POPULATION DYNAMICS AND MANAGEMENT

OF BROWN BEARS ON KODIAK ISLAND, ALASKA

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

with a

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in the

College of Graduate Studies

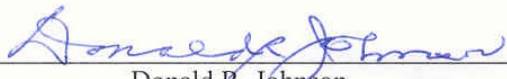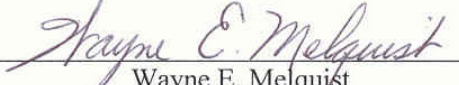University of Idaho

by

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February 2007

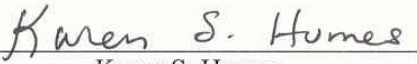Major Professor: Edward O. Garton, Ph.D.

AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Lawrence J. Van Daele, submitted for the degree of Doctor of Philosophy with a major in Natural Resources and titled **"Population dynamics and management of brown bears on Kodiak Island, Alaska,"** has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

Brown bear (*Ursus arctos*) populations along the North Pacific Rim are generally healthy and an important economic resource, yet there are few long-term studies of their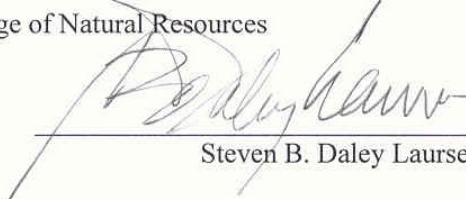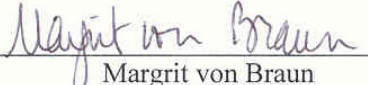 population dynamics and harvest management. This project gathered information on the population dynamics of bears on Kodiak Island, Alaska to develop an easily understood model for use by managers to develop harvest strategies and guidelines.

I investigated a geographically closed brown bear population with no impassable physical barriers from 1982-2004. I hypothesized that Kodiak had a single bear population that could occupy any habitat and would use the best resources available. I investigated 402 marked bears within 4 diverse study areas, including 261 that were radiocollared, yielding 15,539 relocations. Mean home ranges for females were significantly smaller than males, and varied between areas. There was considerable home range overlap and no evidence of territoriality. Topography, vegetation, and salmon availability varied between areas, as did denning habitat and chronology. Elevations used by bears varied by area, reproductive status, and season. Most variations appeared to be related to resource availability. Reproductive fitness and bear densities were comparable in all areas.

Generations of behavioral specialization have resulted in a population that is a radiating continuum in which bears that lived adjacent to each other used similar resources, but those living apart used different resources. Mitochondrial DNA analysis confirmed the hypothesis that bears on Kodiak were a single population; however resource use patterns rejected the hypothesis that all bears used the same "optimal" habitat. This ecological flexibility resulted in a higher carrying capacity than if all bears conformed to uniform habitat use patterns.

I created a model that used population and harvest inputs to derive estimates of population change and the number of trophy-sized bears. Model validation suggested the Kodiak bear population was healthy and productive as it supported a sustainable harvest that yielded consistently large bears. To obtain refined harvest strategies, managers must consider local population parameters, management objectives, harvest characteristics, and confidence levels. There is no single harvest rate that is applicable to all situations.

DEDICATION

This work is dedicated to the brown bears on the Kodiak Archipelago. Without their tolerance and cooperation this project would never have been possible.

Photo by Matthew Van Daele

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INTRODUCTION

This dissertation is divided into 2 chapters, each addressing pertinent aspects of the population dynamics and management of bears on Kodiak Island. Each chapter is written in the style and format of the *Journal of Wildlife Management*.

The first chapter, "Ecological flexibility of brown bears on Kodiak Island, Alaska", addresses the home range sizes, habitat use patterns, denning characteristics, and overall population distribution of bears on the island. Data from marked bears in 4 distinct study areas are analyzed to assess the hypothesis that bears on Kodiak were a single population that could occupy any habitat on the island, and that they moved freely to take advantage of the best resources available.

The second chapter, "Management of brown bear hunting on Kodiak Island, Alaska", builds on the information obtained in the first chapter and uses it to develop a model for sustainable harvest of bears on Kodiak. Brown bear populations along much of the North Pacific Rim are healthy and they provide an important economic resource as trophy hunters seek the largest representatives of the species, yet relatively little research has been published about the population dynamics and harvest management of those brown bears. The purpose of this project was to develop an easily understood model that could be used by bear managers to objectively estimate appropriate harvest strategies and guidelines. We also anticipated that information obtained from Kodiak could be adapted to other coastal bear populations where hunting and other human-caused mortalities are important management considerations.

Chapter 1

ECOLOGICAL FLEXIBILITY OF BROWN BEARS ON KODIAK ISLAND, ALASKA

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Abstract: Brown bear (*Ursus arctos*) population dynamics are challenging to ascertain and generalize because bears are long-lived, widely distributed, and have a great deal of individual variation. We investigated an entire brown bear population by capturing and marking a large sample of bears living in all of the habitats on Kodiak Island, Alaska and following them for over 2 decades. Our study included a geographically closed bear population with no impassable physical barriers within their range. Our hypothesis was that bears on Kodiak were a single population that could occupy any habitat on the island, and that they freely moved to take advantage of the best available resources. We captured 402 bears in 4 diverse study areas from 1982-1997. Of these, 261 were radiocollared (196 females, 65 males). The radiocollared bears yielded 15,539 relocations including 167 bears (142 females and 25 males) with at least 30 relocations. The mean 100% minimum convex polygon (MCP) home range size for all female bears ($\bar{x}$ = 128.6 km^2) was smaller than that of males ($\bar{x}$ = 251.5 km^2). There was no difference in size of MCPs of males in the various study areas; however, mean size of female home ranges in Southwest Kodiak were significantly larger than those in the Terror Lake and Aliulik Peninsula areas. Mean 95% fixed kernel utilization distributions (UD) for all female bears ($\bar{x}$ = 50.1 km^2) were significantly smaller than that of males ($\bar{x}$ = 128.1 km^2). There was no difference in size of UDs of males in the various study areas, but mean size of female UDs in Aliulik were significantly larger than those in the Terror Lake and Zachar/Spiridon areas. In all study areas there was considerable overlap of both MCPs and UDs of individual bears. We observed no overt signs of territoriality or intraspecific spatial exclusion that precluded individual bears access to resources. Topographic features, vegetative resources, and salmon availability varied between study areas. We followed 12 cubs from radiocollared sows from dependency to adulthood. Males ranged significantly farther from their maternal ranges (MCP and UD) than did females. Five females (71.4%) and no males were recaptured within maternal MCP ranges and 3 females (42.9%), and no males were recaptured within maternal UDs. Elevations used by bears varied by study area, by reproductive status, and by season. Bears in northern study areas used higher elevations throughout the year than did bears in southern areas. Overall, females with new cubs used higher elevations throughout the year than all other bears. Den use and chronology also varied by study area. Most females used a single den (95.2%) each year, but there were 4 instances (0.7%) of females not entering dens all winter. Most males also used a single den each winter (76.8%); however, in 13 instances males did not enter dens during the entire year. Bears in the northern study areas spent more time in dens than did bears in southern study areas,

with the most notable difference being between females without new cubs in the Terror Lake area (180 days/year) versus those in the Aliulik (100 days/year). Females with new cubs had similar denning periods in all study areas, and in all areas they emerged significantly later than all other females. Most of the variations in resource use and denning chronology appeared to be resource related. The exception to this pattern was sows with new cubs that stayed in dens longer and used suboptimal habitats when they emerged. Despite ample opportunities to move to and from optimal habitats on Kodiak Island, bears stayed in relatively small areas and adapted to locally available resources. Generations of behavioral specialization within local areas have created a population that is a radiating continuum in which bears that live adjacent to each other have similar resource use patterns, but those living in distant locations with dissimilar habitats have considerably different patterns of resource use. The population distribution and mitochondrial DNA analysis confirmed our hypothesis that bears on Kodiak Island were a single population; however resource use patterns rejected the hypothesis that bears all used the same "optimal" habitat. The ecological flexibility of the population allowed bears to expand to all available habitats on the island. This adaptability expanded the carrying capacity over that which would be expected if bears conformed to a uniform habitat use pattern, and ultimately insulated the population from collapse. The radiating continuum distribution complicates bear management because of local carrying capacities and varying population responses to environmental changes.

INTRODUCTION

The Kodiak Archipelago supports a population of about 3,000 brown bears (*U. a. middendorffi*) (Barnes and Smith 1998) and has a reputation for producing the largest brown bears in North America (Buckner and Reneau 2005). The general life history of Kodiak bears has been the subject of speculation and study since humans first arrived on the island. The first scientific investigations, in the late 1800s, were collecting trips to document the size of Kodiak bears. During the early part of the twentieth century, research focused on bear predation on salmon and cattle (Van Daele 2003). As the value of Kodiak bears as a trophy animal for hunters increased in the 1950s, biologists shifted the emphasis of their research from salmon depredation (Clark 1955, 1957a, 1959, Gard 1971) to gathering baseline biological information on bears (Clark 1957b, Troyer 1961, 1962). As they refined methods of capturing and marking bears (Troyer et al. 1962) and incorporated radio telemetry in 1967 (Berns and Hensel 1972), they became more efficient at estimating bear movements and density. Their studies also provided the first objective data on gender and age ratios (Troyer and Hensel 1969), reproduction (Erickson et al. 1968, Hensel et al. 1969, Gilbert 1970), litter sizes (Troyer and Hensel 1964a), behavior (Troyer and Hensel 1964b), movements (Berns et al. 1980), cannibalism (Troyer and Hensel 1962), dentition (Troyer and Hensel 1969), feeding habits (Atwell et al. 1980), and denning (Lentfer et al. 1972).

Prior to the 1980s, virtually all brown bear research on Kodiak Island was conducted on the southwest portion of the island. Construction of a hydroelectric project on the north end of Kodiak Island was initiated in 1982, and brown bear research commenced simultaneously (Smith and Van Daele 1990). An environmental assessment of the anticipated impacts of the project on brown bears was based on data extrapolated from previous studies (Spencer and Hensel 1980), and it soon became evident that bears on the north end of the island were not conforming to the patterns observed on the southwest part of the island (Van Daele et al. 1990).

Brown bears are an intelligent, long-lived species with a great deal of individual variation. They are distributed across most terrestrial ecoregions in the northern hemisphere (Servheen et al. 1999, Schwartz et al. 2003), thereby demonstrating their adaptability to a wide variety of habitats. This individuality and adaptability can hamper comprehensive investigations of brown bears if the studies are restricted to small numbers of bears, limited areas, or short time periods.

In an effort to investigate an entire brown bear population, we captured and marked a large sample of bears distributed across all habitats on Kodiak Island and followed them for over 2 decades. Our study involved a geographically closed population with no physical barriers to bear movement. Conceivably, a bear could go from one end of Kodiak Island to the other within a couple of days. We hypothesized that bears on Kodiak Island were a single population that could occupy any habitat, and that they moved freely to take advantage of the best available resources. If this were the case, we would be able to identify "critical bear habitat" and manage it similarly island wide. If the hypothesis was not correct and bears were adapting to local habitats, it would demonstrate the adaptability of the species and necessitate localized management.

STUDY AREA

Kodiak, the largest and most complex island in the Kodiak Archipelago, is located in the western Gulf of Alaska (56° 45'–58° 00' N by 152° 09'–154° 47' W), 408 km south of Anchorage, Alaska (Figure 1.1). It is up to 160 km long, varies from 15 to 130 km in width and has a landmass of 8,975 km^2. No point of the island is farther than 21 km from the sea as deep fjords slice into the island. Shelikof Strait separates Kodiak from the mainland on the west, with a 40–65 km swath of extreme ocean currents and windswept waves.

The Archipelago is geologically an extension of the Kenai Mountains and is part of an uplift zone between 2 major tectonic plates. There are numerous faults and seismic activity is common. Complementing the seismic movements is the relentless erosion of shorelines by the sea and the mountaintops by wind, rain, and glaciers. Its most prominent feature is the central spine that runs the length of the island from northeast to southwest. The spine is made up of intrusive rock formations sculpted by prehistoric and active glaciers. The tallest peak along the spine rises to 1,362 m. Most of the valleys on the island contain the remnants of scouring by glaciers that covered most of the islands

about 12,000 years ago. The only portion of the archipelago that escaped that glaciation is in the southwest part of Kodiak. This "refugium" is unlike any other part of the island, with wet tundra expanses bordered by modest mountain ridges. On the border of the refugium is a series of large lakes that fill glacially carved valleys. The largest of these, Karluk Lake, is 21 km long, 4 km wide, and up to 126 m deep. The Karluk drainage is also the longest river system on the island at 68 km.

The Kodiak Archipelago has a sub-arctic maritime climate. Low-pressure systems, spawned along the Aleutian Chain, spin counterclockwise into the Archipelago with easterly winds that bring cool moist weather throughout the year. These systems are periodically disrupted by high-pressure systems that develop over mainland Alaska. The resultant winds from those systems are from the northwest and they typically bring drier weather with more extreme temperatures. Whenever especially strong systems collide, the resultant storms can bring hurricane force winds with heavy rains. Fog is common on the rare days when winds are calm.

Historical weather data from the archipelago was only available from Kodiak city, located near sea level on the northeastern tip of Kodiak Island. From 1973–2003, average February temperatures (the coldest month) ranged from –3.7 to 2.1^{o}C and average August temperatures (the warmest month) ranged from 9.4 to 16.7^{o}C. The highest temperature ever recorded was 26.7^{o}C and the lowest was –26.7^{o}C. Average annual precipitation was 195 cm (range = 138 – 270 cm). Winds were common throughout the year with an average annual wind speed of 4.9 mps; velocities over 22.4 mps have been recorded in every month. Most of the eastern side of Kodiak Island had weather patterns similar to those recorded at Kodiak city. The south and west sides of Kodiak Island had a drier climate with similar temperatures and higher maximum wind speeds. Because of the diverse nature of the landscape on Kodiak Island, the weather varied greatly from one area to the next.

The sea surrounding Kodiak Island remained ice-free throughout the year. Narrow bays that had substantial freshwater influence and protection from most storms became frozen during several months in winter. Nearshore ocean temperatures typically varied from 0.5^{o}C in January to 13°C in August. The daily tides on the east side of the archipelago averaged 2.4 m while those on the west side averaged 4.9 m, with 2 sets of tides being the daily norm. The maximum daily variation on the east side is 4.2 m and on the west side the maximum is 7.2 m. This dramatic tidal difference between each side of the archipelago resulted in substantial tide rips between the larger islands.

Kodiak Island is located 970 km south of the Arctic Circle. The sun is relatively low on the horizon throughout most of the year, and produces long twilight hours. During winter months there is a minimum of 6 hours and 29 minutes of daylight, while in the summer solstice, the sun is above the horizon for 18 hours and 9 minutes.

Sitka spruce (*Picea sitchensis)* were common on the northeastern end of Kodiak Island. It was a relatively new inhabitant to the archipelago, expanding southward from the Kenai Peninsula within the last 800 years. Devil's club (*Echinopanax horridum*), high-bush

blueberry (*Vaccinium ovalifolium*), and bracken fern (*Dryopteris dilatata*) were the principle understory vegetation in forested areas.

A diversity of habitats occurred throughout the remainder of the island, with shrub-grass-forb complexes predominant throughout lowland (<150 m) and mid-slope (150-500 m) areas. Representative species were Sitka alder (*Alnus crispa sinuata*), Kenai birch (*Betula kenaica*), salmonberry (*Rubus spectabilis*), red-topped grass (*Calamagrostis canadensis*), European red elder (*Sambucus racemosa*), willows (*Salix* spp.), fireweed (*Epilobium angustifolium*), and cow parsnip (*Heracleum lanatum*). Cottonwood (*Populus balsamifera*), and willow communities were common along stream bottoms. On southeastern Kodiak Island, extensive areas of regularly-spaced hummocks (0.3 –1.0 m tall) and moist tundra were common.

Alpine vegetation (>500 m elevation) was composed of various mixtures of low willow, ericaceous shrubs (heath), sedge (*Carex macrocheata*), crowberry (*Empetrum nigrum)*, low-bush cranberry (*Oxycoccus microcarpus)*, alpine blueberry (*Vaccinium uliginosum)*, red bearberry (*Arctostaphylos rubra*), and a wide variety of forbs. Nearshore waters supported locally abundant crops of marine vegetation, including bull kelp (*Nereocystis luetkeana*), eelgrass (*Zostera marina*), and bladderwrack (*Fucus gardneri*). Tidal action and storms often deposited parts of these plants on the beach to supplement shoreline vegetation such as goose tongue (*Plantago maritima*), beach pea (*Lathyrus maritimus*), beach greens (*Honckenya peploides*), and beach rye (*Elymus arenarius*). A detailed description of the vegetative aspects of the archipelago is included in Fleming and Spencer (2004) (Appendix 1.1).

Kodiak's diverse habitats provided wintering, resting, and breeding areas for 237 different bird species. There were an estimated 1.5 million seabirds that winter near Kodiak, and 350,000 that nested within the 140 seabird colonies that have been identified along the islands (Kodiak National Wildlife Refuge 1987). About 150,000–200,000 waterfowl, including geese, sea ducks, and puddle ducks, wintered in the area with some staying to breed. There were also at least 40 species of shorebirds that came to Kodiak either as a migration stop or as a breeding area. Terrestrial birds included about 70 species of passerines and upland game birds. There were 18 species of raptors reported on Kodiak, the most common being the bald eagle (*Haliaeetus leucocephalus*). Up to 3,000 bald eagles spent the winter on the islands, with a breeding population of up to 1,000 eagles.

Only 6 land mammals were considered indigenous to Kodiak Island. These original inhabitants were brown bear, red fox (*Vulpes vulpes*), river otter (*Lontra canadensis*), short-tailed weasel (*Mustela erminea*), little brown bat (*Myotis lucifugus*), and tundra vole (*Microtus oeconomus*) (Rausch 1969). Confirmation of original inhabitants was, however, impossible due to the geologic history of the islands. The constant uplifting and erosion of the terrain is not conducive for development of a useable fossil record.

Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) were introduced from southeastern Alaska in the late 1800s. By the 1960s deer had dispersed throughout the

Archipelago. Winter mortality was the most significant limiting factor for the deer population, with estimated population sizes ranging from <50,000 to >100,000 from 1982-2004 (Van Daele 2005). Deer were an important hunting resource for the residents of and visitors to the Kodiak islands.

Mountain goats (*Oreamnos americanus*) were translocated to northern Kodiak Island from the Kenai Peninsula in 1952 and 1953. The first hunting season was authorized in 1968, as the population expanded in number and range. In 2002, the estimated goat population was 1,400 and they occupied all suitable habitats on Kodiak Island (Van Daele and Crye 2004). Other successful translocations to Kodiak included Arctic ground squirrels (*Citellus undulatus*) (prehistoric), reindeer (*Rangifer tarandus*) (1924); muskrat (*Ondata zibethica*) (1925); beaver (*Castor canadensis*) (1925); and snowshoe hares (*Lepus americanus*) (1934) (Burris and McKnight 1973).

Kodiak Island's lakes and streams provided critical spawning and rearing habitat for 5 species of Pacific salmon *(Oncorhynchus* spp.), steelhead (*O. mykiss*), arctic char (*Salvelinus alpinus)* and Dolly Varden (*S. malma*). There were about 350 streams involved in this vital process. The first salmon to return to most streams on the island each year were the sockeye (red) salmon (*O. nerka).* Each year about 6,000,000 sockeye returned. Another species that returned to Kodiak in late May was the chinook (king) salmon *(O. tschawytscha*). These were the largest of the salmonids, but they also had the most restricted distribution on the archipelago, occurring in large numbers in only the Ayakulik and Karluk drainages. Average annual returns were about 40,000 chinook salmon.

In mid-summer chum (dog) salmon *(O. keta)* returned to spawn in Kodiak streams. Each year about 800,000 chums came back to Kodiak. Another mid-summer returnee and the most abundant salmonid in both distribution and number was the pink (humpback) salmon (*O. gorbuscha*). The strength of the return of pinks varied between 5,000,000 in odd years and 11,000,000 in even years. The last salmon to come back to Kodiak were the coho (silver) salmon (*O. kisutch*), arriving in late summer and averaging an annual return of approximately 400,000 fish.

In 2003, the estimated resident human population of Kodiak Island was 14,181, and had been relatively stable over the previous 20 years. Over 90% of the populace lived on northeastern Kodiak Island, with the other residents dispersed in 6 outlying villages. Roads were restricted to the northeast coast of the island, and the immediate vicinity of villages. Kodiak's inland habitat was contiguous and intact. The only large-scale anthropogenic disruption of inland habitat, the Terror Lake hydroelectric project, was completed with minimal direct or indirect adverse impact to bears or their habitat due to a conscious effort to work with and around the bears (Smith and Van Daele 1990). Coastal areas had much greater human activity that influenced bear activities, but it was generally restricted to isolated areas and small numbers of people.

Commercial fishing was vital to the economy of the region. Fishing and fish processing occurred year-round, but during summer months residents and transients expanded their

activities to remote coastal areas in pursuit of salmon. Salmon management for sustained yield was a high priority on the archipelago, and bear predation was factored into escapement rates. Residents of Kodiak generally had a higher tolerance and a greater understanding of bears than most other people. There was an on-going effort by various agencies to educate residents and visitors about bears, minimize attracting bears to human habitat, and maintain a lower bear density on northeastern Kodiak Island where most human activities occurred (Van Daele 2002).

METHODS

There were 4 major bear research projects on Kodiak Island from 1982-2004, all of which included radio telemetry (Figure 1.1). Each of these studies addressed specific management questions. The Terror Lake hydroelectric (TLH) investigation was designed to address concerns that bears would be displaced or otherwise disturbed by construction and operation of a hydroelectric facility in a remote area of Kodiak Island (Smith and Van Daele 1990). The Zachar/Spiridon (ZSP) study investigated the relationship between bears and deer hunters at a time when there were increasing encounters, which were resulting in hunters losing their game and bears being shot in defense of life or property (Barnes 1994). The southwest Kodiak (SWK) study was designed to assess annual use patterns of salmon spawning areas by bears and explore the possibility of developing an objective method of determining population trends (Barnes 1990). The Aliulik Peninsula (ALK) research was primarily descriptive in design, investigating the population dynamics of bears living in a unique habitat on the extreme south end of Kodiak (Barnes and Smith 1997). This paper presents a meta-analysis of data collected during and subsequent to those projects.

We used comparable capture, handling, and processing techniques in each of these investigations. Bears were captured by chemically immobilizing them with Etorphin (M99[®], Lemmon Co., Sellersville, Pennsylvania, USA) or tiletamine hydrochloride and zolazepam hydrochloride (Telazol[®], Fort Dodge Laboratories, Fort Dodge, Iowa, USA). The drugs were administered from darts fired from Palmer capture equipment by biologists in small helicopters (Bell 206 or Hughes 500). Immobilization dosages were typically 5 ml for subadults, 7 ml for females, and 10 ml for adult males (etorphin @ 1.0 mg/ml; Telazol[®] @ 200 mg/ml). Bears immobilized with etorphin were reversed with a comparable dose of dipenorphine (2.0 mg/ml) (M50-50[®], Lemmon Co., Sellersville, Pennsylvania, USA). No antagonist was used with Telazol[®].

For each captured bear, we noted gender, reproductive status, and estimated age. We also collected standard morphological measurements (total length, heart girth, neck circumference, and skull length and width), hair and blood samples, and an upper or lower first premolar tooth. Matson's Laboratory (Milltown, Montana, USA) and the Alaska Department of Fish and Game (ADF&G) laboratory in Anchorage provided cementum-aging analysis of the teeth (Matson et al. 1993). Green punch tattoos were

applied to both sides of the upper lip and to the front of the lower lip. Groin tattoos were applied with an electric tattoo gun. Numbered plastic tags were affixed to each ear.

We deployed conventional VHF radio collar transmitters (Telonics Inc., Mesa, Arizona, USA) on a sample of subadult and adult bears in each study area. The sample was purposefully biased toward adult females because they would provide the most information on productivity and cub survival, and because of concerns about neck injuries the collars could cause to subadults and males. Most collars placed on subadults and adult males included cotton spacers or some other breakaway device. All collars included inverse mortality sensors (signal pulse rate slowed down when transmitter was immobile more than 12 hours). Active transmitters were replaced at 2 to 3-year intervals so that long-term information on individual bears could be collected.

Collared bears were typically radio tracked from a fixed-winged aircraft (Piper PA-18, Aviat Husky, or Bellanca Scout) weekly by experienced pilot/observer teams, but windy or foggy weather commonly delayed these flights. We reduced the flight schedule to twice monthly during the winter months. Tracking flight frequency was increased during spring emergence to ascertain cub production and survival. During each flight, we attempted to locate all active radio transmitters and recorded location (plotted on 1:63,360 U.S. Geological Survey [USGS] topographic maps), habitat, activity, and information about other bears associated with the collared individual. If necessary, an additional day of aerial radio tracking was used to find missing transmitters. Whenever possible, we investigated transmitter locations when we suspected a collar had been shed or the bear died. Cause and time of death were estimated whenever carcasses were found. All location data were digitized to obtain coordinate information and all data were transferred to Microsoft Excel® (Microsoft Corporation, Seattle, Washington, USA) spreadsheets for storage and initial analysis.

During this study, home range analyses were used for several purposes. The first was to estimate the effective sizes and boundaries of the 4 study areas (TLH, ALK, ZSP, and SWK) and the habitat components available to bears within each. Because relocations were only collected during daylight hours and at times when flying conditions were favorable, we could not expect relocation data to be unbiased samples of critical habitats. Taken collectively for an individual, however, they provided an objective estimate of areas used during the time the bear was studied. A second use was to estimate the sizes of home ranges and use distributions within each study area and to statistically compare them. A third analysis we used was to investigate the level of home range overlap within and between each study area. Finally, we compared the size of bear home ranges on Kodiak Island to those reported for other brown bear populations.

We used 95% minimum convex polygons (MCPs) derived from relocation data from all bears within each study to determine the boundaries of each study area. We then spatially analyzed each area with ArcView 9.1 GIS software (Environmental Systems Research Institute, Redlands, California, USA) and used a recently developed vegetative cover map for the Kodiak Archipelago (Fleming and Spencer 2004) to determine the amount of each major cover type within the bears' home ranges. Fleming and Spencer's

(2004) vegetative cover map included 64 distinct cover types, which we consolidated into 8 categories that reflected bear habitat (rock-ice, alpine, tall shrub, low shrub, grassland, heath, wetlands and freshwater) (Appendix I).   Marine waters were excluded from this analysis.

Cover type and salmon availability data within each study area allowed us to compare resource availability and use between study areas. Salmon availability data were derived from ADF&G weir counts, aerial surveys, and field estimates during the study period (Kuriscak 2004 and ADF&G files, Kodiak, Alaska). The number of days reliable feeding opportunities were available to bears (*food days*) were estimated from field observations. To surmount concerns about sampling bias due to timing of relocations, and potential variations due to the unique proclivities of individual bears, we collectively analyzed bears by study area rather than by individual bear. Multiple (MANOVA), univariate Analyses of Variance (ANOVA), and Tukey honestly significant difference (HSD) tests provided the analytical tools for comparisons between areas and resources within areas, and chi-square tests were used to compare resource availability and use (Johnson and Wichern 2002, Zar 1999) (SAS 9.1 for Windows, SAS Institute Inc., Cary, North Carolina, USA).

We calculated 100% MCPs to facilitate comparison to other bear populations. Only bears with ≥ 30 relocation points were included in these analyses. The MCP boundaries and areas were calculated with the Hawth's Analysis Tools extension (Version 3.2, Edmonton, Alberta, Canada) to Arc View 9.1. We analyzed the applicability of using a minimum sample of 30 in a manner similar to that described below for 95% fixed kernels. While fixed kernel areas provided an accurate measure of the utilization distribution (UD) of bears, the MCP provided a more complete representation of the total area used. In combination, these metrics were used to ascertain the distribution and concentrations of resources used by Kodiak bears.

We determined that the most appropriate analytical tool for calculating the areas regularly used by bears (UDs) was the fixed kernel (95%, with the smoothing parameter selected by least squares cross validation with a minimum window width of 500m) (Worton 1989). Fixed kernel home ranges of bears were calculated using BIOTAS software (Ecological Software Solutions, [http://www.ecostats.com/software/biotas/biotas.htm], accessed 2004 September 01). We included winter relocations, including denning locations, in UD analyses because we judged that the reduced winter flight schedules and coupled with occasional movements of den sites surmounted any potential problems with autocorrelation. Fixed kernel data were also analyzed to determine the appropriate minimum sample size for relocations (Seaman et al. 1999). This analysis was limited to data from bears that were relocated at least 100 times, assuming that home range at that sample size represented the total home range. We calculated the percentage of the total home range that was obtained at each iteration of 10 relocations (e.g. 10, 20, 30, etc.) to ascertain when or if an asymptote was achieved.

We explored an alternative method of deriving home range and UDs by measuring the distance between capture and death locations of marked bears. We analyzed data from

radiocollared bears that had $\geq$30 relocations and were later found dead or shot by hunters at least a year after they were captured and marked. The 100% MCP and 95% fixed kernel areas of those bears were regressed against the linear distances between capture and death locations.

Cubs that were captured along with their mothers were tattooed, but not radiocollared. We investigated dispersal after family break-up by collecting information on where cubs were recovered as adults and determining distances of those locations to the nearest edge of their mother's home range (MCP and UD)(t-tests). In all cases, recapture occurred due to hunter harvest. For this analysis we used only bears that were marked as dependent cubs (0-2 years), killed as adults (>5 years old), and had mothers with sufficient numbers of relocations to determine their MCP and UD sizes.

Individual bears occasionally made unexpected forays outside their typical ranges. To objectively evaluate these erratic movements, we analyzed relocations that were at least as far away from the edge of a bear's UD as the maximum distance across the UD. In other words, if the maximum distance across a bear's UD was 10 km and the relocation was 12 km outside of the UD, that relocation would be considered erratic.

Mean seasonal (biweekly) elevations used by bears in each study area provided another estimate of habitat use because much of the Kodiak Island resource characteristics and availability were directly related to height above sea level. Elevation data were derived from USGS 1:63,360 topographic maps, and were cross-referenced with aircraft altimeters in the field and digital elevation models in the laboratory.

We recorded the locations of all the dens we found and attempted to determine if they were excavated or within natural cavities. Aspect and slope of den sites were derived using ArcView GIS 9.1 software and digital elevation and topographic models for the Kodiak Archipelago. Detailed analyses of den entrance and emergence dates included only those bears that had $\leq$30 days between the last time the bear was observed out of the den and the first time it was determined to be in a den, or vice versa. Den entrance and emergence dates were calculated as the mid-point between "out" and "in" observation dates and we used multiple regression analyses (SAS 9.1 for Windows) to investigate the factors influencing denning periods. Denning characteristics between areas and between reproductive categories were compared with ANOVA and Tukey HSD tests.

RESULTS

Capture, Collaring, and Data Collection

We captured 402 bears from 1982-1997. Of these, 261 were radiocollared (196 females, 65 males). The radiocollared bears yielded 15,539 relocations (female $\bar{x}$ = 68.9; SE = 3.29; male $\bar{x}$ = 30.5, SE = 3.17), including 167 bears (142 females and 25 males) with at least 30 relocations (Table 1.1).

Analysis of relocation data for female bears with $\geq$100 relocations ($n = 60$) revealed that UDs reached 100% levels (SE = 4.0%) and changed little once 30 relocations were obtained. Males were not included in the analysis because only 1 radiocollared male had over 100 relocations. MCP data for the same bears did not reach an asymptote, as home range sizes continued to increase as the number of relocations increased. At 30 relocations, average 100% MCPs were 54% (SE = 3.1%) of the level obtained with 100 relocations, with a range of 5% to 100%. There was no difference between study areas in the proportion of the MCP home range represented by 30 relocations (ANOVA, $F_{3, 56} = 1.99$, $P = 0.125$) or the number of relocations obtained for bears that had $\geq$30 relocations ($n = 89.4$; SE = 3.11; ANOVA, $F_{3,139} = 1.92$; $P = 0.129$). These results indicated that we could compare MCP ranges between study areas, even though we knew they were not exact measures of total MCPs.

Home Range and Utilization Distribution

The mean 100% MCP size for female bears ($\bar{x} = 128.6$ km^2; $n = 143$; SE = 12.4) was smaller (t = 3.82, $P < 0.001$) than that of males ($\bar{x} = 251.5$ km^2, $n = 24$, SE = 26.7) (Table 1.2). There was no difference in the size of male MCPs between study areas (ANOVA, $F_{3, 20} = 0.65$, $P = 0.592$); however, mean size of female MCPs varied by study area (ANOVA, $F_{3, 139} = 7.51$, $P < 0.001$). The variation between areas was due to larger home ranges in SWK than in TLH ($P < 0.01$) and ALK ($P < 0.01$) (Tukey HSD).

The mean 95% fixed kernel UD for female bears ($\bar{x} = 50.1$ km^2, $n = 143$; SE = 1.9) was smaller (t = 8.35, $P < 0.001$) than that of males ($\bar{x} = 128.1$ km^2, $n = 24$, SE = 20.2). The size of 95% fixed kernels of males was similar among study areas (ANOVA, $F_{3, 20} = 0.011$, $P = 0.956$). In contrast, mean size of female UD ranges differed by study area (ANOVA, $F_{3, 140} = 5.18$, $P < 0.002$). Further analysis revealed that the source of that variation was that UDs in ALK were significantly larger than those in TLH ($P < 0.01$) and ZSP ($P < 0.01$) (Tukey HSD).

We found that 15.5% ($n = 22$) of female bears with $\geq$30 relocations had at least 1 erratic movement. The proportion of bears with erratic movements, by study area, was 24.3% (ZSP), 21.2% (SWK), 9.9% (TLH) and 7.4% (ALK). Of the 56 erratic movements we recorded, most occurred in September (42.9%) and August (19.6%). Only 4 were observed from November through May (7.1%). Erratic movements were recorded every year and there was no apparent relationship between food availability and erratic movements. We recorded erratic movements by lone females as well as females with cubs of all ages (lone females - 44.1% of the erratics, females with new cubs – 26.5%, with yearlings – 17.6%, with 2-year olds - 11.8%).

In all study areas there was considerable overlap of both MCP (Figure 1.2) and the 95% fixed kernel UDs (Figure 1.3) of individual bears. We observed no overt signs of territoriality or intraspecific spatial exclusion that precluded individual adult bears access to resources, although temporal displacement was common in some places. There was no

overlap of MCPs for female bears in the TLH study area with females from any other study area. Females in the ALK study area were also isolated from females in all other study areas. One female from the SWK area had a small portion of her MCP overlap with bears in the ZSP area. Three females from the ZSP had small portions of their MCP overlap with bears in the SWK area. There was no overlap of the UDs of females from different study areas.

We recorded distances between capture and death locations for 170 marked bears during this study ($\bar{x}$ = 9.39 km, SE = 0.78; TLH - n = 73, ZSP- n = 23, SWK- n = 44, ALK- n = 30). Distances between capture and death sites did not vary between study areas (ANOVA, $F_{3, 166}$ = 0.84, P = 0.48). Analysis of bears with ≥30 relocations (n = 77) revealed no correlation between the capture-death distances and 95% fixed kernel UDs for individual bears (r^2 = 0.005, ANOVA, $F_{1, 75}$ = 0.352, P = 0.55). There was, however, a positive relationship between capture-death distances and MCP home ranges (r^2 = 0.203, y = 9.41x + 75.48; ANOVA, $F_{1, 75}$ = 19.06, P < 0.0001). This suggests that capture-death distances can be used to estimate relative dispersal and home range information, but they do not provide accurate estimates of the size of UDs.

Habitat Availability and Use

Study area sizes, as defined as the composite 95% MCP home range of all bears captured in each area, were 1,974.3 km^2 in SWK, 1,269.2 km^2 in ZSP, 882.7 km^2 in TLH, and 414.3 km^2 for ALK. TLH, ZSP, and SWK had similar vegetative composition, with tall shrub habitats making up the majority of the areas (44.7%, 45.6%, and 43.3%, respectively). TLH and ZSP had greater areas of alpine tundra and barren rock/ice than did SWK (39.8%, 38.1%, and 26.6%), and SWK had a greater percentage of freshwater and wetland habitat (9.4% versus 3.9% for TLH and 3.1% for ZSP). The primary habitat in ALK was heath and grassland (54.7%). Even though there was considerably less area within ALK, it still had 45.0% more heath habitat than did the other 3 study areas combined (113.1 km^2 versus 78.0 km^2). Tall shrub habitat made up only 25.6% of ALK, and alpine tundra and barren rock/ice made up only 7.6% of the area (Figure 1.4). Vegetative composition within composite UDs for each study area was not significantly different from the composition within composite 95% MCPs (TLH – x^2 = 3.54, P = 0.831; ZSP – x^2 = 13.96, P = 0.052; SWK – x^2 = 12.34, P = 0.090; ALK – x^2 = 4.78, P = 0.687).

Salmon resources within each study area varied in species availability, run timing, and biomass (Table 1.3). TLH averaged 429.4 kg/km^2 annually with a peak period of the run of 82 days, ZSP averaged 327.7 kg/km^2 with a peak period of 52 days, SWK averaged 2,963.1 kg/km^2 with a peak period of 112 days, and ALK averaged 1,759.5 kg/km^2 with a peak period of 22 days.

Comparisons of resource categories (MANOVA), including the 8 vegetative types and salmon availability for each study area, revealed differences in the ways bears used those resources both in amount used (P<0.0001, n = 143, Wilk's λ = 383.2) and proportions used (P<0.0001, n =143, Wilk's λ = 60.21). Two eigenvalues accounted for 95% of the

variability, and canonical analysis suggested that most of the variation was due to differences in use of Grassland, Heath, Salmon, and Tall Shrub resources. An ANOVA indicated differences (P<0.0001) in resource use within each of the areas. Further analysis with Tukey HSD clarified the relationships, suggesting that resources used by bears in TLH and ZSP were similar in all but 1 category, while there were significant differences (P<0.05) in the use of at least 6 categories between all other study areas (Table 1.4).

Cub Dispersal

We recovered information from 12 bears that were captured as dependent cubs, later recovered as adults, and also had mothers' who were radiotracked long enough to obtain MCP and UD data. Male bears ($\bar{x}$ = 17.37 km, n = 5, SE = 9.00, range = 2.98 – 52.46) were recovered farther from their mothers' MCP home ranges (t = 2.24, P = 0.02) than females ($\bar{x}$ = 0.62 km, n = 7, SE = 0.46, range = 0.00 – 3.17). Five of 7 females (71.4%), and no males were recovered within maternal MCP ranges. Similarly, male bears ($\bar{x}$ = 16.47 km, n = 5, SE = 9.17, range = 1.30 – 52.26) were recovered significantly (t = 1.91, P = 0.04) farther from their maternal 95% fixed kernel UDs than females ($\bar{x}$ = 1.80 km, n = 7, SE = 0.86, range = 0.00 – 12.59). Three of 7 females (42.9%), and no males were recovered within maternal 95% fixed kernel UDs.

Seasonal Movements

An evaluation of seasonal (biweekly) mean elevations revealed that elevations used by bears varied by study area (ANOVA, $F_{3,92}$ = 31.59, P < 0.0001), by reproductive status (females with new cubs versus all other bears)(t = 2.39, df = 190, P = 0.018), and by season (ANOVA, $F_{23,72}$ = 2.57, P = 0.001). Bears in the northern study areas (TLH and ZSP) used significantly higher elevations throughout the year than did bears in the southern areas (SWK and ALK) (Tukey HSD, P < 0.01). Bears in SWK used higher elevations than those in ALK (Tukey HSD, P < 0.01). Overall, females with new cubs used higher elevations throughout the year than all other bears (t = 20.17, df = 15,532, P < 0.0001). The differences between study areas held true for both females with new cubs (northern areas higher than southern areas – Tukey HSD, P < 0.01), and for all other bears (northern areas higher than southern areas, and SWK higher than ALK) (Tukey HSD, P < 0.01) (Figures 1.5 and 1.6).

Differences in seasonal elevation use in each study area appeared to be a consequence of both topographic relief and resource availability in the different areas. In TLH, the area with highest terrain, mean denning elevation was higher than any other area ($\bar{x}$ = 670.7 m, n = 253, SE = 17.0; ANOVA, $F_{3, 723}$ = 81.6, P < 0.0001; Tukey HSD, P < 0.01). The TLH area was the only area in which we had sample sizes sufficiently large to compare mean elevations of male (n = 27) and female (n = 226) den sites, and we found no differences between them (t = 0.87, P = 0.38). Use of dens in the high country from

January through March was responsible for high mean elevations during those months. Den emergence for most TLH bears occurred throughout April and into May, and most bears moved to lower elevations to seek carrion, roots, and newly emergent vegetation. The emergence of developing vegetation progressed into higher elevation through June and into early July providing the primary food source for bears at that time. In early July alpine sedges provided feeding opportunities for some bears in TLH, along with salmonberries in mid-slope areas. From late July and through mid-August, spawning salmon, especially in the Terror and Kizhuyak drainages drew most of the bears into low elevation areas (Table 1.3). By late August, elderberries and blueberries in mid-slope areas provided additional nutrients. Autumn feeding opportunities included late run pink and silver salmon, cranberries, devil's club berries, crowberries, bearberries, cow parsnip seeds, and carcasses of deer shot by hunters. Movement into denning areas began in mid-October and continued through December.

Seasonal mean elevation patterns by bears in ZSP were comparable to those noted in TLH. The terrain in this area was lower than TLH, and the mean elevation of den sites was significantly lower than TLH, but higher than the other 2 study areas ($\bar{x}$ = 590.2 m, n = 111, SE = 14.5; ANOVA, $F_{3, 723}$ = 81.6, $P < 0.0001$; Tukey HSD, $P < 0.01$). Several ZSP individuals traversed into the central highlands of the island to den in mountainous terrain. The most obvious seasonal difference between TLH and ZSP was the extent of use of alpine feeding areas in July. The ZSP bears had more extensive alpine feeding opportunities and made more use of them than any other group of bears we investigated. Spawning salmon were more plentiful in the Zachar, Spiridon, Uyak, and South Arm Uganik drainages than those in TLH. Berry resources were similar to TLH, with lower levels of blueberries but more cranberries and crowberries.

Bears in SWK occupied an area characterized by relatively low ridges separated by broad flat valleys. Mean den elevations in this area were lower than TLH and ZSP, but higher than ALK ($\bar{x}$ = 457.7 m, n = 136, SE = 16.9; ANOVA, $F_{3, 723}$ = 81.6, $P < 0.0001$; Tukey HSD, $P < 0.01$). The lower terrain resulted in lower vegetative diversity than the northern study areas. SWK had few alpine feeding opportunities and few blueberries. Primary food sources were abundant and long-lasting salmon runs and extensive elderberry and salmonberry crops. Salmon were common in all of the major drainages in SWK, beginning in late May and persisting through November. The impact of these resources on SWK bear distribution is evident as these bears moved into lower elevations earlier and remained in them longer than did TLH and ZSP bears (Barnes 1990).

The terrain in ALK is essentially a broad, flat tundra shelf on the south end with relatively low ridges comparable to SWK on the north end. Mean den elevations of bears in ALK were significantly lower than any other study area on Kodiak Island ($\bar{x}$ = 290.7 m, n = 111, SE = 17.6; ANOVA, $F_{3, 723}$ = 81.6, $P < 0.001$; Tukey HSD, $P < 0.01$). The area provided adequate food for bears but had the lowest diversity of resources. Windrowed marine vegetation such as kelp and bladderwrack, and associated decomposer fauna on beaches provided consistent and high quality nutritive opportunities throughout the year, and carrion from dead marine mammals and deer was sporadically available. Sedges were palatable in spring and early summer and crowberries,

bearberries, and cranberries became available throughout the peninsula in autumn. Spawning pink salmon were only readily available for a few weeks in late summer on 2 streams, one of which was not dependable from 1 year to the next.

Females with new cubs remained in higher elevations than all other females throughout the year ($t = 2.39$, $P = 0.02$). This held true for all study areas, and was most evident from April through June. Den site elevations of females with new cubs were not different from those of other bears ($t = 1.02$, $P = 0.31$), but the new families stayed in higher elevations in spite of the paucity of food resources in those areas. They traveled to lower elevations when salmon became abundant and followed patterns similar to other bears during late summer and autumn.

Denning

Den use and chronology varied by study area. Most females used a single den (95.2%) each year, but some switched during winter, using 2 (3.8%) or 3 separate dens (0.4%). Four instances of females not entering dens all winter were recorded (0.7%). Most males also used a single den each winter (76.8%); however, in 13 instances radiocollared males did not enter dens during the entire year. There were no cases of males using multiple dens in a single season. Bears in ALK had the most anomalous denning activities with only 76.0% of the females and 25.0% of the males using single dens (Table 1.5). Mean den entrance dates in the northern areas (TLH and ZSP) were similar, as were those in the southern areas (ALK and SWK); however, the bears in the northern areas entered dens later than their counterparts in the south (ANOVA, $F_{3, 340} = 35.5$, $P < 0.001$; Tukey HSD, $P < 0.01$) (Table 1.6). Lone (potentially pregnant) females generally entered dens earlier than females with cubs, however, this difference was only significant in the ALK area ($t = 4.11$, $P<0.001$), and approached significance in TLH ($t = 1.51$, $P = 0.07$), and SWK ($t = 1.65$, $P = 0.05$).

Most den sites faced northerly directions (67.0%; n = 727), with all study areas having at least 60% of the dens with northerly aspects (Figure 1.7). Slopes of den sites ranged from flat ground (0°) to steep (77°) ($\bar{x} = 56.7^{o}$, SE = 0.59, $n = 727$) (Table 1.7). Slopes used differed between study areas, with dens in ALK being on flatter ground ($\bar{x} = 40.1^{o}$, SE = 2.31, $n = 111$) than dens in other areas (ANOVA, $F_{3, 723} = 63.3$, $P < 0.001$; Tukey HSD, $P < 0.01$). Although we were not able to visit each den site, it appeared from aerial observations that most were excavated annually. Some natural rock cavities were used, but those were not commonly available on many parts of the island.

Den emergence patterns for lone females and females with yearling and older cubs mirrored entrance patterns, with ALK bears emerging earlier than all other bears, and SWK bears emerging earlier than those in TLH and ZSP (ANOVA, $F_{3, 339} = 52.6$, $P < 0.001$; Tukey HSD, $P < 0.01$) (Table 1.8). Males in the northern study areas spent less time in dens than did females, but sample sizes were not sufficient to detect similar patterns in the southern areas. As a consequence of these denning patterns, bears in the northern study areas spent more time in dens than did bears in the southern study areas,

with the most notable difference between females without new cubs in TLH (180 days/year) versus those in ALK (100 days/year) (Table 1.8). Multiple regression analysis of factors that might influence denning periods (days food was available, salmon biomass, salmon availability, den slope, den elevation, bear age) of females without new cubs revealed that the best model for predicting denning periods ($R^2 = 0.49$; $P<0.0001$) was: *den days = 134.94 + 0.02(den elevation) – 0.20(food days).*

Interestingly, females with new cubs had virtually identical mean emergence times in all study areas, and in all areas they emerged later than all other females (TLH: $t = 5.92$, $P <0.001$; ZSP: $t = 8.68$, $P < 0.001$; SWK: $t = 6.37$, $P < 0.001$; ALK: $t = 3.79$, $P < 0.001$). There was also less difference in denning periods between study areas than was noted for other females (Table 1.8). Multiple regression analysis of the factors potentially impacting the denning periods of females with new cubs yielded a lower correlation coefficient ($R^2 = 0.27$; $P = 0.001$) than was noted for other females. The best model for this group of bears was: *den days = 181.81 + 0.02(den elevation) – 0.38(food days) – 0.12(den slope).*

DISCUSSION

Methods of accurately determining home ranges for wildlife individuals and populations have been a perennial subject of debate. The most basic method is calculation of the area within a MCP that connects the outermost relocation points (Mohr 1947, Hayne 1949). Researchers have measured and reported it for a wide variety of species and habitats, yet disagreement remains on the minimum number of points necessary to provide an accurate estimate, and the inherent bias of comparing home ranges derived from varying sample sizes (Kernohan et al. 2001). A plethora of alternative home range analysis methods have evolved since we began our Kodiak bear studies. These include fixed kernel, adaptive kernel, harmonic mean, cluster analysis, grid cell count, Dunn estimator, and Fourier series smoothing (White and Garrott 1990, Millspaugh and Marzluff 2001). Some authors have suggested that use of conventional VHF radio telemetry, especially aerial telemetry, can rarely, if ever, yield adequate sample sizes or distributions to provide meaningful data (Arthur and Schwartz 1999). Leban et al. (2001) conversely note that when radiotelemetry resources are limited, monitoring a higher number of radiocollared animals while collecting fewer locations per animal appears to be more accurate than more intensive monitoring of fewer animals. Commensurate with these discussions is concern about autocorrelation between successive locations adversely impacting analyses (Aebischer et al. 1993, Otis and White 1999), and consideration of how the study animal perceives its world when it is establishing and living within its home range (Gautestad et al. 1998).

Our analysis of MCP home ranges provided a good representation of the total areas in which bears traveled. It was, nevertheless, an incomplete picture because most MCPs increased in area the longer we tracked the bears. The rate of expansion was consistent between study areas, so we were able to make viable comparisons among areas; nevertheless, it was virtually impossible to objectively compare the MCPs of Kodiak

bears to those obtained from other areas. There were simply too many variables in the data collection methods and study durations to allow a detailed analysis. McLoughlin et al. (2000) list annual female home ranges for 30 brown bear populations, including 2 from our studies. They found that only 1 bear population (Admiralty Island, Alaska) had smaller home ranges than Kodiak. It is important to note, however, that the MCPs they reported for TLH (28 km^2) and SWK (71 km^2) were considerably smaller than were those we calculated in this investigation (70 km^2 and 219 km^2, respectively). When we compared the mean MCP for all Kodiak bears that had $\geq$30 relocations (128.2 km^2) with the McLoughlin et al. (2000) synopsis, it was still smaller than all but 5 of the MCPs reported from other areas.

McLoughlin et al. (2000) suggest that high habitat quality will result in small MCP home ranges and much home range overlap. This is consistent with our findings for Kodiak, as home ranges were relatively small and there was considerable overlap within all study areas. Even with the high degree of overlap, we did not detect any overt signs of spatial territoriality by bears. The only places where intraspecific strife was consistently observed was along portions of salmon spawning streams where fish were concentrated and easily caught (e.g. falls, riffles, and other shallow areas).

The lack of overlap of MCPs and UDs between study areas was an artifact of how the study areas were dispersed rather than a function of distinct subpopulations of bears. Had we captured bears in locations between the study areas, we suspect we would have seen a continuum of overlapping home ranges rather than distinct study areas. This hypothesis is supported by genetic analyses of bears from the entire archipelago (Talbot et al. 2006). That study found that despite evidence of substructuring of maternal lineages on Kodiak Island, genetic evidence from nuclear microsatellite loci indicates that bears on Kodiak comprise a single interbreeding population. They also noted that levels of genetic diversity at loci adequate for use in genetic tagging in other populations of brown bears in Alaska are insufficiently variable for similar use in Kodiak populations.

Perhaps a more accurate reflection of bear habitat quality on Kodiak was bear density. Estimates derived by Barnes and Smith (1998) suggest that bear densities (independent bears/1,000 km^2) in the study areas were: TLH – 199.8; ZSP – 221.2; SWK – 212.0; and, ALK – 218.6. Even though densities were comparable in all areas ($\bar{x}$= 214.36 independent bears/1000 km^2), there were considerable variations in average MCP and UD sizes between study areas. This implies that in spite of obvious differences in resource availability, the bears were flexible and able to successfully adapt to their local environments.

To further investigate bear distribution on the island, we analyzed resource availability and the MCP and UD sizes within the study areas. Hilderbrand et al. (1999) found that the proportion of meat in the diet of brown bears was significantly correlated with mean adult female body mass, mean litter size, and mean population density. Although bears throughout Kodiak had access to deer, and in some areas to mountain goats and reindeer, those mammals were only minor components to the overall diet of most bears; consequently salmon were the primary meat source. Willison and Halupka (1995) noted

that salmon were a keystone species in many coastal terrestrial ecosystems along the Pacific Rim and they also provide an influx of marine nutrients in these ecosystems (Hilderbrand and Robbins 1999).

Females in SWK had the largest MCPs of any female bears on Kodiak. This was in spite of the fact that bears in SWK had access to an estimated 13,976 kg/bear/year of salmon (versus an average of 3,893 kg/bear/year in the other areas) and the peak run of salmon lasted longer than any other area (102 days in SWK versus an average of 52 days for the other areas). Hilderbrand et al. (2004) estimated that bears on the Kenai Peninsula, Alaska, an area immediately north of the Kodiak Archipelago that is occupied by bears only slightly smaller than those on Kodiak, needed 1,003 kg/bear/year to sustain themselves. Within our study areas, the amount of salmon available annually ranged from 1,482 kg/bear/year in ZSP to 13,976 kg/bear/year in SWK, suggesting that bears on all Kodiak study areas had access to more than enough salmon to satisfy their needs.

The UDs in SWK were only slightly larger than those in the northern areas. This reflects that while bears in SWK had to range relatively far to acquire resources, they focused on specific areas once they got there. We noted many bears in that area going to salmon spawning areas as soon as fish arrived and moving to other streams when fish numbers waned or intraspecific competition became too intense (Barnes 1990). This pattern may have also been influenced by a preference for fresh salmon whenever possible because they have more lipids and proteins when they enter spawning streams than after they spawn (Gende et al. 2004).

Bears in SWK reduced their use of salmon streams when elderberries ripened. Even though salmon were still readily available, most bears supplemented their diets with berries. Local Alutiiq Native elders speculated that the reason bears consumed substantial amounts of elderberries was to purge themselves of tapeworms (*Diphyllobothrium ursi*) they acquired from eating salmon. Another reason may be that elderberries were the most abundant berries in the area and they grew in concentrated shrub fields with large clumps of fruit on each bush. Berries have a lower nutritive value than salmon and require more effort to consume. Welch et al. (1997) reported that bears depend on plants that permit large bite sizes or high bite rates through berry clustering and bush configuration that reduce leaf-to-fruit ratios. Rode and Robbins (2000) found that a mixed diet of salmon and fruit enhanced weight gain more than a diet limited to either only salmon (too much protein) or only fruit (too much carbohydrate).

Female bears in ALK had the largest UDs on Kodiak (significantly larger than the northern areas). Even though those bears had relatively small MCPs, there were few concentrated food sources on the peninsula, so the bears had to traverse much of the area to satisfy their needs. Salmon were only available for a relatively short period in limited areas, and berries and sedges were seasonally plentiful but widely dispersed throughout the study area. The most reliable food source was windrowed marine detritus that collected on beaches that surrounded the peninsula. The detritus contained an expansive variety of marine flora including bull kelp, bladderwrack, and sea lettuce (*Ulva* spp.). As it decomposed on the beach it also attracted a rich array of invertebrate faunal

decomposers such as beach hoppers (*Traskorchestia traskiana*) and insect larvae. Myrmecophagy is seasonally important for some brown bear populations in North America and Scandinavia (Mattson 2001, Swenson et al. 1999), but there are no ants on the Kodiak Archipelago. The beach hoppers may be an ecological equivalent to ants as a food resource for bears on Kodiak. Even when windrowed marine detritus was not evident on beaches, some bears were observed digging into sand and rocks apparently in pursuit of amphipods.

Although seasonally abundant after vernal and autumnal storms, windrowed detritus was present in ALK throughout the year. Beach foraging also provided bears with emergent coastal vegetation in spring and early summer and occasional bounties such as dead gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae)*, or fin (*Balaenoptera physalus*) whales that washed ashore, and deer that succumbed during winter.

The northern study areas had the smallest UDs because of the rich variety of resources found in relatively small tracts in those locations. Both areas had a mix of coastal and inland habitats and topographic relief that provided resources from early spring to late autumn, allowing bears the option of elevational movements rather than going long distances.

Another way to investigate seasonal resource use was by examining the biweekly mean elevations used by bears. These data reflected the seasonal availability of emergent vegetation as it progressed from sea level to the alpine in spring and early summer, and salmon at low elevations, and berries in low and mid-slope habitats. As expected, bears with access to more topographic diversity (TLH and ZSP) used a wider elevational range than those that lived in areas with more moderate terrain. Similarly, analysis of the cover types within the various study areas showed significant differences in resources chosen by bears. Although we did not have detailed, unbiased data on resource use by individual bears, the suite of analyses we used, coupled with the large, long-term, and widely distributed sample of individuals, provided a robust platform for investigating resource use by bears on different parts of the island during times of varying resource availability. If we had relied on a smaller sample of bears with more relocations during a shorter time, such an analysis would not have been feasible.

Further evidence of fidelity to home areas was adherence to the well-documented tendency for female brown bears to stay in or near maternal home ranges. During our studies, most female cubs used home ranges (MCP) that overlapped those of their mothers. Although all male cubs dispersed from maternal home ranges, the farthest any dispersed was only 52 km.

Erratic movements by bears occurred in all of the study areas throughout the study period, however, in every case (except those when bears were killed during their erratic ventures) the bears eventually returned to their usual areas. These unexplained short-term forays away from normal home ranges reiterated the bears' physical ability to use much larger areas.

Denning behavior also reflected the ability of Kodiak bears to adapt to their local environs. They usually sought sites that would remain dry throughout winter, because of the slope, aspect, substrate, elevation, or a combination of those factors. Even though sufficient den sites existed in what we would categorize as "ideal denning habitat", most bears denned near their foraging areas and showed a great deal of fidelity to den sites, continuing the pattern noted by Van Daele et al. (1990).

In TLH and ZSP, most dens were in steep alpine habitats. Natural cavities were used when available, but most dens were dug in suitable substrate. Denning usually commenced at the same time as sub-freezing temperatures in the high country, and den integrity was bolstered by frozen ground and deep snow that persisted through winter. Some bears in the ZSP area broke the pattern of denning near foraging areas by peregrinating to the rocky central spine of the island each year to den.

In SWK, most bears dug their dens in mid-slope shrub fields. These lower elevation dens did not have consistent snow cover or frozen ground much of the winter, but their integrity was maintained by the root systems of the shrubs above. Some SWK bears moved to higher ground to den in habitats similar to those in the northern areas, but they were the exception.

While some of the bears in ALK moved to the northern part of their peninsula to den in the highest terrain available in their district, most opted to dig dens in hummocks in the tundra. Tundra dens were the antithesis to what would normally be considered ideal denning habitat on Kodiak. The terrain was relatively flat, open, and rarely covered with snow. Heath and low shrub root systems provided some integrity to the dens, but they often flooded and sometimes collapsed. Coincident with the poor quality dens was a propensity to change dens during winter, and, perhaps, earlier emergence. Twenty percent of the females in ALK used more than 1 den during winter as opposed to only 1.5% for females that denned in other areas on Kodiak.

Denning chronology was as diverse as the den configurations and resource availabilities between the study areas. In the northern areas, where resources dwindled as winter commenced and diverse topography allowed denning options in higher elevations, adult females entered dens in early November, with males following a couple weeks later. In SWK, females had access to salmon for a longer period and entered their dens in late November. We did not have a sufficient sample size to determine when collared males in SWK or ALK entered their dens, but incidental observations indicated that most also inaugurated denning a couple weeks after the females. Lone (possibly pregnant) female bears in ALK entered dens about the same time as the females in SWK, but females with cubs waited until mid-December. A reverse pattern characterized den emergence, with females without neonates in ALK coming out of dens in late March, SWK females in late April, and females in the northern areas emerging in early May. The result was a difference of nearly 2.5 months in the average denning periods of female bears without neonates on opposite ends of the island.

In contrast to the denning patterns noted above, denning chronology was similar among study areas for females with neonates. In all areas, sows with new cubs emerged in late May, notably later than other bears, after spending over 6 months in their dens. Most of these new families did not follow the post-emergence movement patterns shared by other bears, foregoing feeding opportunities at lower elevations until early summer. Infanticide by adult males has been well documented in brown bear populations (Swenson et al. 1997, Miller et al. 2003, McClellan 2005), and while the reasons for that behavior have been debated, spatial and temporal segregation between males and maternal females occurs throughout the range of the brown bear (Ben-David et al. 2004, Dahle and Swenson 2004, Wielgus and Bunnell 1995). It appeared that even after the physiological strain of fasting for more than half the year, parturition, and suckling new cubs for most of that time (Hilderbrand et al. 2000), there was still a selective advantage on Kodiak Island for most females with neonates to select habitats separate from other bears, even if that meant delaying replenishment of their bodily reserves.

Male bears throughout Kodiak denned for shorter periods than their female counterparts and in spite of larger home ranges, used den sites similar to the females in their areas. Overall, 23% of the males we followed during this study did not enter dens during a winter (as opposed to less than 1% of the females). The highest proportion of non-denning males was in ALK (75%). Even though our sample size of radiocollared males was not large, incidental sightings concurred with those observations.

Denning chronology appeared to be driven by food availability. Ambient temperatures were comparable throughout Kodiak, but for bears on northern Kodiak food was available later in the spring and dwindled earlier in the fall as compared to the southern parts of the island. Marine detritus was available to bears in ALK virtually year-round. Multiple regression analysis confirmed that food availability was the most important variable driving the number of days bears were in dens. This pattern was complicated somewhat by the reproductive category of the bear. As noted earlier, females with neonates had comparable denning periods regardless of what part of the island they occupied, suggesting that the demands of parturition and protecting new cubs superseded conventional denning patterns. Males typically denned for shorter periods than did females in all areas, including many males that did not den during a winter. This may have been attributable to their larger home range sizes and larger body sizes that gave them an advantage over females in finding and competing for adequate food for as resources dwindled in most areas with the approach of winter.

Differential uses of feeding and denning habitats by bears in the various study areas on Kodiak were a testament to the adaptability of the species. Whenever possible, bears were able to use a plethora of resources to satisfy their needs without moving long distances. If bears can satisfy their needs without extensive forays, efficient use of the local resources can improve the fitness of the population. Long-lived species such as bears invest a great deal in a small number of offspring. Maternal females teach their cubs when and where to find the most nutritious foods, and where to rest and den. The cubs also learn to recognize the social status of other bears in the vicinity, thereby reducing intraspecific encounters both when they are with their mothers and after family

break-up. Consequently, there is a strong incentive to remain close to home if resources are adequate. Male movement out of the maternal home range may be a function of a natural tendency to wander, maternal intolerance, adult male intolerance, or most likely a combination of factors. We could not ascertain the exact reasons, but it was common to see subadults actively chased by other bears during the spring and early summer. Because of the sedentary nature of female bears in Kodiak, the limited dispersal of young males and the larger home ranges of adult males afforded some of the few possibilities for genetic mixing.

Even though there were no physical barriers preventing movement between resources, generations of behavioral specialization within local areas have created a population that is a radiating continuum in which bears that live adjacent to each other are similar in their resource use and activity patterns, but those living in different habitats on the island are considerably different due to behavioral specialization for their areas. This radiating continuum may lead to local carrying capacities. If local resources dwindle, most bears would probably not pioneer new locales, but would stay in familiar habitats. In situations such as Kodiak, where virtually all habitats are used by high densities of bears, opportunities to be successful in new areas are limited because transient bears would have to compete with resident bears that have superior knowledge of the local situation.

MANAGEMENT IMPLICATIONS

The population distribution patterns and the mitochondrial DNA analysis confirmed our hypothesis that Kodiak Island bears are a single population; however, resource use patterns lead to a rejection of the hypothesis that all bears used the same type of "optimal" habitat. The ecological flexibility of the population as a whole has allowed it to expand to all available habitats on the island, thereby expanding the carrying capacity over that which would be expected if they conformed to a uniform habitat use pattern. This diversification ultimately insulates the population from collapse. The radiating continuum appears to be similar in some ways to the metapopulation concept proposed by Levins (1970) and expanded on by Harrison (1991) and Hansson (1991), in that it includes a series of "subpopulations" that use different resources and may be subjected to localized extinctions and recolonizations should there be catastrophic alterations of resource availability. Unlike the concepts presented by those authors, Kodiak bears were not distinct subpopulations, they were not genetically diverse, and they were not dispersed over large distances.

The results of this study highlight the dangers of making management decisions based on limited knowledge of a brown bear population. The radiating continuum distribution and differential resource use can be expected to result in varying population responses to environmental changes.   Many of the conclusions derived from data on one part of the island are not directly applicable to bears in other areas, even though the bears are part of the same population. Similarly, any estimation of the impacts of an environmental event, such as normal interannual variation or long-term climate change, must consider all components of the bear population because what may be beneficial for bears in one area

could be neutral or detrimental in other areas. This same caution holds true for all bear populations – the species is too diverse to lend itself to simple or straightforward answers.

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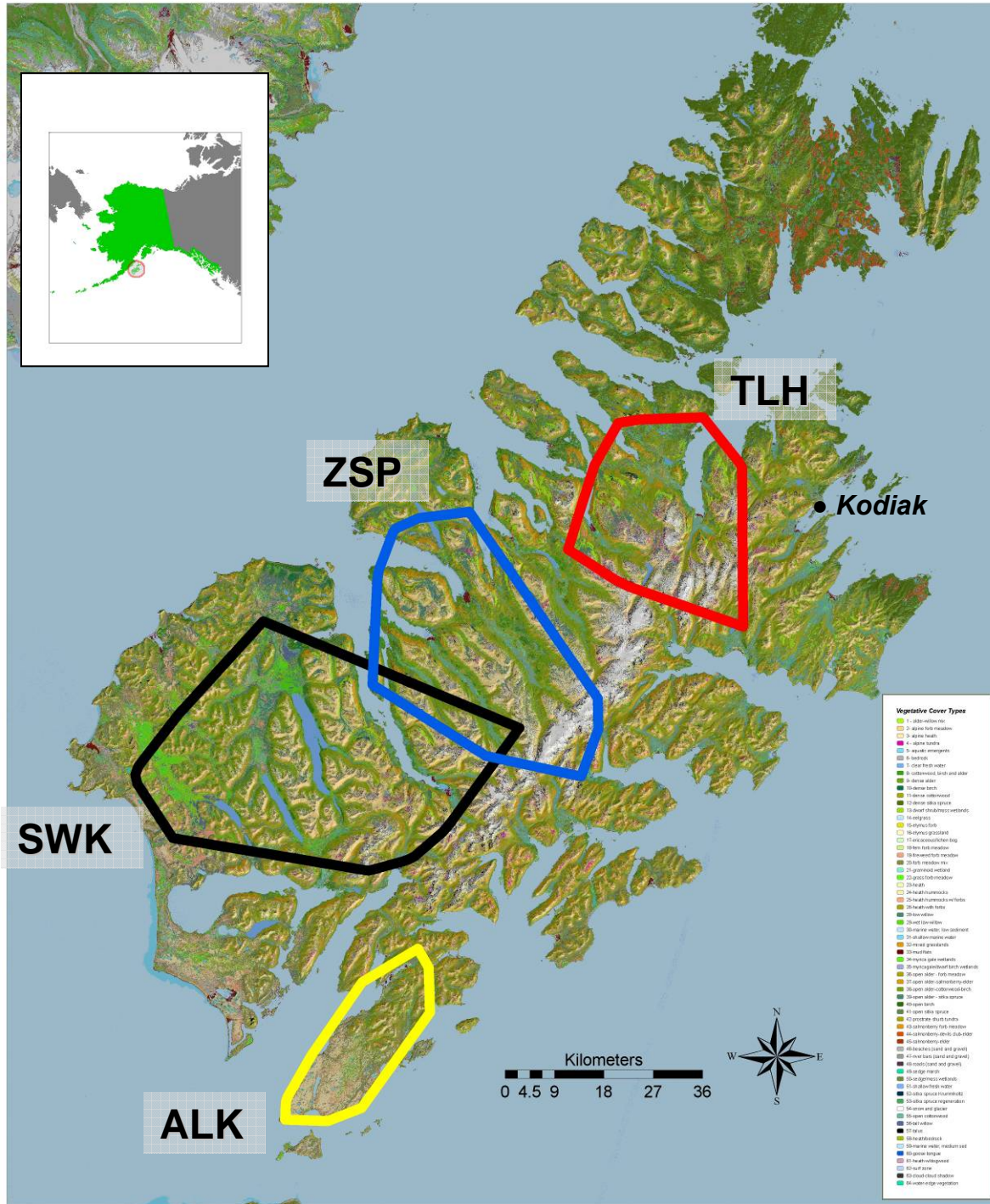
Figure 1.1. Kodiak Archipelago, Alaska, including the 4 brown bear study areas. (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula) and vegetative cover types, 1982 – 2004.
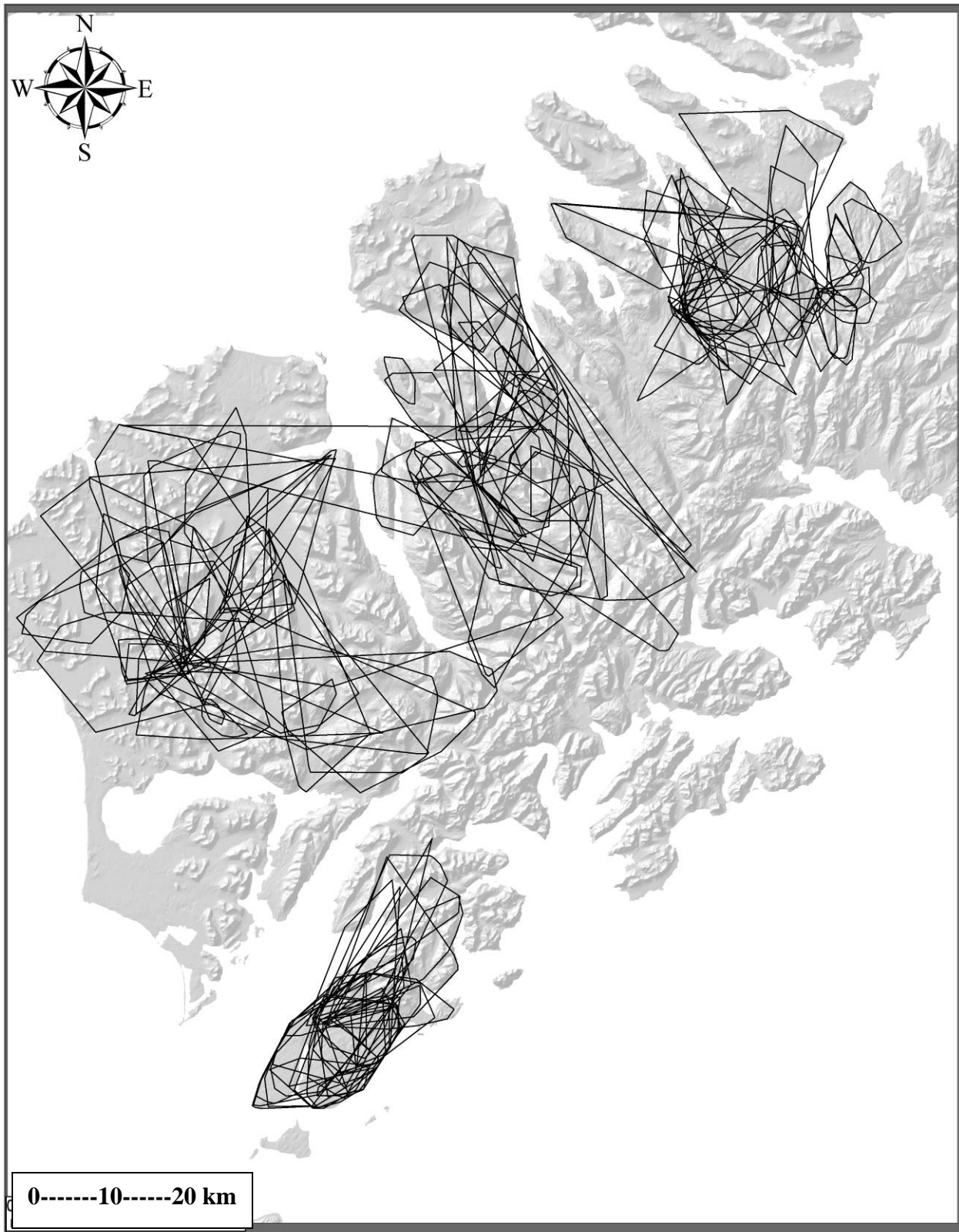
Figure 1.2. Minimum convex polygon (100%) home ranges for all female bears with ≥30 relocations, Kodiak Island, Alaska, 1982 – 2004.
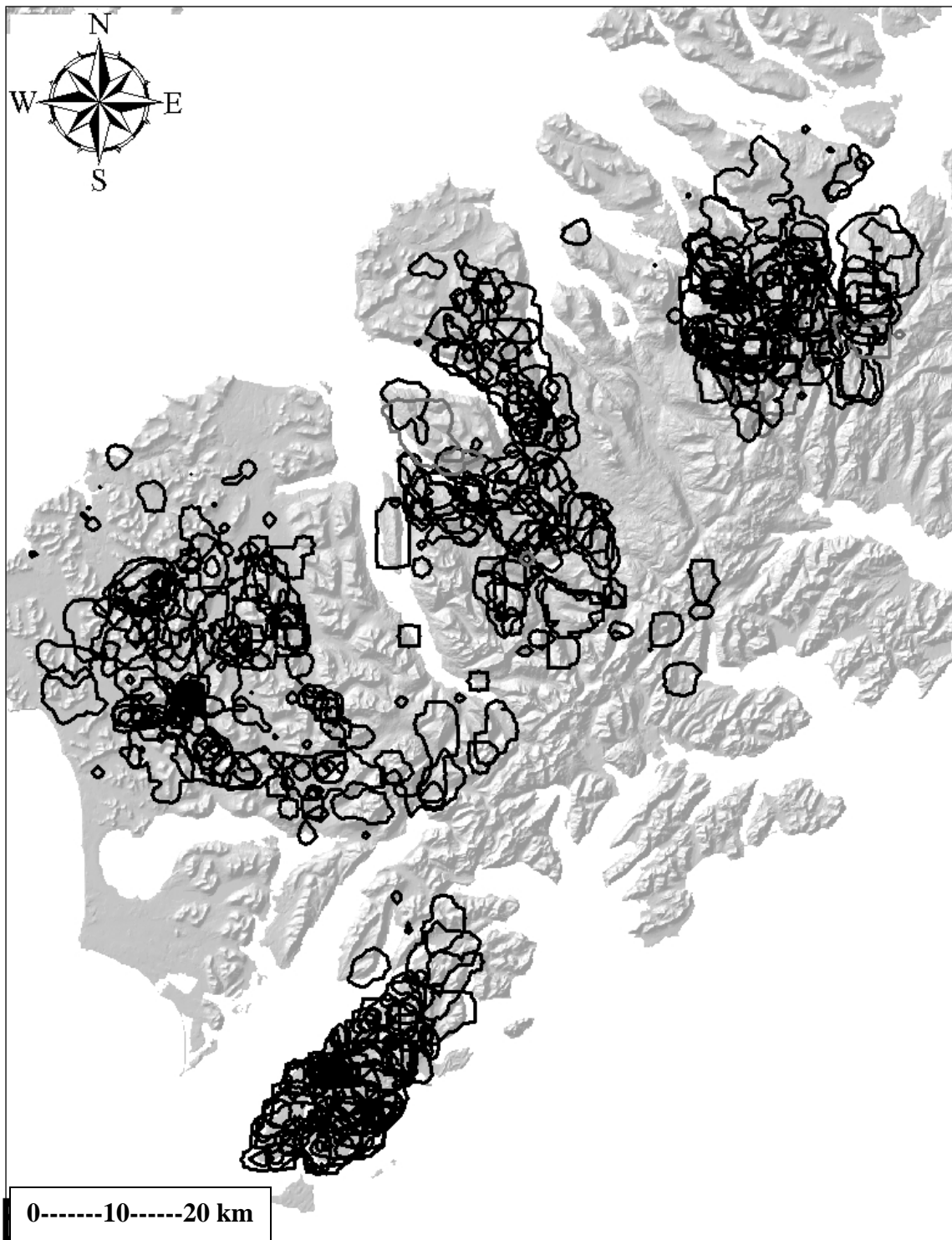
Figure 1.3. Fixed kernel (95%) utilization distribution areas for all female bears with $\geq$30 relocations, Kodiak Island, Alaska, 1982 – 2004.
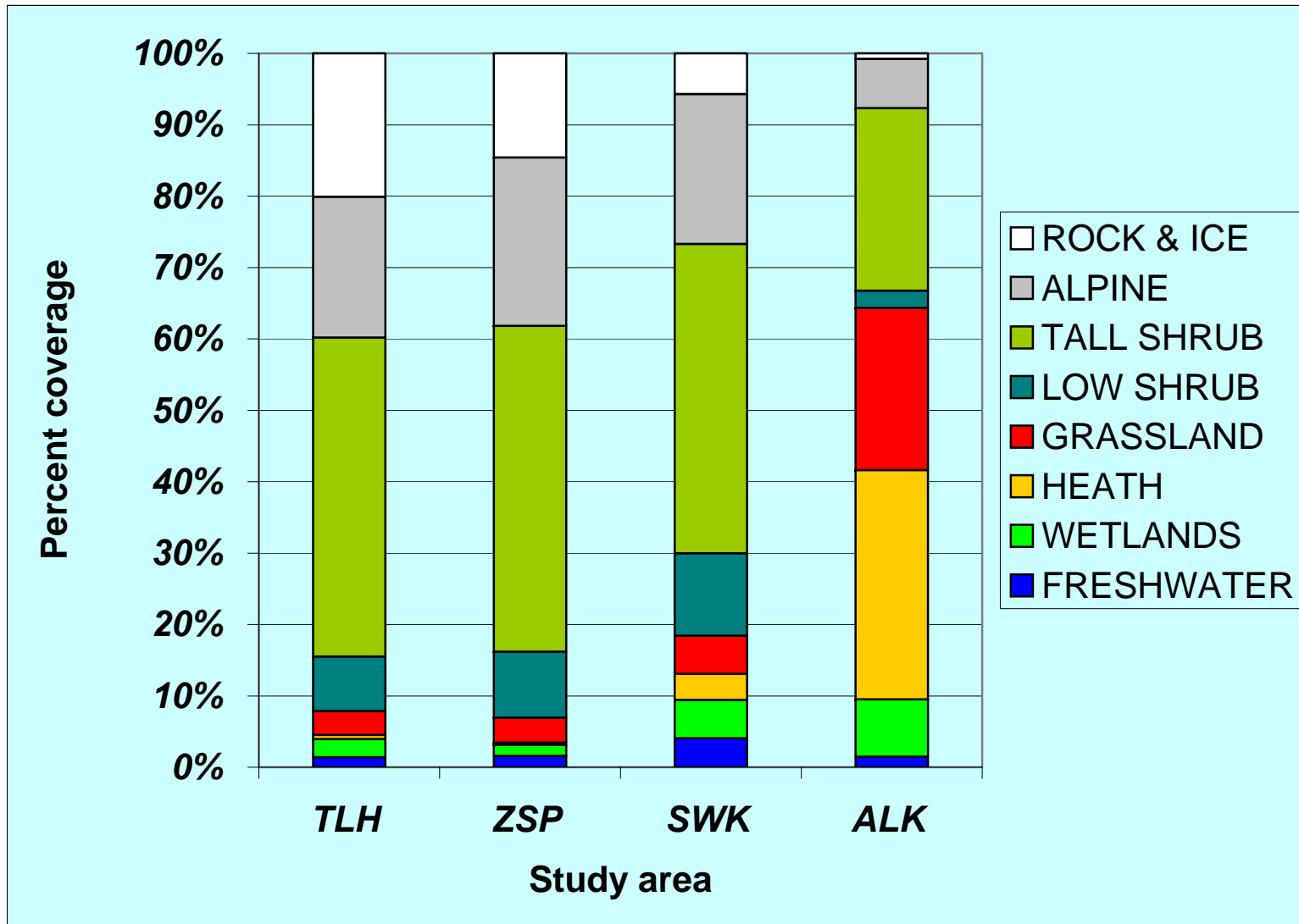
Figure 1.4. Vegetative cover types (percentage of total area excluding marine habitat) within each study area (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula), Kodiak Island, Alaska, 1982-2004.

Table 1.1. Summary of information collected from bears captured on Kodiak Island, Alaska from 1982 – 2004.

Study Area	Gender	Captured	Radiocollared	Total relocations	Bears with ≥30 relocations	Bears with known fate	% known fate
Terror Lake	Male	56	38	1,159	15	38	67.9%
	Female	95	60	4,449	45	40	42.1%
	Total	151	98	5,608	60	78	51.7%
Zachar / Spiridon	Male	11	11	381	5	7	63.6%
	Female	44	44	3,607	37	15	34.1%
	Total	55	55	3,988	42	22	40.0%
Southwest Kodiak	Male	28	8	153	2	15	53.6%
	Female	92	57	2,992	33	39	42.4%
	Total	120	65	3,145	35	54	45.0%
Aliulik Peninsula	Male	30	8	210	3	18	60.0%
	Female	46	35	2,588	27	12	26.1%
	Total	76	43	2,798	30	20	26.3%
TOTAL	Male	125	65	1,903	25	78	62.4%
	Female	277	196	13,636	142	106	38.3%
	Total	402	261	15,539	167	174	43.3%

Table 1.2. Home range and utilization distribution calculations by study area for radiocollared female bears with ≥ 30 relocations, Kodiak Island, Alaska, 1982 – 2004.

Study area	Home range	$\underline{n}$	Mean (km^2)	Median (km^2)	Standard deviation (km^2)	Standard error (km^2)	Range (km^2)
Terror Lake	100%MCP[a]	45	70.0	45.5	55.6	8.3	11.7 – 217.2
	95% FK[b]	45	45.1	40.6	16.6	2.5	98.5 – 2,029.4
Zachar / Spiridon	100%MCP	37	135.5	75.8	156.8	25.8	7.5 – 817.7
	95% FK	37	43.8	41.1	19.3	3.2	119.1 – 1,619.1
Southwest Kodiak	100%MCP	33	218.6	155.1	221.4	38.5	5.7 – 1,063.3
	95% FK	33	54.3	48.3	28.3	4.9	20.5 – 165.0
Aliulik Peninsula	100%MCP	28	107.3	102.6	61.1	11.5	17.4 – 270.3
	95% FK	28	61.7	56.6	22.3	4.2	115.5 – 1,727.2
TOTAL	100%MCP	143	128.6	76.6	148.4	12.4	5.7 – 1,063.3
	95% FK	143	50.1	46.5	22.4	1.9	16.3 – 165.0

a – 100% MCP = 100% minimum convex polygon home range
b – 95% FK = 95% fixed kernel utilization distribution

Biweekly Elevations
Females with new cubs - all study areas
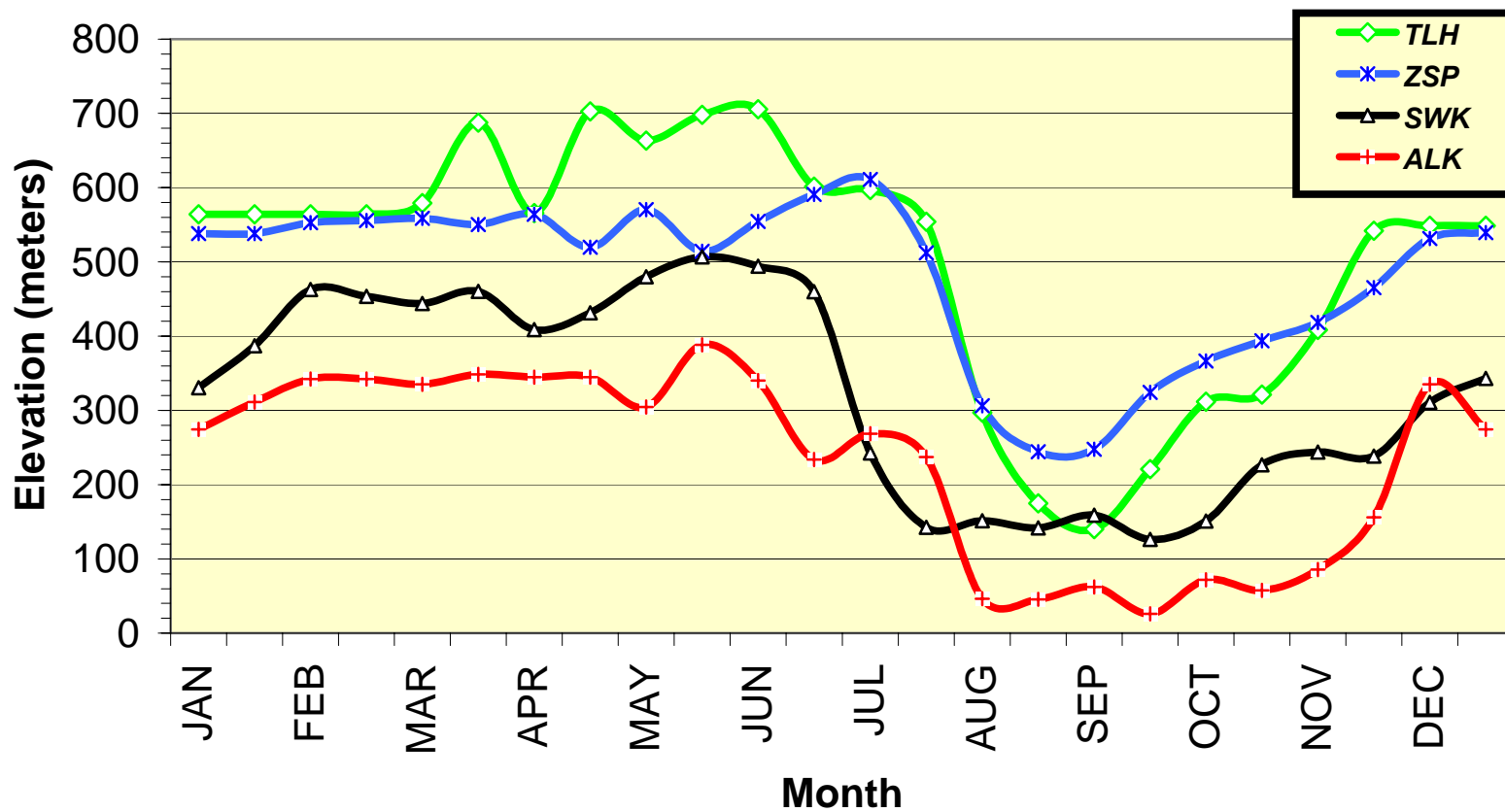
Figure 1.5. Biweekly mean elevations of radiocollared female bears that were with new cubs by study area (TLH – Terror Lake, ZSP –Zachar/Spiridon, SWK – Southwest Kodiak, ALK – Aliulik Peninsula), Kodiak Island, Alaska, 1982 – 2004.

Biweekly Elevations

All bears (except females with new cubs)
all study areas
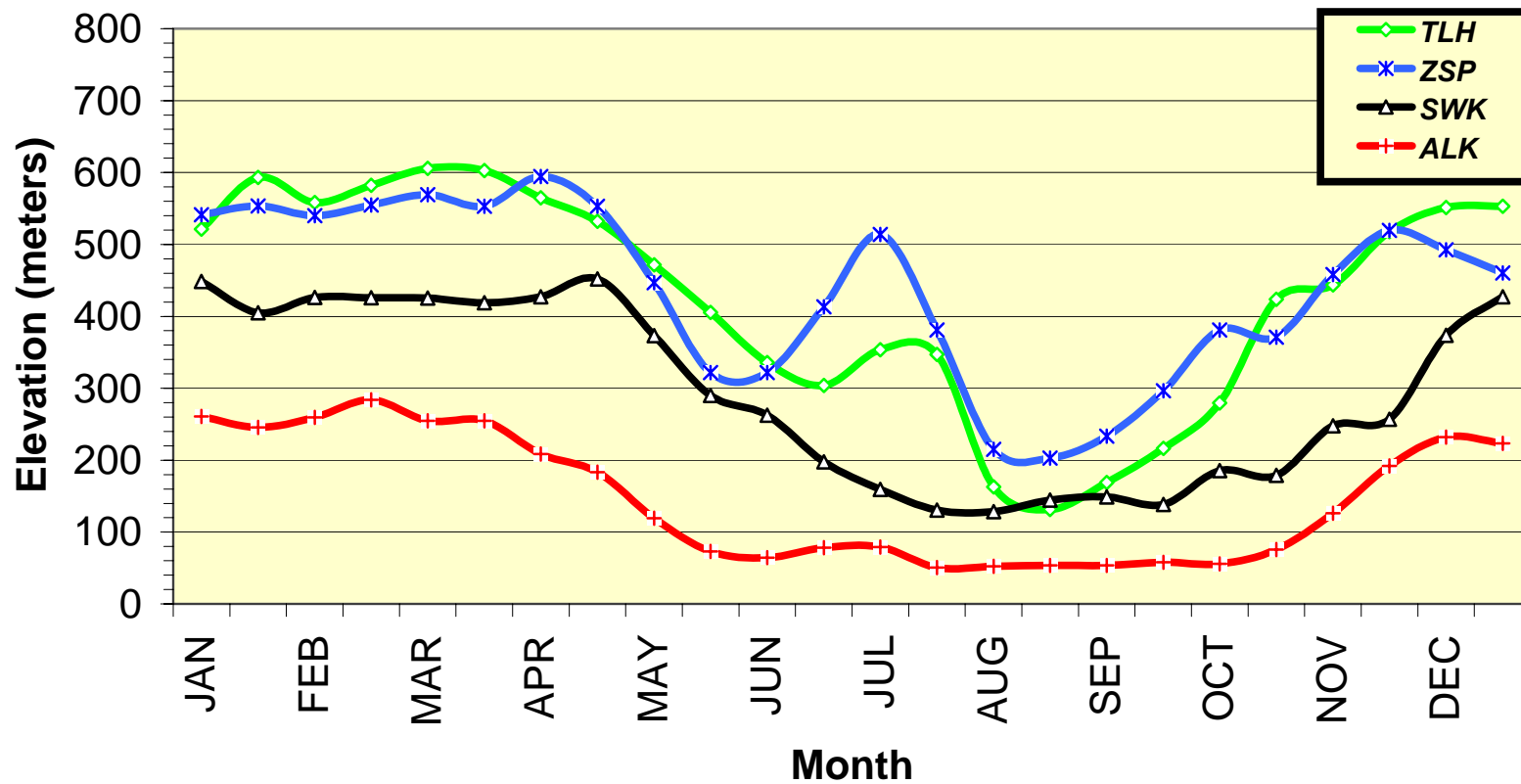
Figure 1.6. Biweekly mean elevations of radiocollared bears that were not with new cubs by study area (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula), Kodiak Island, Alaska, 1982 – 2004.
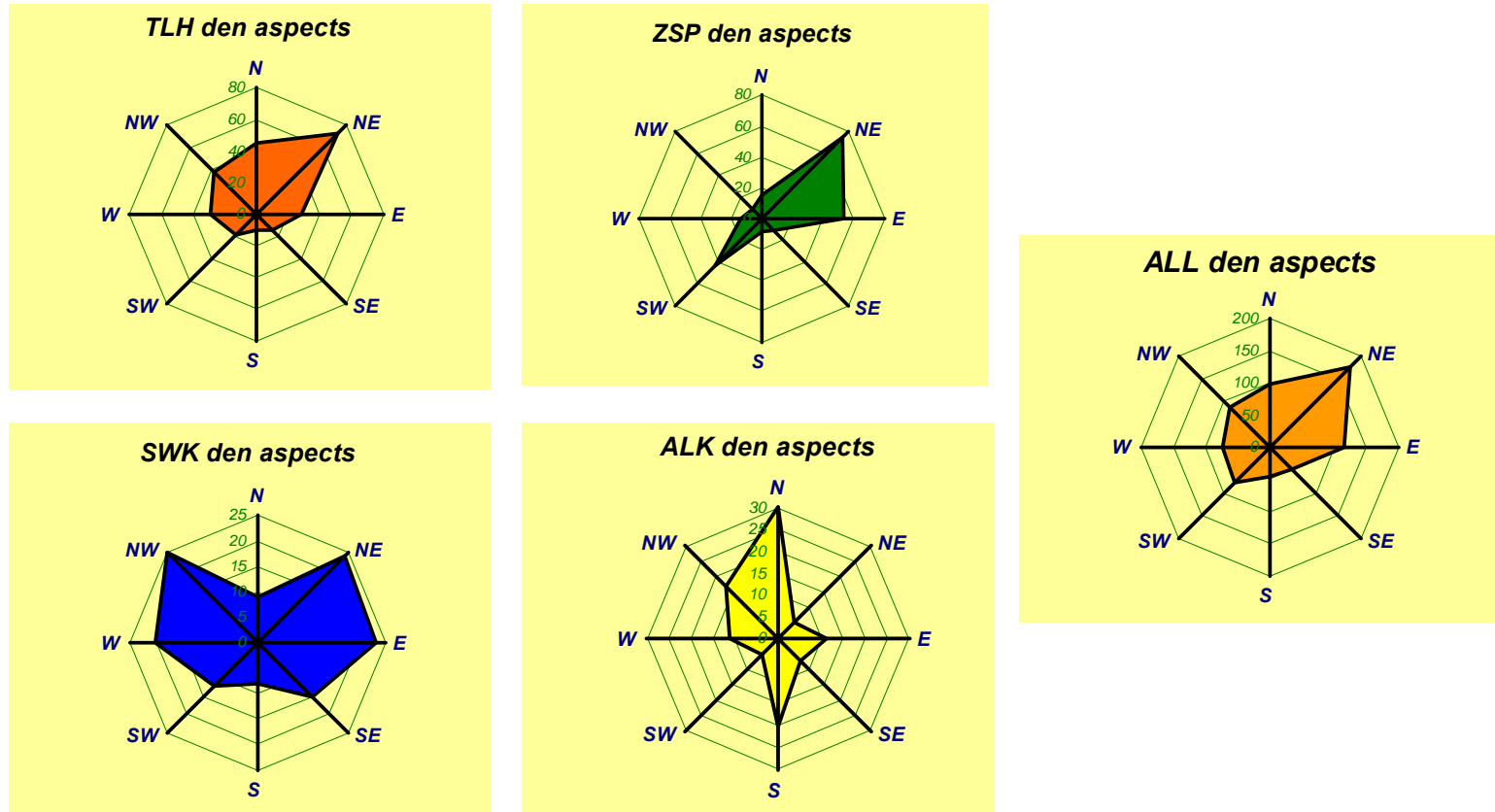
Figure 1.7. Aspects of brown bear den sites, by study area (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula) and overall, on Kodiak Island, Alaska, 1983-1997. The numerical value is the number of den sites.

Table 1.3. Estimated availability of spawning salmon to bears in each study area on Kodiak Island, Alaska, 1982-2004.

Study area	Species	Annual escapement[a]	Available biomass[b] (kg)	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 – 05 Oct	15 SEP – 30 Sep
	TOTAL	181,400	347,840	10 Jun – 05 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 – 05 Oct	15 Sep – 30 Sep
	TOTAL	185,000	383,580	10 Jul – 05 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	01 Aug – 20 Aug
	Silver (coho)	73,500	264,600	15 Aug – 05 Oct	15 Sep – 30 Sep
	TOTAL	2,787,500	5,645,330	25 May – 05 Oct	05 Jun – 25 Sep
Aliulik Peninsula	King (chinook)	0	0	-----	-----
	Sockeye (red)	0	0	-----	-----
	Chum (dog)	14,300	48,620	01 Aug – 15 Sep	05 Aug – 01 Sep
	Pink (humpy)	375,800	563,700	15 Jul – 10 Sep	10 Aug – 30 Aug
	Silver (coho)	2,000	7,200	15 Aug – 05 Oct	15 Sep – 30 Sep
	TOTAL	392,100	619,520	15 Jul – 05 Oct	10 Aug – 01 Sep

a – Mean estimates based on weir counts, aerial surveys, and field estimates (Alaska Department of Fish and Game files).
b – Mean 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 files).

Table 1.4. Resource use by brown bears in various study areas (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula) on Kodiak Island, Alaska, 1982-2004.

| Resource category	Amount used ($\bar{x}$)	ANOVA significance[a]	Study area comparisons (Tukey HSD; $P<0.05$)
Rock – ice	2.99 km^2	$P<0.0001$	TLH>ZSP, SWK, ALK
Alpine	6.84 km^2	$P<0.0001$	TLH>ALK; ZSP>ALK, SWK; SWK>ALK
Tall Shrub	20.15 km^2	$P<0.0001$	TLH>ALK; ZSP>ALK; SWK>ALK
Low shrub	4.03 km^2	$P<0.0001$	ZSP>ALK; SWK>ALK, TLH, ZSP
Grassland	3.97 km^2	$P<0.0001$	ALK>TLH, ZSP, SWK; SWK>TLH, ZSP
Heath	5.04 km^2	$P<0.0001$	ALK>TLH, ZSP, SWK
Wetlands	2.53 km^2	$P<0.0001$	ALK>TLH, ZSP: SWK>TLH, ZSP
Freshwater	1.28 km^2	$P<0.0001$	SWK>TLH, ZSP, ALK
Salmon	1,072,756 kg	$P<0.0001$	SWK>TLH, ZSP, ALK

a – results of univariate analysis of variance statistic testing the hypothesis that all of the study areas had an equal amount of a given resource.

Table 1.5. Number of dens used per denning period for radiocollared bears, Kodiak Island, Alaska, 1982 – 2004.

Study area	Gender	Complete denning periods[a]	No den (%)		One den (%)		Two dens (%)		Three dens (%)	
Terror Lake	Females	202	1	(0.5)	196	(97.1)	5	(2.5)	0	(---)
	Males	34	8	(23.5)	26	(76.5)	0	(---)	0	(---)
	Total	236	9	(3.8)	222	(94.1)	5	(2.1)	0	(---)
Zachar / Spiridon	Females	164	0	(---)	162	(98.8)	2	(1.2)	0	(---)
	Males	14	2	(14.3)	12	(85.7)	0	(---)	0	(---)
	Total	178	2	(1.1)	174	(97.8)	2	(1.1)	0	(---)
Southwest Kodiak	Females	117	0	(---)	116	(99.1)	1	(0.9)	0	(---)
	Males	4	0	(---)	4	(100.0)	0	(---)	0	(---)
	Total	121	0	(---)	120	(99.2)	1	(0.8)	0	(---)
Aliulik Peninsula	Females	75	3	(4.0)	57	(76.0)	13	(17.3)	2	(2.7)
	Males	4	3	(75.0)	1	(25.0)	0	(---)	0	(---)
	Total	79	6	(7.6)	58	(73.4)	13	(16.5)	2	(2.5)
TOTAL	Females	558	4	(0.7)	531	(95.2)	21	(3.8)	2	(0.4)
	Males	56	13	(23.2)	43	(76.8)	0	(---)	0	(---)
	Total	614	17	(2.8)	574	(93.5)	21	(3.4)	2	(0.3)

a – includes all bears that were known to enter dens and later emerge from dens, regardless of whether we could accurately ascertain the timing of den entrance and emergence. In the case of bears that did not enter dens, those that were observed out of dens during the entire winter were included.

Table 1.6. Den entrance dates for radiocollared bears, Kodiak Island, Alaska, 1982 – 2004.

Study area	Reproductive status	n^a	Mean (date)	Standard deviation (days)	Standard error (days)	Range (date)
Terror Lake	Lone females	67	06 Nov	11.11	1.36	14 Oct – 14 Dec
	Females with cubs	34	10 Nov	15.69	2.69	21 Oct – 20 Dec
	Males	5	30 Nov	35.83	16.02	04 Nov – 26 Jan
Zachar / Spiridon	Lone females	49	08 Nov	16.50	2.36	03 Oct – 11 Dec
	Females with cubs	56	08 Nov	18.34	2.45	12 Sep – 24 Dec
	Males	6	20 Nov	18.53	7.56	27 Oct – 15 Dec
Southwest Kodiak	Lone females	29	20 Nov	18.85	3.50	19 Oct – 28 Dec
	Females with cubs	50	28 Nov	22.54	3.19	17 Oct – 19 Jan
	Males	2	02 Jan	15.56	11.00	24 Dec – 13 Jan
Aliulik Peninsula	Lone females	37	23 Nov	15.83	2.60	30 Oct – 27 Dec
	Females with cubs	22	13 Dec	20.28	15.83	08 Nov – 19 Jan
	Males	0	--	--	--	---

a – includes only those bears that had ≤30 days between the last time the bear was determined to be out of a den and the first time it was observed in a den. Den entrance date was calculated as the mid-point between "out" and "in" observation dates.

Table 1.7. Den site characteristics for radiocollared bears, Kodiak Island, Alaska, 1982 – 2004.

Study area	Den site characteristic	n	Mean	Standard deviation	Standard error	Range
Terror Lake	Elevation	253	670.7 m	264.0 m	16.6 m	91 – 1189 m
	Slope	253	57.70 $^\circ$	14.38 $^\circ$	0.90 $^\circ$	10 - 74 $^\circ$
Zachar / Spiridon	Elevation	227	588.6 m	219.0 m	14.5 m	61 – 1189 m
	Slope	227	62.37 $^\circ$	9.39 $^\circ$	0.62 $^\circ$	27 – 75 $^\circ$
Southwest Kodiak	Elevation	136	457.8 m	196.8 m	16.9 m	137 – 914 m
	Slope	136	58.70 $^\circ$	8.60 $^\circ$	0.74 $^\circ$	20 – 77 $^\circ$
Aliulik Peninsula	Elevation	111	287.4 m	184.9 m	17.5 m	30 – 655 m
	Slope	111	40.10 $^\circ$	24.33 $^\circ$	2.31 $^\circ$	0 - 73 $^\circ$

Table 1.8. Den emergence dates for radiocollared bears, Kodiak Island, Alaska, 1982 – 2004.

Study area	Reproductive status	$\underline{n}$[a]	Mean (date)	Standard deviation (days)	Standard error (days)	Range (date)	Mean denning period (days)[b]
Terror Lake	Females with new cubs	48	27 May	20.24	2.92	20 Mar – 08 Jul	202
	Other females	127	09 May	17.06	1.51	31 Mar – 12 Jul	180
	Males	21	24 Apr	15.11	3.30	31 Mar – 24 May	146
Zachar / Spiridon	Females with new cubs	38	27 May	16.28	2.64	15 Apr – 28 Jun	200
	Other females	88	01 May	15.83	1.69	14 Mar – 17 Jun	173
	Males	9	23 Apr	12.17	4.06	08 Apr – 12 May	154
Southwest Kodiak	Females with new cubs	19	27 May	17.53	4.02	19 Apr – 02 Jul	188
	Other females	82	26 Apr	19.48	2.15	11 Mar – 02 Jun	149
	Males	2	09 Mar	50.91	36.00	01 Feb – 14 Apr	66
Aliulik Peninsula	Females with new cubs	7	20 May	16.40	6.20	03 May – 08 Jun	177
	Other females	46	23 Mar	39.24	5.78	20 Dec – 23 May	100
	Males	0	---	---	---	---	--

a – includes only those bears that had ≤30 days between the last time the bear was observed in the den and the first time it was observed away from the den. Den emergence date was calculated as the mid-point between "in" and "out" observation dates.

b – difference between mean den entrance and den emergence dates by reproductive category. To calculate the denning period for "females with new cubs", we used the mean den entrance date for lone females and the mean den emergence date for females with new cubs. To calculate the denning period for "other females", we used the mean den entrance date for females with cubs and the mean den emergence dates of lone females and females with yearling and older cubs.

Appendix 1.1. Area of habitats and vegetative cover types within each study area (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula), Kodiak Island, Alaska, 1982 – 2004.

Habitat type	Vegetative cover type[a]	Study area (km^2)			
		TLH	ZSP	SWK	ALK
ROCK & ICE		*162.34*	*170.75*	*108.70*	*2.61*
	Bedrock	60.83	66.15	75.52	1.95
	River bars (sand and gravel)	4.24	6.30	2.49	0.16
	Roads (sand and gravel)	0.05	0.09	0.08	0.28
	Snow and glacier	77.60	85.46	20.28	0.01
	Talus	19.62	12.76	10.33	0.20
ALPINE		*159.95*	*275.92*	*399.90*	*24.35*
	Alpine forb meadow	56.12	114.79	199.29	10.42
	Alpine heath	24.00	69.39	105.60	6.56
	Alpine tundra	15.89	9.61	12.81	0.79
	Prostrate shurb tundra	61.50	80.32	80.71	6.50
	Sitka spruce krummholtz	2.44	1.82	1.49	0.08
TALL SHRUB		*361.37*	*534.06*	*825.27*	*90.09*
	Alder-willow mix	33.02	27.56	31.66	1.32
	Cottonwood, birch and alder	4.30	28.38	15.31	0.39
	Dense alder	81.51	159.91	265.75	23.55
	Dense birch	1.98	2.69	4.56	0.75
	Dense cottonwood	9.02	29.68	13.02	0.46
	Dense Sitka spruce	10.92	0.00	0.00	0.00
	Open alder - forb meadow	101.94	111.33	263.30	33.49
	Open alder-salmonberry-elder	34.06	53.97	87.21	16.97
	Open alder-cottonwood-birch	16.11	28.23	29.18	0.85
	Open alder - Sitka spruce	16.21	18.15	0.56	0.15
	Open birch	7.55	25.74	35.99	1.56
	Open Sitka spruce	14.30	8.76	0.00	0.00
	Sitka spruce regeneration	0.00	0.00	0.00	0.00
	Open cottonwood	26.65	36.00	40.72	4.56
	Tall willow	3.81	3.64	38.00	6.05

Appendix 1.1 (continued). Area of habitats and vegetative cover types within each study area (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula), Kodiak Island, Alaska, 1982 – 2004.

Habitat type	Vegetative cover type[a]	Study area (km^2)			
		TLH	ZSP	SWK	ALK
LOW SHRUB		*61.83*	*108.56*	*220.32*	*8.52*
	Low willow	43.07	83.46	140.41	4.04
	Wet low willow	2.74	4.69	63.55	2.42
	Salmonberry forb meadow	9.15	12.14	8.94	1.72
	Salmonberry-devils club-elder	0.00	0.00	0.00	0.00
	Salmonberry-elder	6.87	8.28	7.41	0.34
GRASSLAND		*27.26*	*40.49*	*101.29*	*79.90*
	Elymus forb	0.15	0.29	0.31	0.86
	Elymus grassland	0.64	0.40	0.47	1.19
	Fern forb meadow	4.66	14.79	23.17	6.66
	Fireweed forb meadow	5.50	1.76	22.36	1.84
	Forb meadow mix	15.09	22.59	54.24	67.57
	Grass forb meadow	1.17	0.60	0.72	1.37
	Mixed grasslands	0.05	0.05	0.03	0.40
HEATH		*4.69*	*3.82*	*69.47*	*113.11*
	Heath	0.42	0.86	1.18	6.19
	Heath hummocks	0.70	0.26	7.25	75.96
	Heath hummocks w/ forbs	3.49	2.11	60.63	30.37
	Heath with forbs	0.04	0.12	0.02	0.13
	Heath/bedrock	0.02	0.40	0.04	0.04
	Heath w/dogwood	0.01	0.07	0.36	0.43

Appendix 1.1 (continued). Area of habitats and vegetative cover types within each study area (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula), Kodiak Island, Alaska, 1982 – 2004.

Habitat type	Vegetative cover type[a]	Study area (km^2)			
		TLH	ZSP	SWK	ALK
WETLANDS		*20.53*	*17.96*	*102.81*	*28.31*
	Dwarf shrub/moss wetlands	1.72	0.34	33.35	3.32
	Ericaceous/lichen bog	0.00	0.00	0.00	0.05
	Graminoid wetland	3.19	4.43	2.00	1.46
	Mud flats	2.39	5.16	3.45	3.45
	Myrica gale wetlands	3.06	1.56	36.17	2.72
	Myrica gale/dwarf birch wetlands	0.43	0.68	12.38	2.13
	Beaches (sand and gravel)	1.11	1.38	0.66	1.07
	Sedge marsh	0.77	0.66	0.72	0.81
	Sedge/moss wetlands	7.85	3.75	14.09	13.29
FRESHWATER		*11.27*	*18.86*	*77.47*	*5.24*
	Aquatic emergents	0.58	0.20	0.54	0.85
	Clear fresh water	7.04	12.62	67.60	1.76
	Shallow fresh water	0.56	1.56	1.21	0.27
	Water-edge vegetation	3.08	4.48	8.13	2.37
MARINE		*73.49*	*98.74*	*69.08*	*62.15*
	Eelgrass	1.51	3.98	1.75	3.35
	Marine water, low sediment	70.61	92.59	64.30	57.49
	Shallow marine water	1.23	1.41	2.92	0.40
	Marine water, medium sediment	0.07	0.74	0.08	0.51
	Goose tongue	0.05	0.02	0.03	0.36
	Surf zone	0.00	0.01	0.00	0.02
	Cloud, cloud shadow	0.01	0.01	0.00	0.01
TOTAL AREA		*882.72*	*1,269.18*	*1,974.32*	*414.27*

a – vegetative cover types as described in Fleming and Spencer (2004).

Chapter 2

MANAGEMENT OF BROWN BEAR HUNTING ON KODIAK ISLAND, ALASKA

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Abstract: Brown bear (*Ursus arctos*) populations along much of the North Pacific Rim are healthy and provide an important economic resource as trophy hunters seek the largest representatives of the species, yet relatively little research has been published about the population dynamics and harvest management of those brown bears. The purpose of this project was to gather information on the population dynamics of bears on Kodiak Island, Alaska during a long-term study, and to develop an easily understood model that could be used by managers of coastal bear populations to objectively estimate appropriate harvest strategies and guidelines. There were bear research projects in 4 separate study areas on Kodiak from 1982-2004, all of which included marked bears. The annual adult male survival rate was comparable in all study areas at 0.809. The overall survival rate for all independent females was 0.867, with one area significantly lower than the others at 0.800. Adolescent annual survival rates were 0.563 for males and 0.889 for females. The major cause of death for males was hunter harvest (91%), while most females died of natural causes (54%). The annual harvest density for all areas during this study was 17.07 independent bears/1,000 km^2, and the harvest rates of independent bears ranged from 6.68% to 10.33%. The number of bears harvested remained relatively consistent during the study period, but we saw an increase in the number and the percentage of the harvest that consisted of trophy-sized (total skull size>71 cm) males. Male bears dominated the harvest in all areas and the age structure of the male bear population directly impacted the number of large bears available to hunters with 56.1% of the males in the oldest age class (>20 years) being trophy-sized. We created a deterministic model using Microsoft Excel software that operated with user inputs of either measured or estimated data for a variety of population parameters. Model output included estimates of the projected population (by gender) of independent bears in subsequent years, a calculation of the annual population change, and an estimate of the number of bears that will be in the trophy size class. Model predictions were similar to the results of consecutive intensive aerial surveys in 3 of 4 study areas. The population dynamics and harvest data collected on Kodiak during this study provided an opportunity for a comprehensive analysis of a closely managed coastal brown bear population that was subjected to annual hunting pressure. Information from bears in all segments of the population, and bears that used a variety of habitats demonstrated that brown bear management must be adaptable to be successful. All indicators suggested that the Kodiak bear population was healthy and productive even as it supported a sustainable harvest that consistently yielded some of the largest bears in North America. To obtain refined harvest strategies, however, managers must consider local population parameters, the management objectives for the area of interest, characteristics of the

harvest, and the level of confidence for each of those factors – there is no single harvest rate that is applicable to all situations. We found that when we used our model to explore an assortment of harvest strategies with hunters and managers, it facilitated productive discussions about a multiplicity of options and the potential biological ramifications of various management scenarios.

INTRODUCTION

Brown bear populations have been severely depleted in much of North America and Europe as human populations expanded in size and altered natural habitats (McLellan 1998, Zedrosser 2001). There has been a concerted effort to reverse that trend during the past half-century as biologists expanded their knowledge of bear life history, population dynamics, habitat requirements, and bear/human interactions and converted that information into management actions (Servheen et al. 1999). In some cases, those actions have helped bear populations improve (Boyce et al. 2001, Schwartz et al. 2005) or become reestablished (Clark et al. 2002). The coastal areas of Alaska and the Russian Far East have lower human population densities and there are still extensive areas of intact habitat. Consequently, many bear populations in those regions have not been as severely impacted as their counterparts. Brown bear populations along much of the North Pacific Rim are healthy and provide an important economic resource as trophy hunters seek the largest representatives of the species (Seryodkin 2006, Alaska Department of Fish and Game [ADF&G] 2005), yet little research has been published about population dynamics and harvest management of those brown bears. On the Kodiak Archipelago, Alaska, where 8 of the 10 largest bears ever harvested in North America were taken, hunters spent an estimated $4.5 million on Kodiak brown bear (*U. a. middendorffi)* hunts in 2003 (ADF&G files).

Because of the high economic value of bear hunting along the North Pacific Rim, managers are tasked with maintaining productive populations with stable to increasing proportion of large male bears in the harvest. The challenge of doing this is exacerbated by the logistics of working with a notoriously secretive species in a remote and oftentimes inhospitable region. Most managers recognize the importance of minimizing the harvest of productive females in brown/grizzly bear populations (McLellan et al. 1999), but an appropriate harvest strategy for males is more complex. While increasing the average skull size of harvested males is attractive, it can only be accomplished with caution. Harvest strategies that target large male bears, especially in spring, may reduce the proportion of such bears in the population and ultimately reduce the mean skull size and health of the population. Research has also shown that in some bear populations harvest strategies that target adult males can reduce productivity (Weiglus et al. 2001).

Since the 1960s bear harvests have been closely regulated and monitored on the Kodiak Archipelago (Van Daele 2003). The Constitution of the State of Alaska (Section 08.04)

mandates that wildlife populations "…shall be utilized, developed, and maintained on the sustained yield principle…" On Kodiak, a desire for "high quality hunting experiences" and management for a large number of "trophy-sized" bears further direct bear hunting management strategies. Traditionally a "trophy" bear was defined as a bear with a hide size of at least 0.93 m (measured as the sum of length of the hide from the tip of the nose to the anus plus the length from the tip of the center claw on the right front foot to the tip of the center claw on the left front foot, divided by 2). Most hunting associations now define a "trophy" bear as one with a total skull size (zygomatic breadth plus total length) of at least 71.1 cm (Buckner and Reneau 2005). While harvesting a large male is the goal of most hunters, many are satisfied with taking any Kodiak bear, regardless of size. In addition to managing harvests, ADF&G is expected to reduce adverse bear/human encounters and provide opportunities for the increasing number of individuals and commercial operators seeking bear viewing opportunities on the islands.

To balance the public mandates, ADF&G established the following management objectives for Kodiak bears: 1) Maintain a stable brown bear population that will sustain an annual harvest of 150 bears composed of at least 60% males; 2) Maintain diversity in the gender and age composition of the brown bear population, with adult bears of all ages represented in the population and in the harvest; and, 3) Limit human-caused mortality of female brown bears to a level consistent with maintaining maximum productivity (Van Daele 2005). While the objectives provide some harvest guidelines, they are somewhat nebulous in what comprises a female mortality rate that is at "a level consistent with maintaining maximum productivity." To date, the harvest strategies for Kodiak bears, like those in many other areas along the North Pacific Rim, have been adaptive, building on hunter success rates, skull sizes, gender ratios and perceived bear population responses, and altering regulations as appropriate (or politically feasible). This system can be successful, but it requires a great deal of subjective judgment tempered with extensive experience and public relations skills.

The purpose of this project was to gather information on the population dynamics of Kodiak bears during a long-term study and to develop an easily understood model that could be used by bear managers to objectively estimate appropriate harvest strategies and guidelines (Bunnell and Tait 1980). We also anticipated that information obtained from Kodiak could be adapted to other coastal bear populations where hunting and other human-caused mortalities are important management considerations.

STUDY AREA

The Kodiak Islands are in the western part of the Gulf of Alaska (56 25'–58 40' north latitude by 152 00'–154 50' west longitude), approximately 400 km south of Anchorage, Alaska (Figure 2.1). They are an archipelago of 3 large islands (Kodiak, Afognak, and Shuyak) and innumerable smaller islands, reefs, and offshore rocks. The archipelago's diverse habitats provided wintering, resting, and breeding areas for 237 different species of birds, 6 indigenous land mammals, and several introduced mammals. The most widespread and common large mammals were the introduced Sitka black-tailed deer (~60,000) (*Odocoileus hemionus sitkensis*)

and the indigenous brown bears (~3,000). The islands' lakes and streams provided critical spawning and rearing habitat for 5 species of Pacific salmon *(Oncorhynchus* spp.), steelhead (*O. mykiss*), arctic char (*Salvelinus alpinus),* and Dolly Varden (*S. malma*). Each summer about 50,000,000 salmon returned to the 350 spawning streams on the archipelago.

This project was restricted to Kodiak Island, the largest and most complex of the islands. Its most prominent feature is the central spine that runs the length of the island from northeast to southwest. The spine is made up of intrusive rock formations sculpted by prehistoric and active glaciers. The tallest point is Koniag Peak at 1,362 m. The only portion of the archipelago that escaped glaciation is in the southwest part of Kodiak. This "refugium" is unlike any other part of the island, with wet tundra expanses bordered by modest mountain ridges. On the border of the refugium are a series of large lakes that fill glacially carved valleys. No point on Kodiak is farther than 21 km from the sea. Most of Kodiak Island had not been altered by human intervention. In 2003, the estimated resident human population of 14,181 on Kodiak Island, and had been relatively stable for the previous 20 years. The vast majority of the people lived along the limited road system on the northeast corner of the island. There were 6 small villages and numerous seasonally occupied cabins and lodges along the coast. Kodiak National Wildlife Refuge managed the southern and western two-thirds of the island. A more detailed description of the study area can be found in Van Daele (2007).

During this project (1982 – 2004) there were 2 brown bear hunting seasons each year: spring (01 April – 15 May) and fall (25 October – 30 November). The Archipelago was divided into 30 hunt areas during each season. Within 29 of those areas a set number of drawing (lottery) permits were allocated each year, and competition for permits was intense. The other hunting area was in the vicinity of most of the human activity on the northeast part of Kodiak Island, and hunters in that precinct could obtain a permit by registering in person at the ADF&G office in Kodiak (Van Daele 2005).

All Kodiak bear hunters were required to check in at the Kodiak ADF&G office and attend a short orientation briefing. Although hunters were allowed to hunt any time during the open season, they were limited to a self-defined hunt period of 15 consecutive days. The bag limit was 1 bear every 4 years. Either gender could be taken, but females with cubs, and their cubs, were not legal game. Hunters could not hunt the same day they had been flying in a fixed-winged aircraft and helicopters could not be used for any aspect of the hunt. The use of dogs and artificial lights were also prohibited. The hide and skull of all harvested bears had to be salvaged, but meat could be left in the field. Hunters that did not reside in Alaska were required to employ the services of a registered Big Game Guide unless they were accompanied in the field by a relative (second degree of kindred) who was an adult Alaska resident.

When the hunt was completed, all hunters were required to check out at the Kodiak ADF&G office. Successful hunters were further required to bring the hide and skull of harvested bears to the Kodiak ADF&G office for inspection and Council on the International Trade of Endangered Species (CITES) sealing. Unlike most other areas of the state, bears taken on the Kodiak Archipelago could not be sealed at any other office. Hides were checked for size, hair quality,

evidence of gender, and tattoos. Skulls were measured (length and width) and a premolar tooth was extracted for aging. Hunters also provided information on where and when they killed the bear, how many other bears they saw, how long they hunted, and what commercial services they used during their hunt.

METHODS

Capture

There were 4 major bear research projects on Kodiak Island from 1982-2004, all of which included marked bears. The Terror Lake hydroelectric (TLH) and Zachar/ Spiridon (ZSP) studies included the north and central parts of Kodiak Island, while the southwest Kodiak (SWK) and Aliulik Peninsula (ALK) areas were on the south and west parts of the island. We used comparable capture and radio telemetry techniques in each of these investigations. Each captured bear was permanently marked with green punch tattoos applied to the inside of the left and right upper lip and to the inside-front of the lower lip. Groin tattoos were applied with an electric tattoo gun. Numbered plastic tags were affixed to each ear and a sub-sample of captured bears were radiocollared and tracked periodically. Van Daele (2007) includes a detailed description of the capture and relocation methods used.

Data Collection

Survival data were collected during radio telemetry flights for bears with active radiocollars. Information on natural mortalities was available only for bears with active radiocollars. Whenever practical, all radiocollared bears that died were investigated as soon as possible after death was detected, and we attempted to determine the time and cause of the mortality. Human-caused mortalities of marked bears were noted when their hides and skulls were brought in to biologists for inspection. Alaska State regulations required that any bear killed on the Kodiak Archipelago by either a hunter or in defense of life or property must have the hide and skull brought to the ADF&G office in Kodiak to be checked. During the course of this project, only 6 individuals were authorized to conduct those inspections, thereby giving us an excellent likelihood of detecting any marked bears.

We investigated the relationship between the age of male bears and total skull size by analyzing data from bears harvested on Kodiak from 1961 to 2004. Bear ages were determined by counting cementum annuli from premolar teeth (Matson et al. 1993) and skull measurements were collected at the time of sealing.

Brown bear population estimates were developed for 9 study areas with the "intensive aerial survey technique" detailed in Barnes and Smith (1998) and Miller et al. (1997). Data from the aerial surveys were extrapolated to develop a Kodiak Archipelago-wide bear density and population estimate. We did not conduct aerial surveys on northeastern Kodiak, Afognak or the

other northern islands where dense Sitka spruce (*Picea sitchensis*) forest made it difficult to observe bears, so the population estimates for those areas were tentative (Barnes et al. 1988).

Data Analysis

Program MARK (White and Burnham 1999) provided analyses of estimated adult survival rates for bears in each study area. We used the Burnham live and dead encounter option (Burnham 1993) with annual data (yearly time steps) from radiocollared bears. Bears that died as a direct result of research activities (capture mortalities) were excluded from the analysis. Comparison between study areas was accomplished by analyzing comparable study periods (5 consecutive years), while we used data from all years in the development of specific study area survival estimates. We also used Program MARK to analyze recovery data from all captured adult bears (Brownie et al. 1985, Cooch and White 2005) to explore an alternate procedure for determining survival rates. In all cases, we created several different models and compared them using Akaike information criterion (AIC) to verify the strongest, most parsimonious model that fit the data.

Model Development

We created a deterministic model using Microsoft Excel® (Microsoft Corporation, Seattle, Washington, USA) software. We sought to develop a model that would operate with user inputs of either measured or estimated data for a variety of population parameters. The intention of the model was to be parsimonious, transparent, easily understood by managers and the public, and able to run on most conventional computers. Model output included estimates of the projected population (by gender) of independent bears in subsequent years, a calculation of the annual population change, and an estimate of the number of bears that will be in the trophy-size class. Detailed documentation of the model is included in Appendix 2.1.

Model verification was accomplished by comparing the population changes (independent bears) noted in portions of each study area during consecutive intensive aerial surveys with model predictions for those areas for comparable time periods. Model input included data collected from each of the study areas (initial estimated population of independent bears, annual productivity and survival, average annual harvest, and other human caused mortality, etc.) and estimates of parameters that were not measured.

Sensitivity analysis was accomplished by inputting a range of 10 variables within the 95% confidence interval for each study area and monitoring which variables had the greatest impact on the output. If parameters were estimated rather than measured, we used a 10% confidence interval. Confidence intervals about the model estimates of population growth rate (λ) were calculated by analyzing the suite of results from the sensitivity analysis.

RESULTS

Survival Rates

We investigated survival rates of 33 adult male bears radiocollared over a 9-year period.   This resulted in an annual survival rate of 0.722 (SE = 0.052) and a 95% confidence interval of 0.607 – 0.812. We also examined the annual adult male survival rate based on 108 bears permanently marked within all study areas and later recovered dead by hunters or researchers. These data yielded a rate of 0.809 (SE = 0.026) and a 95% confidence interval of 0.754 – 0.854 (Table 2.1). In both tests, the strongest models were those that treated all males as a single population with no differences between study areas, recapture, recovery, or fidelity rates (AICc weights = 0.569 and 0.459, respectively). Both of these methods yielded comparable estimates, however because of the larger sample size, tighter confidence intervals, and smaller standard errors, we felt that the estimates derived from the recovery model (Brownie et al. 1985) were the most applicable for males.

Initial analysis of adult female survival rates included 162 radiocollared bears over a 5-year period. The periods were not the same years, but each included a consecutive block of time within each area. The samples included: TLH – 53 bears from 1983-87; ZSP –47 bears from 1989-1993; SWK – 31 bears from 1983-1987; and, ALK – 29 bears from 1992-1996. AIC results suggested similar recovery, recapture and fidelity rates for each area, corresponding with evidence from capture and radiotelemetry observations in the field. The overall survival rate for all independent females was 0.867 (SE = 0.015) with a 95% confidence interval of 0.834 - 0.894 (Table 2.1). The strongest model suggested that survival rates in SWK were lower than those in the other 3 study areas (AICc weight = 0.402). These results coincided with the statistical comparisons of the areas that revealed considerable overlap of the 95% confidence intervals for TLH (0.831 – 0.948, SE = 0.029), ZSP (0.827 – 0.949, SE = 0.030), and ALK (0.874 – 0.981, SE = 0.024) survival rates, but little overlap with SWK (0.719 – 0.866, SE = 0.037).

When TLH was analyzed separately, we followed 54 radiocollared adult females for 7 consecutive years (1982-1988). The strongest model was the one that consolidated all parameters (time, survival, recapture, recovery, or fidelity rates) (AICc weight = 0.976). It resulted in an annual survival rate of 0.886 (SE = 0.022) and a 95% confidence interval of 0.835 – 0.923 (Table 2.1).

Within the ZSP area, we followed 45 radiocollared adult female bears for 9 consecutive years (1988-1996). The strongest model also consolidated all parameters (time, survival, recapture, recovery, or fidelity rates) (AICc weight = 0.997). It resulted in an annual survival rate of 0.880 (SE = 0.023) and a 95% confidence interval of 0.828 – 0.917 (Table 2.1).

In SWK, 53 radiocollared adult females were followed for 6 consecutive years (1983-1988). Once again, the best model was the one that consolidated all parameters (time, survival, recapture, recovery, or fidelity rates)(AICc weight = 0.966). It resulted in an annual survival rate of 0.800 (SE = 0.032) and a 95% confidence interval of 0.730 – 0.855 (Table 2.1).

The ALK area yielded survival information from 29 radiocollared adult female bears for 5 consecutive years (1992-1996). As was noted in all other areas, the best model was the one that consolidated all parameters (time, survival, recapture, recovery, or fidelity rates) (AICc weight = 0.950). It resulted in an annual survival rate of 0.913 (SE = 0.030) and a 95% confidence interval of 0.835 – 0.956 (Table 2.1).

When we examined the annual adult female survival rate based on bears that were permanently marked and later recovered dead by hunters or researchers (Brownie et al. 1985), the data yielded comparable estimates to the Burnham live and dead encounter analyses. Unlike the analysis of male data, the recovery analysis included smaller numbers of recovered females and provided wider confidence intervals and larger standard errors (TLH – 0.817 [0.743 – 0.872, SE = 0.033], ZSP 0.749 [0.610 – 0.850, SE = 0.062], SWK 0.760 [0.674 – 0.829, SE = 0.040], and ALK (0.795 [0.628 – 0.900, SE = 0.069]. Consequently, we felt that the estimates derived from the live-dead encounter models were the most applicable for female survival rates.

We were able to collar 25 cubs (16 males and 9 females) soon after they were weaned (2- or 3-year olds) and follow them through their adolescence (age 5). Of the 16 males, 13 (81.3%) lived to age 4 and 9 (56.3%) lived to age 5. For the 9 females, 8 (88.9%) lived to age 4 and all 8 were still alive at age 5 (88.9%).

Harvest

We investigated the cause of deaths of all the radiocollared bears used for the survival rate analyses (Table 2.1). The major cause of death for males was hunter harvest (91%), while most females died of natural (non-anthropogenic) causes (54%). There were no significant differences between the causes of death reported for females from the various study areas (ANOVA, $F_{3,11}$ = 1.43, P = 0.286), however, there was a significant difference between males and females (x^2 = 148.42, df = 3, P<0.001).

During the study period (1982-2004), overall annual harvest density for the study areas was 17.07 independent bears/1,000 km^2, ranging from 13.34 in TLH to 22.58 in ALK (Table 2.2). The harvest rates of independent bears ranged from 6.68% in TLH to 10.33% on the ALK, and males dominated the harvest in all areas (68.4%), ranging from 63.7% in TLH to 72.2% in ALK.

The number of bears harvested remained relatively consistent during the study period, but was higher than during the previous 20 years (Table 2.3). We also saw an increase in the number and percentage of the harvest that consisted of trophy-sized males (Figure 2.2).

We analyzed data from 3,267 male bears that were harvested on the Kodiak Archipelago, had unbroken skulls at the time of sealing, and had a premolar tooth that was suitable for aging. Data from these samples revealed that the percentage of skulls reaching trophy size (n = 283) increased with the age of the bear, with 56.1% of the males in the oldest age class (>20 years)

being trophy-sized (>71 cm). Bears in the >68 cm category (n = 710) also increased with age, including 91.2% of the males in the oldest age class (Figure 2.3). The relationship between male skull size and age was also evident when we compared the average annual skull sizes and ages for bears harvested from 1982-2004. The correlation between these data was significant ($P <$ 0.001) with $r^2 = 0.77$ (n = 22).

Nonresident hunters were significantly (t = 14.18; $P < 0.001$; df = 41) more successful in their bear hunts ($\bar{x}$ = 65.8%;) than were resident hunters ($\bar{x}$ = 35.6%) on the Kodiak Archipelago from 1982-2004. We did not detect any significant difference in the percentage of adult females in the harvests of resident ($\bar{x}$ = 21.0%; P = 0.17; df = 41) and nonresident hunters ($\bar{x}$ = 18.2%). There was a significant difference (t = 2.06; P = 0.046, n = 39) in the percentage of female bears taken during the spring hunting season ($\bar{x}$ = 17.1%;) as compared to the fall hunting season ($\bar{x}$ = 21.3%).

Model

When we sought to validate the model by comparing model predictions of independent bear population levels with the results of consecutive intensive aerial surveys of areas within each study area, there were similar results in 3 of the 4 study areas. The intensive aerial surveys in the Terror Lake vicinity suggested an 18.0% increase in the bear population between 1987 and 1997 (Table 2.4). When the TLH model was run for a 10-year period, it predicted an increase of 16.6%. The intensive aerial surveys of the Spiridon Lake area indicated a 13.7% increase in the population between 1995 and 2000. A 5-year run of the ZSP model predicted a 17.2% increase. The Sturgeon River drainage is in the western part of the SWK study area. Intensive aerial surveys in 1987 and 1998 suggested a 20.2% decline in the bear population, while an 11-year run of the model predicted a 19.0% decline. The one study area that did not conform to the pattern of having intensive aerial survey data agree with model predictions was ALK. Intensive aerial surveys in 1993 and 2002 indicated a 17.2% decline, while the model predicted a 2.0% decline for a 9-year period. Extrapolation of intensive aerial survey data from all of the survey units on Kodiak Island, coupled with model predictions, indicated a 16.7% increase in the Archipelago-wide bear population from 1995 – 2005 (Table 2.5).

Sensitivity analysis revealed that changes in female survival rates had the greatest impact on the rate of population change predicted by the model when we tested a range of inputs for each of the study areas. The second most influential parameter proved to be annual productivity. Estimates of the population growth rates (lambda) within the study areas were: TLH - $\bar{x}$ = 1.010 (SE = 0.002, range = 1.007-1.014); ZSP - $\bar{x}$ = 1.024 (SE = 0.002, range = 1.021 – 1.028); SWK - $\bar{x}$ = 0.979 (SE = 0.003, range = 0.973 – 0.985); and, ALK - $\bar{x}$ = 0.995 (SE = 0.002, range = 0.985 – 0.999).

DISCUSSION

The population dynamics and harvest data collected on Kodiak from 1982-2004 provided an opportunity for a comprehensive analysis of a closely managed coastal brown bear population that was subjected to annual hunting pressure. Information from bears of all segments of the population and bears that used a variety of habitats demonstrated that brown bear management must be as adaptable and intelligent as the bears themselves to be successful. All indicators suggested that the bear population was healthy and productive even as it supported a sustainable harvest that consistently yielded some of the largest bears in North America.

Survival Rates

Survival rates for adult female bears on Kodiak were comparable in the northern study areas (TLH, ZSP) and the southern-most study area (ALK) in spite of considerable differences in available habitat and denning patterns. Adult female bears in southwest Kodiak (SWK) did not follow a similar pattern, as their annual survival rates were significantly lower than all other areas. We recorded 47% more of the radiocollared females in SWK dying during the study period than in any other area. Those deaths included both human-induced and natural mortalities. The sample of female bears in SWK had comparable age distribution to the radiocollared bears in the other areas, and the relative annual variation in the food availability noted during the SWK study period was comparable to the other study areas and periods. Consequently, the difference in survival was probably not a result of a biased sample.

This result was surprising because bears in SWK had the greatest access to salmon resources both in biomass and in the length of time salmon were available (Van Daele and Barnes 2007). Closer analysis of the survival differences noted in SWK revealed that female bears in that area had greater minimum convex polygon home range sizes than any of the other study areas. The larger home range sizes were not reflected in the 95% fixed kernel utilization distribution areas, however, as the SWK females relied on areas comparable in size to those used by bears in the northern study areas. The reason for this apparent discrepancy was due to the bears in SWK seeking out areas where spawning salmon provided seasonally concentrated food sources. Coincident with this movement pattern, the bears in that area were more likely to interact with other bears frequenting the same small areas. Although bears in northern Kodiak would seasonally concentrate in small areas (<2.5 km^2) such as the heads of Terror and Uganik Bays in densities of 5,400 independent bears/1000 km^2, in southwest Kodiak bears at Frazer and Thumb Rivers congregated at densities of up to 10,000 independent bears/1000 km^2 and at O'Malley River at up to 16,200 independent bears/1000 km^2 (Barnes 2006) for several months each year.

While adult female bears in SWK shared similar causes of mortality to those on other parts of Kodiak, the magnitude of those mortality factors seemed to be exacerbated by increased home range sizes and increased intraspecific encounters at food concentration areas. The annual survival rate of adult females in SWK ($\bar{x} = 0.800$) was comparable to that of males island wide

($\bar{x}$ = 0.809), and the 100% minimum convex polygon home range sizes also had analogous similarities (SWK, $\bar{x}$ = 218.6 km^2; all males, $\bar{x}$ = 251.5 km^2) (Van Daele 2007). This implies that because both of these groups of bears ranged in much larger areas than did female bears on other parts of Kodiak, they were exposed to greater risks from humans and other bears.

A comprehensive literature review by Schwartz et al. (2003) reported that brown bear annual survival rates in North America ranged from 0.89 - 0.96 ($\bar{x}$ = 0.93) for adult females and from 0.62 – 0.94 ($\bar{x}$ = 0.85) for adult males. The rates we observed in Kodiak (0.87 and 0.81, respectively) were lower than most noted in that synopsis, but their synopsis did not include any high-density coastal brown bear populations that were subjected to human harvests. Schwartz et al. (2003) also noted that subadult female survival was generally comparable to adult female survival rates, and that subadult male survival rates were usually lower than the subadult females and all independent bears. Garshelis et al. (2005) noted subadult female annual survival rates of 0.92 and subadult male survival rates of 0.69 in Alberta. The data we collected on Kodiak followed similar patterns with subadult females at 0.89 and subadult males at 0.56, again reflecting a lower annual survival rate than in non-hunted and interior populations.

We could not definitively ascertain if hunter harvest of males was compensatory for natural mortality (Burnham and Anderson 1984, Schaub and Lebreton 2004), but radio telemetry data indicated that adult male bears were over 175% more likely to be killed by hunters than adult females on Kodiak Island. This discrepancy was a result of hunter selectivity, larger male home ranges and use sizes, and hunting regulations that protected maternal females. Conversely, the adult females we radiotracked on Kodiak were over 10 times more likely to die of natural causes than were the radiocollared males.

We found significant differences in the productivity (Barnes and Van Daele 2006) and survival rates of bears in the different study areas on Kodiak. In spite of this, densities varied only slightly (Van Daele 2007) and bears in each of the areas appeared to have similar reproductive fitness as they adapted to their local habitats.   Females in SWK had the greatest reproductive rate on Kodiak (0.421 weaned cubs/female/year) and the lowest annual survival rate (0.800). Conversely, females in ALK had the lowest reproductive rate (0.328 weaned cubs/female/year) and the highest annual survival rate (0.913). Population dynamics data, coupled with home range and habitat use data (Van Daele 2007), provided no evidence of a source–sink dynamic between the Kodiak study areas similar to what is suspected in portions of the Greater Yellowstone Ecosystem grizzly bear population (Schwartz et al. 2006).   The only possible exception on Kodiak might have been the northeastern part of the island where liberal harvests were designed to reduce bear densities and harvests exceeded sustainable levels. Unfortunately we did not have sufficient data to test that possibility.

There has been a plethora of articles documenting infanticide by adult male brown bears and speculation on its potential impacts on bear populations (McClellan 1994, Swenson et al. 1997, Miller et al. 2003), and guides and hunters documented several incidents on Kodiak during our studies. We have also noted instances of adult males killing and eating adult females, both

maternal and barren, at various times of the year (Troyer and Hensel 1962, Smith and Van Daele 1991). Bunnell and Tait (1981) created a simulation model that predicted that hunter harvest of adult males would dramatically disrupt regulatory mechanisms of a bear population by reducing effectiveness of intrinsic controls. Determining what impact hunter harvests have on the dynamics of Kodiak bear populations is confounded by the ability of the bears to use a wide array of habitats and food resources, thereby making assessment of carrying capacity difficult and measuring impacts of density-dependent processes impractical.

Although density-dependent processes may ultimately regulate all populations, the range of population densities where density affects vital rates and the mechanisms by which density influences population dynamics have not been demonstrated for any bear populations (Taylor 1994). McLellan (1994) reviewed research from several brown bear populations and concluded that the hypothesis of a biological mechanism for density-dependent population regulation has not been conclusively demonstrated for any population and that a prudent manager should not assume that a reduction of density would cause an increase in recruitment or survival of a harvested bear population.

Harvest

From the 1950s through 1970s bear managers on Kodiak noted a decline in the harvest of trophy-sized bears, but no detectable change in population density that could be attributed to hunting pressure (Troyer 1961, Troyer 1962, Troyer and Hensel 1969, Kodiak National Wildlife Refuge 1976). To address that concern, regulations were promulgated to better disperse hunting pressure around the Archipelago, reduce season lengths, and require that skulls be measured and premolar teeth collected for aging. Impacts of the revised regulations were apparent within the next decade, and continued throughout this study. Harvest levels and male:female ratios were stable to increasing Archipelago-wide and the number and percentage of trophy-sized bears in the harvest steadily increased. Estimated population densities were stable to increasing in most harvest subunits. When survey data detected a decline in bears in the Southwest Kodiak Island subunit, regulations protecting females were initiated and within a decade bear numbers rebounded (Van Daele 2005).

Skull size-age data collected as a result of the regulation changes clearly demonstrated that age structure of the male bear population has a direct impact on the number of large bears available to hunters. On Kodiak, over 90% of male bears have the potential to reach skull sizes exceeding 68 cm, and over half of the bears can attain trophy size if they live long enough. Therefore, when managing for a population that retains a segment of large males, it is important to establish regulations that consider survival rates of adult males as well as productive females. During this study, hunting regulations for Kodiak bears were crafted to distribute harvest throughout the archipelago and reduce hunter efficiency. While season dates included times when hide quality was at its peak, they are also set to afford protection to females that have longer denning periods. Prohibiting harvest of maternal females and their dependent cubs further protected productive females.

The estimated annual harvest rate of 5.5% of the total bear population on the Kodiak Archipelago was close to the suggested approximate maximum 5.7% exploitation rate from Miller's (1990a) population simulation studies on brown bears in Southcentral Alaska. Other investigators have suggested that sustainable level of human-caused mortality of brown bear populations is about 6% (Bunnell and Tait 1981, Hovey and McLellan 1996), but it has also been noted that habitat quality impacts bear productivity, so human-caused mortality should be reduced in marginal habitats (Austin et al. 2004, Eberhardt 1990, McLellan 1994).

Model

Choosing the appropriate level of resolution for a population model is a pragmatic compromise between the complexity of the ecosystem on one hand and the need to solve a problem with limited data and in a reasonable amount of time on the other (Starfield and Bleloch 1986). Wildlife managers and the public are often overwhelmed and sometimes intimidated by models that incorporate complex algorithms hidden within "black boxes" of convoluted formulae, stochastic iterations, and immeasurable variables. While demands for such sophisticated modeling techniques are legitimate, too often managers respond by either avoiding using the models or by dismissing them as unrealistic or misleading. Consequently, the thought and effort that went into development and testing are diminished.

Our model performed well when its predictions were compared to data from intensive aerial surveys of portions of the study areas and study periods. The only area where estimates did not closely agree was in ALK. In that case, we suspected that the model was more accurate than the intensive aerial survey. The second survey in ALK was plagued by poor weather conditions that prevented adequate coverage of the entire area. Model predictions were also superior to aerial surveys in that they provided not only estimates of the total number of independent bears, but also estimates by gender and of number of trophy males in the population.

The simplicity of the model developed during this project is simultaneously its greatest asset and its greatest limitation (Appendix 2.1). By using a deterministic model that employs data derived from long-term studies, impacts of interannual variations were dampened and we obtained concise results. This is attractive to managers and members of the public who prefer definitive answers that can be easily comprehended. The drawback to this is that there is no variation or confidence interval, and results may be misleading if care is not taken to explain the quality of the data used to derive those results and the potential impacts of errors.

Although the purpose of this project was to produce a simple model to be used in a public forum, there are several ways to surmount its limitations. Managers using the model should elucidate constraints on the model to users and they must explain that the anticipated level of projection accuracy is based on the quality of the input data (Taylor et al. 2002). With this in mind, the model could be run several times using variables that were within confidence levels of each parameter that was measured (Jerina et al. 2003). This would give everyone an idea of how

accurate the results might be and where more research is needed to improve estimates. Although such an exercise could be more easily accomplished by conventional computational techniques such as Monte Carlo simulation or bootstrapping, we found that having a simple model that could be manipulated in a public forum made a greater impact on decision-makers than did more sophisticated methods. If more detailed population simulations were desired, the model could be modified to include stochastic variables, input ranges, and feedback loops (Wielgus et al. 2001, Schwartz et al. 2006). Starfield and Bleloch (1986) recommended starting off with a simple model that addressed a specific objective and building modules that could be attached to that model as more data became available or if additional objectives were defined. Future iterations of the model could conceivably include feedback from potentially limiting factors, such as the impact of adult male density on cub survival, and variations in productivity due to annual food availability.

MANAGEMENT IMPLICATIONS

Integration of research and management data is necessary to assure management for a sustainable brown bear population and quality hunting experiences. Analysis of harvest patterns, denning chronology, and home ranges provide managers with critical components for bear management strategies. From these analyses, seasons and regulations provide a suite of management tools that can be tailored to efficiently target specific areas and segments of the bear population. We found that because of relatively small home ranges of bears on Kodiak and the adaptability of bears to their surroundings (Van Daele 2007), it was best to manage the Archipelago as 6 subunits, each reflecting the unique aspects of bear biology in the areas. Application of the model to each subunit gave us an assessment of current harvest strategy, and allowed us to develop an "ideal" strategy that would stabilize the bear population while maintaining opportunities for high quality hunting experiences.

The concept of a "high quality hunting experience" is subjective and can only be defined with extensive public input. We found that when we used our model to explore an assortment of harvest strategies with hunters and managers, it facilitated productive discussions about a multiplicity of options. While consensus may not always be possible, a legitimate and understandable model allows exploration of potential biological ramifications of various management scenarios and assists in framing a debate of pros and cons of different proposals. These deliberations also expose areas where further research is needed.

Miller (1990b) cautioned that using gender and age ratios to set allowable harvest objectives is more likely to result in overexploitation than using total adult females for setting guideline harvests. Our model came to the same conclusion, with female survival and productivity the most sensitive parameters driving population trend; however, on Kodiak we had an increasing population on many parts of the island, and an agency supported comprehensive bear management plan, developed by stakeholders (ADF&G 2002), that recommended maintenance of the bear population within a "wildlife-acceptance capacity." Rather than attempting to estimate biological carrying capacity, "acceptance capacity" was defined as a population that

was no more than 10% larger than the current (2001) estimated bear population level. The plan also recommended maintaining the tradition of bear hunting, consistent with a conservative management and regulatory regime that avoided overharvest of the resource (ADF&G 2002).

The increasing number and percentage of trophy males in the harvest during the past 30 years was encouraging, however, model results suggested that the number of trophy-sized males in the harvest may be reaching an asymptote, and higher levels may not be sustainable. To stabilize the population, maintain the current annual harvest of trophy-sized males, and avoid overcrowding of hunters, the model suggested increasing harvest of adult females in some subunits. It also suggested harvest rates ranging from 5.6 – 7.9 % of the estimated independent bear population would be appropriate in various harvest subunits on Kodiak.

Harvest rates developed during this project were comparable to previously published estimates for sustainable brown bear harvest levels. To obtain refined harvest strategies, however, managers must consider several population parameters, management objectives for the area of interest, characteristics of the harvest, and the level of confidence for each of those factors – there is no single harvest rate that is applicable to all situations.

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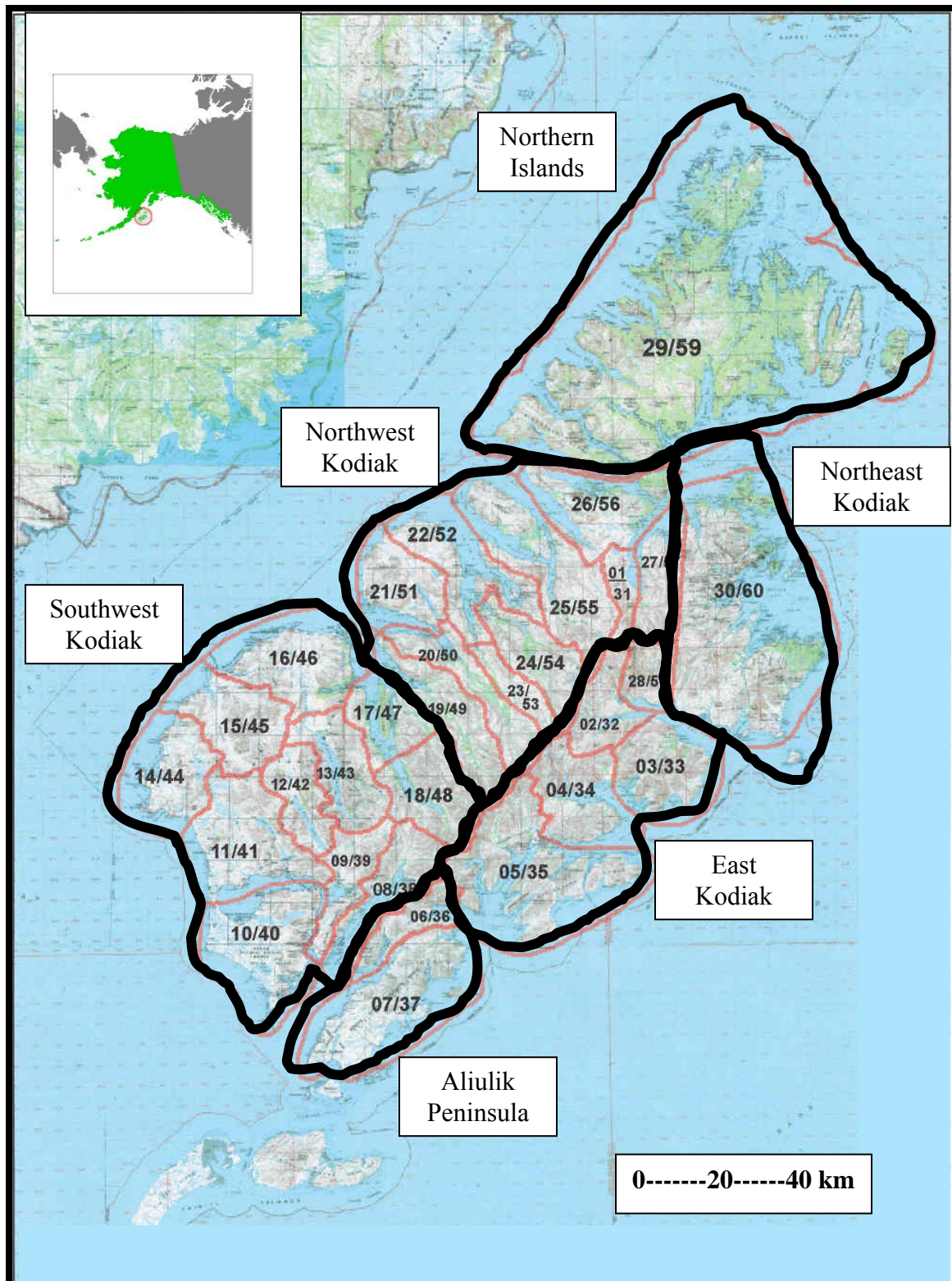
Figure 2.1. Brown bear hunt areas (Game Management Unit 8) and bear management subunits, Kodiak Archipelago, Alaska.

Annual harvest of trophy bears
(total skull size >71 cm)
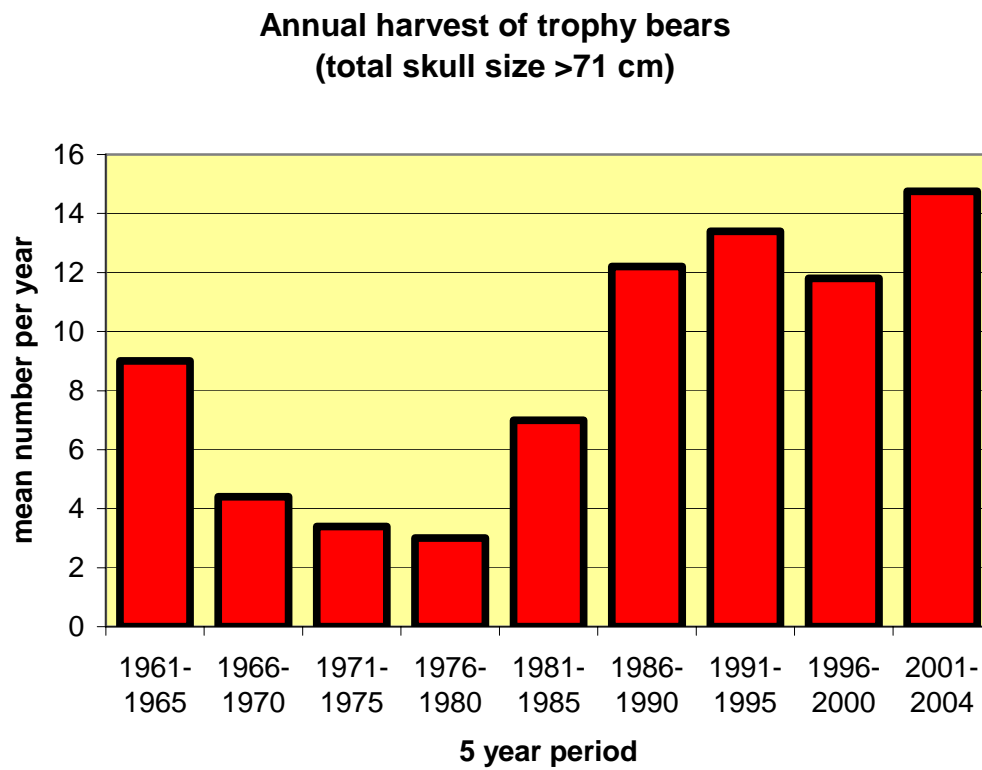
Figure 2.2. Mean number of brown bears with total skull sizes exceeding 71 cm (trophy-sized bears), by 5-year period, harvested on the Kodiak Archipelago, Alaska, 1961 – 2004.
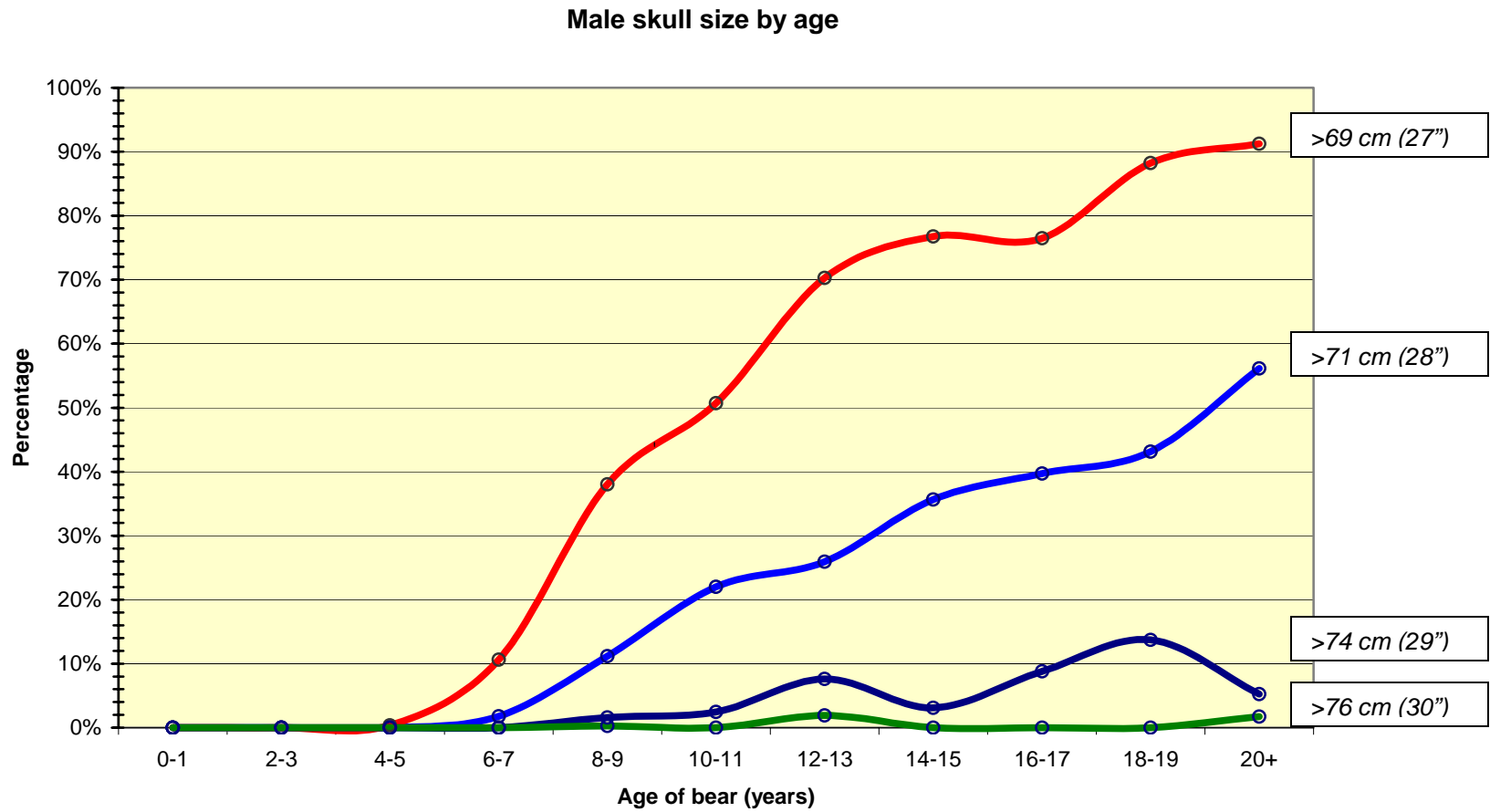
Figure 2.3. Skull sizes and ages of male bears killed by hunters on the Kodiak Archipelago, Alaska, 1961 – 2004.

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Table 2.1. Annual survival rates and mortality factors for radiocollared adult bears, Kodiak Island, Alaska, 1982 – 2004.

Area / Gender	Annual survival rate (95% CI)	Cause of death				
		Natural	Hunter	DLP[a]	Illegal	Total
All males[b]	0.809	1	20	1	0	22
	(0.754 – 0.854)	(5%)	(91%)	(5%)	(----)	
All females[c]	0.867	21	13	4	1	39
	(0.834 - 0.894)	(54%)	(33%)	(10%)	(3%)	
Terror Lake females[c]	0.886	5	2	2	0	9
	(0.835 – 0.923)	(56%)	(22%)	(22%)	(----)	
Zachar / Spiridon females[c]	0.880	3	4	1	0	8
	(0.828 – 0.917)	(38%)	(50%)	(12%)	(----)	
Southwest Kodiak females[c]	0.800	10	6	0	1	17
	(0.730 – 0.855)	(59%)	(35%)	(----)	(6%)	
Aliulik Peninsula females[c]	0.913	3	1	1	0	5
	(0.835 – 0.956)	(60%)	(20%)	(20%)	(----)	

a – bears killed under defense of life or property provisions.
b – survival rates calculated using procedures outlined by Brownie et al. (1985) and Program MARK (White and Burnham 1999).
c – survival rates calculated using procedures outlined by Burnham (1993) and Program MARK (White and Burnham 1999).

Table 2.2. Annual human harvest of brown bears within the 4 study areas, Kodiak Island, Alaska, 1982 – 2004.

Study area	Independent bears / year/1000 km^2	Annual harvest			
		Bears / year	Male	Female	% harvest of independent bears
Terror Lake	13.34	16.17	63.7 %	35.5%	6.68%
Zachar / Spiridon	16.46	24.61	70.7%	28.8%	7.44%
Southwest Kodiak	17.82	47.70	66.8%	32.9%	8.41%
Aliulik Peninsula	22.58	14.00	72.7%	26.7%	10.33%

Table 2.3. Mean annual harvest of brown bears, by 5-year period, on the Kodiak Archipelago, Alaska, 1961-2004.

Regulatory Years	Mean annual fall harvest			Mean annual spring harvest			Mean annual total harvest			Mean annual trophy[b] %
	Male	Female	Total	Male	Female	Total	Male	Female	Total	
1961-65	62.5%	37.5%	32.0	60.4%	38.0%	103.6	60.8%	37.9%	135.6	6.97%
1966-70	61.2%	37.9%	44.8	59.1%	38.7%	81.2	59.8%	38.4%	126.0	3.49%
1971-75	52.0%	46.9%	54.2	63.1%	35.6%	87.2	58.8%	39.9%	141.4	2.41%
1976-80	59.0%	41.0%	35.6	63.6%	36.0%	96.6	62.3%	37.4%	132.2	2.27%
1981-85	58.0%	41.2%	50.0	71.4%	28.6%	112.4	67.2%	32.5%	162.4	4.32%
1986-90	52.7%	46.3%	60.0	67.6%	32.2%	108.8	62.2%	37.3%	168.4	7.26%
1991-95	64.0%	35.2%	53.4	67.2%	32.1%	106.6	66.1%	33.1%	160.0	8.38%
1996-2000	68.6%	31.4%	52.8	74.8%	25.0%	107.2	72.8%	27.1%	160.0	7.38%
2001 – 04[a]	72.2%	27.8%	53.0	75.9%	24.1%	112.3	74.7%	25.3%	165.3	9.11%

a – four-year average
b – "trophy" bears are those with a total skull size (maximum length + maximum width) >71 cm.

Table 2.4. Results of intensive aerial surveys of brown bears on Kodiak Island, Alaska, 1987-2002.

Survey area	Year	Replicate surveys	Survey rate (min/km^2)	Bears[a] observed $/1,000\ km^2$	Sightability[b]	Estimated bear[a] density $/\ 1,000\ km^2$	Standard error	Area surveyed (km^2)	Estimated bears[a] in area
Terror Lake	1987	3	1.5	75	33%	234	29.75	355	83
Terror Lake	1997	4	1.7	92	33%	276	31.70	355	98
Spiridon Lake	1995	4	1.9	38	33%	118	24.26	287	34
Spiridon Lake	2000	4	1.8	44	33%	134	23.28	287	38
Sturgeon River	1987	4	1.6	120	41%	293	22.32	264	77
Sturgeon River	1998	4	1.9	94	41%	227	4.43	264	60
Aliulik Peninsula	1992/93	8	1.6	108	53%	209	16.95	350	73
Aliulik Peninsula	2002	5	1.4	92	53%	173	18.32	350	61

a – independent bears (does not include dependent cubs).
b – percentage of bears expected to be seen during the survey (based on radio telemetry data).

Table 2.5. Estimates of brown bear numbers and density in each harvest subunit on the Kodiak Archipelago, Alaska, 1995 and 2005.

Bear harvest subunit	Area (km^2)	1995[a] Density[c]	1995[a] Independent bears[d]	1995[a] Total bears[e]	2005[b] Density[c]	2005[b] Independent bears[d]	2005[b] Total bears[e]	Difference Independent bears[d]	Difference Total bears[e]
Northern Islands	2,281	101	231	330	132	300	430	+69	+100
Northwest Kodiak	2,983	200	596	808	224	668	908	+72	+100
Northeast Kodiak	1,005	63	63	90	70	71	101	+8	+11
East Kodiak	1,738	146	253	471	230	400	744	+147	+273
Southwest Kodiak	3,498	204	712	1,019	219	765	1,094	+53	+76
Aliulik Peninsula	837	219	183	262	208	174	249	-9	-13
TOTAL	12,342	165	2,038	2,980	193	2,378	3,526	+340	+547

a – estimated bear density in 1995 (based on aerial surveys and extrapolation from 1987 – 1994) (Barnes et al. 1988, Barnes and Smith 1998).
b – estimated bear density in 2005 (based on aerial surveys and extrapolation from 1987 – 2005).
c – estimated density of independent bears per 1,000 km^2.
d – estimated number of independent bears (excludes dependent cubs)
e – estimated number of bears in the harvest subunit (includes dependent cubs and independent bears).

Appendix 2.1. Population model documentation

Kodiak brown bear population model documentation

This is a deterministic model for use on Microsoft Excel® (Microsoft Corporation, Seattle, Washington, USA) software. It was developed to operate with user inputs of either measured or estimated data for a variety of population parameters. It is designed to be parsimonious, transparent, easily understood by managers and the public, and able to run on most conventional computers. Model output includes estimates of projected population (by gender) of independent bears in subsequent years, a calculation of annual population change, and an estimate of the number of bears that will be in the trophy size class.

The first input variable to the model is an estimate of the initial population level. This includes only independent bears (>3 years old) and an estimate of the percentage of those that are males. The projected population is the sum of the initial population, plus the influx of new subadults from resident sows minus the number of bears that died. In making these calculations we assume: 1) we know initial population size and gender ratio; 2) immigration/emigration has no net impact on the population; 3) productivity and mortality rates are known; and, 4) all factors are deterministic.

Mortality calculations consist of 4 facets: 1) hunter harvest of adult bears; 2) adult bears killed in defense of life or property (DLP); 3) illegal and unreported human kills of adult bears; and, 4) all adolescent mortality. Hunter harvest includes reported harvest by gender (input variable). The number of those that are adults is calculated by multiplying the total harvest by a correction factor (input variable) for the proportion of adults in the harvest of each gender. DLP kills are input variables by gender (only adults are included). Those that are of unknown gender are assigned a specific gender by multiplying them by the percentage of each gender in the reported DLP kill. Unreported and illegal kills are calculated as a percentage of the reported legal harvest and the reported DLP (both input variables). Percentages by gender are calculated to be the same as in the reported kill. These data are added to the reported kills for total harvest estimates.   Unreported DLP kills are also calculated as a percentage of the reported DLP kill (input variable). Gender percentages are calculated to be the same as in the reported kills. These data are added to the reported DLPs for the total DLP estimates. Natural mortality is gender-specific and incorporated as input variables. This is a 2-step process that includes an input of the total estimated percentage that is due to natural (non-human-caused) circumstances. The resultant natural mortality rate is multiplied by the estimated adult population size, by gender, to calculate the number of adult bears that die of natural causes. Total estimated annual adult mortality is the sum of all the above.

Subadult (adolescent) mortality is calculated by multiplying the estimated annual adolescent (3- and 4-year olds) mortality, an input variable, by the estimated number of subadults of each gender in the population. The estimated number of subadults is obtained from the productivity estimates. Total mortality is the sum of the adult and subadult mortality estimates. Throughout the mortality calculations we make the

following assumptions: 1) estimates of unreported and illegal kills are accurate; 2) gender ratios of unknown and unreported kills are the same as the reported rates; 3) adolescent mortality rates are different from adult rates and can consistently be estimated; 4) the number and percentage of males in the population do not impact mortality rates; 5) natural mortality rates are consistent; and, 6) the number of subadults in the initial population is closely correlated to the number of subadults in the projected population.

Annual productivity is derived by multiplying the estimated number of cubs weaned per productive female per year (input variable), times the estimated number of productive females. Mortality calculations are made prior to productivity calculations, thereby reducing the number of productive females available. The estimated number of productive females includes those between 7-25 years old. This is calculated by developing a life table (based on female survival rates and the initial population) and subtracting the number of females in the population at year 7 from the number in the population at year 26.

The percentage of weaned cubs of each gender is an input variable that is multiplied by the total number of cubs weaned to obtain the estimated number of male and female subadults coming into the population. Productivity estimates take into consideration the age of first successful weaning, weaning age of the cubs, reproductive intervals, new cub production and survival, and the age of female reproductive senescence. The calculated annual productivity is derived by multiplying the estimated number of cubs weaned per productive female per year (input variable), times the estimated number of productive females. Throughout the productivity estimations, we make the following assumptions: 1) cub production is constant; 2) weaned cub gender ratios can be accurately determined and are constant; 3) adult male numbers and percentages have no impact on productivity; and, 4) cementum age data are accurate.

The number of trophy males in the population is calculated by multiplying the percentage of $\geq$10-year old males that are projected to have 71 cm (28") or greater total skull sizes (input variable) by the projected number of males that are at $\geq$10 years old, based on a life table. The life table is derived from the initial male population multiplied by the estimated male survival rates (subadult plus adult rates). In making these calculations we assumed: 1) there is a consistent percentage of $\geq$10 year old males that have $\geq$71 cm skull sizes and that percentage can be gleaned from harvest data; 2) cementum age data are accurate; and, 3) there is a direct relationship between male bear age and the percentage of trophy-sized bears, and an inverse linear relationship of the number of males available in each age category (i.e., fewer bears in older age categories).

Model verification consisted of comparing extrapolated results with intensive aerial survey (IAS) data from IAS areas nearest to or within a study area. The initial population was multiplied by the intrinsic rate of increase (lambda) to obtain the projected population size for the next year (t+1). Similar calculations were performed to project population sizes for subsequent years. Changes in density estimates from 2 temporally distinct IASs were compared to the changes in the initial population estimate used for the model and the extrapolated estimate for a comparable time span. Subtracting the latest

estimate from the initial estimate and dividing the difference by the initial estimate calculated the percent change.

Appendix 2.1 (continued). Example of the Kodiak bear harvest model with input variables for the Terror Lake study area, Alaska (yellow and beige cells require user input, blue cells are calculated by the model, red cells are the model output).

Initial Population	242		**New Population Level**	246	
independent males→	80	33%	independent males→	80	33%
independent females→	162	67%	independent females→	166	67%

Annual production	0.342		**Population change**	1.55%	3.8
calculated annual production→	35		independent male change→	0.44%	0.4
new independent males→	14		independent female change→	2.09%	3.4
new independent females→	21		*Lambda* →	1.016	

Annual mortality	31	12.9%	**Initial Trophy males→**	3.39	19.3%
total independent males→	14		**New Trophy males→**	3.40	
total independent females→	18				

independent males killed by hunters→	11.14	63.5%	4.6%	percentage of 10+ yr old males >71cm→	22%
independent females killed by hunters→	6.4	36.5%	2.6%		
independent bears killed by hunters→	17.54		7.2%	percent male cubs→	40%
estimated percent adult males in harvest→	51.2%			percent female cubs→	60%
estimated percent adult females in harvest→	46.2%				
estimated unreported & illegal harvest→	3%	(% of reported)		male adolescent survival→	56%
				female adolescent survival→	89%

adult males reported DLP→	0.57			
adult females reported DLP→	0.91		total calculated adult female mortality→	11.4%
adult unknowns reported DLP→	0.00		estimated % that is natural (female) →	56.0%
estimated unreported DLP→	100%	(% of reported)		

natural adult male mortality→	0.5%		total calculated adult male mortality→	19.2%
natural adult female mortality→	6.4%		estimated % that is natural (male) →	2.9%

Appendix 2.1 (continued). Example of the Kodiak bear harvest model with input variables for the Terror Lake study area, Alaska (yellow and beige cells require user input, blue cells are calculated by the model, red cells are the model output).

ADULT MORTALITY

Reported kills

Total males killed by hunters→	11.14	Percent of total males that are adults→	51.2%
Adult males killed by hunters→	5.70		
Total females killed by hunters→	6.4	Percent of total females that are adults→	46.2%
Adult females killed by hunters→	2.96		
Total adults reported as hunter kill→	8.66		

males killed DLP→	0.57	Estimated males killed DLP→	0.57
females killed DLP→	0.91	Estimated females killed DLP→	0.91
Unknown gender DLP→	0		
Total reported DLP→	1.48	**Total estimated DLP (reported) →**	1.48

Natural & other unreported mortality

% unreported & illegal that were male→	66%	% males in harvest * est unreported kill →	0.17
% unreported & illegal that were female→	34%	% females in harvest * est unreported kill →	0.09
Total unreported and illegal kill→	3%	* the reported harvest →	0.26
male unreported DLP →	100%	* the estmated reported male DLP →	0.57
female unreported DLP →	100%	* the estmated reported female DLP →	0.91
Total unreported DLP→	100%	* the reported DLP →	1.48
natural independent male mortality→	0.5%	* the est independent male population→	0.44
natural independent female mortality→	6.4%	* the est independent female population→	10.35
		sum of estimated total natural mortality→	10.79

Appendix 2.1 (continued). Example of the Kodiak bear harvest model with input variables for the Terror Lake study area, Alaska (yellow and beige cells require user input, blue cells are calculated by the model, red cells are the model output).

Estimated annual adult mortality

adult males harvested by hunters→	5.87	Estimated percent adult males in harvest→	51.2%	
adult females harvested by hunters→	3.05	Estimated percent adult females in harvest→	46.2%	
Total hunter harvest of adults→	8.92			

		Estimated adult males killed by hunters→	5.70	65.9%	2.4%
males killed DLP→	1	Estimated adult females killed by hunters→	2.96	34.1%	1.2%
females killed DLP→	2	Estimated total adults killed by hunters→	8.66		3.6%
Total DLP kill→	3				

adult male natural mortality→	0.44	Total estimated adult mortality→	22.7	bears
adult female natural mortality→	10.35	Including:	7.5	males
Total adult natural mortality→	10.79	Including:	15.2	females

SUBADULT MORTALITY

male adolescent survival→	56%	male adolescent survival X male cubs→	7.81	subadult males
female adolescent survival→	89%	female adolescent survival X female cubs→	18.61	subadult females

Total estimated adolescent mortality→	8.4	bears
Including:	6.1	males
Including:	2.3	females

TOTAL MORTALITY (all independent bears)

Total estimated annual mortality→	31.1	bears
Including:	13.6	males
Including:	17.5	females

Appendix 2.1 (continued). Example of the Kodiak bear harvest model with input variables for the Terror Lake study area, Alaska (yellow and beige cells require user input, blue cells are calculated by the model, red cells are the model output).

PRODUCTIVITY

Cub production→ **0.342** mean weaners/adult female/year X adult females → **34.86** # total cubs

percent male cubs→ **40%**   percent male cubs X total cub production → **13.94** # male cubs

percent female cubs→ **60%**   percent female cubs X total cub production → **20.91** # female cubs

Total new subadults→ **34.86**