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MANAGEMENT OF BROWN BEAR HUNTING ON KODIAK ISLAND, ALASKA

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Abstract: Brown bear (*Ursus arctos*) populations are hunted along much of the North Pacific Rim, yet little research has been published about the population dynamics and harvest management of these bear populations. The purpose of our work was to investigate the population dynamics of bears on Kodiak Island, Alaska during a long-term study, and to develop an intuitive model that could be used by managers of coastal bear populations to objectively determine appropriate harvest strategies. We conducted research on 4 separate study areas on Kodiak from 1982-2004, all of which had marked bears. The annual adult male survival rate (0.81) was similar in all study areas. The overall survival rate for all independent females was 0.87, with one area lower than the others at 0.80. Subadult (≤5 years old) annual survival rates were 0.56 for males and 0.89 for females. The major cause of death for males was hunter harvest (91%), while most females died of non-anthropogenic causes (54%). The annual harvest density for all areas was 17.07 independent bears/1,000 km^2, and the harvest rates of independent bears ranged from 6.7% to 10.3%. The number of bears harvested was relatively consistent during the study period, but we detected an increasing trend in the number and percentage of the harvest that consisted of trophy-sized (total skull size ≥71 cm) males. Male bears dominated the harvest in all areas; 56.1% of the males in the oldest age class (>20 years) were trophy-sized. We created a deterministic model using Microsoft Excel software that estimated projected population (by sex) of independent bears, annual population change, and the number of trophy-sized bears. Model predictions were similar to the results of consecutive intensive aerial surveys in 3 of 4 study areas. Our model facilitated productive discussions with the public about the potential biological ramifications of various management options. Population and harvest data suggested that the Kodiak bear population was healthy and productive with an estimated λ of 1.014, even as it supported a sustainable harvest that consistently yielded some of the largest bears in North

America. Our investigation demonstrated that brown bear management must be adaptable to be successful and that to refine harvest strategies, 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 .

Key words: *Ursus arctos middendorffi*, Kodiak Island, brown bear, Alaska, coastal, management, trophy, sustainable harvest, survival, population model, hunting, population dynamics.

Brown bear populations have been severely depleted in much of North America and Europe, as human populations expanded and altered natural habitats (McLellan 1998, Zedrosser et al. 2001). There has been a concerted effort to reverse that trend during the past half-century as biologists gained a better understanding of bear life history, population dynamics, habitat requirements, and bear-human interactions, and converted that information into management actions (Servheen et al. 1999, Boyce et al. 2001, Clark et al. 2002, Schwartz et al. 2005, Bischof et al. 2008).

Coastal areas of Alaska and the Russian Far East have been spared from many of the anthropogenic impacts affecting brown bear habitat, and lower human population densities have insulated many bear populations in those regions from severe impacts experienced by their conspecifics elsewhere. Brown bear populations along much of the North Pacific Rim provide an important economic resource via trophy hunting (Seryodkin 2006, Van Daele 2007a). On the Kodiak Archipelago, Alaska, where 8 of the 10 largest bears harvested in North America were taken, (including the World Record [Buckner and Reneau 2005]), hunters spent an estimated $5 million on Kodiak brown bear (*U. a. middendorffi)* hunts in 2010 (Alaska Department of Fish and Game [ADF&G] files). In Kamchatka, bear management has become more complex since the fall of the Soviet Union in 1991, because of a dramatic increase in natural resource extraction and a surge in bear poaching by financially strapped residents (Chestin 1998). Hunters and managers also noted that with increased trophy hunting pressure the number of large bears decreased (Valentsev et al. 2001) and considerable debate was sparked after government officials curtailed all spring hunting in an effort to conserve the integrity of the population (Mooza 2005).

Little research has been published about population dynamics and harvest management of these bears. Managers generally recognize the importance of minimizing the harvest of productive females in brown/grizzly bear populations (McLellan et al. 1999), but defining an appropriate harvest strategy for males is complex (Milner et al. 2007, Zedrosser et al. 2007). 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 of harvested bears and health of the population. Research has also suggested 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). On Kodiak, a desire for high quality hunting experiences and management for a large number of trophy-class bears constrains bear hunting management strategies. A trophy bear has been defined as a bear with a hide size at least 10 square feet (sum of length of the hide from the tip of the nose to the anus, plus the width 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, exceeds 3.08 m); however, most hunting associations now define a trophy bear as one with a total skull size (zygomatic breadth plus total length) of at least 28” (71 cm; Buckner and Reneau 2005). While harvesting a large male is the goal of most hunters, many are satisfied with taking any Kodiak bear. In addition to managing harvests, ADF&G is also expected to reduce adverse bear/human encounters and provide bear viewing opportunities on the islands.

ADF&G has 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 sex 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 2007a). While the objectives offer specific harvest guidelines, they are vague relative to what comprises a female mortality rate that is at “a level consistent with maintaining maximum productivity.” To date, the harvest strategies for Kodiak bears have been adaptive; data on hunter success rates, skull sizes, sex ratios and perceived bear population responses have been used as feedback to refine regulations as appropriate (or politically feasible). Management was further refined to reflect the relatively small home ranges of bears on Kodiak and the adaptability of bears to their surroundings (Van Daele 2007b), by parsing the Archipelago into 6 management subunits (Figure 1; Table 6), each reflecting the unique aspects of bear biology in the areas.

In 2001, a Citizens Advisory Committee was established by ADF&G to work closely with the agency and Kodiak National Wildlife Refuge (Kodiak NWR) to develop a management plan addressing the wide variety of issues that affect bears, including hunting, habitat, and viewing. The resulting *Kodiak Archipelago Bear Conservation and Management Plan* recommended maintaining the tradition of bear hunting, consistent with a conservative management and regulatory regime that avoided overharvest, stabilized population levels, and maintained opportunities for high quality hunts (ADF&G 2002). Although the plan was advisory in nature, government management agencies expressed a commitment to implement all of the regulations that were feasible and within their legal jurisdictions, and to work with an on-going advisory committee on all future bear management issues. This collaboration required a comprehensive analysis of bear research and harvest data and development of a population model that was transparent and easily understood by the general public. We also anticipated that information obtained from Kodiak could be adapted to other coastal brown bear populations where hunting and other human-caused mortalities are important management considerations.

STUDY AREA

The Kodiak Archipelago is 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 1). It includes 3 large islands (Kodiak, Afognak, and Shuyak) and innumerable smaller islands, reefs, and offshore rocks. The most widespread and common large mammals were the introduced Sitka black-tailed deer (~60,000) (*Odocoileus hemionus sitkensis*) and the indigenous brown bears (~3,500). 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.

Kodiak is the largest and most complex island on the Archipelago. 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. A series of large lakes that fill glacially carved valleys are found on the border of the refugium. No point on Kodiak is farther than 21 km from the sea. Most of Kodiak Island has not been altered by human interventionThe 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 NWR managed the southern and western two-thirds of the island. A more detailed description of the study area can be found in (Van Daele 2007b).

During this project there were 2 hunting seasons for brown bears 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 limited number of drawing (lottery) permits (472) was 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 an unlimited number of permits were available to hunters who registered in person at the ADF&G office in Kodiak (Van Daele 2007a).

All Kodiak bear hunters were required to check in at the Kodiak ADF&G office and attend an orientation briefing. The bag limit was 1 bear every 4 years. Either sex could be taken, but maternal females and dependent 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, bait, 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. Hides were checked for size, hair quality, evidence of sex, 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

There were 4 major bear research projects on Kodiak Island during 1982-1996, all of which included radio telemetry (Terror Lake hydroelectric [TLH], Smith and Van Daele 1990; Zachar/Spiridon [ZSP], Barnes 1994; southwest Kodiak [SWK], Barnes 1990; Aliulik Peninsula [ALK], Barnes and Smith 1997). In each of these studies, we captured bears in the late spring or early summer and permanently marked them with green punch tattoos applied to the inside of the left and right upper lip and to the inside-front of the lower lip. We affixed numbered, plastic tags to each ear and radiocollared a sub-sample of captured bears. Van Daele (2007b) includes a detailed description of the capture and relocation methods.

We monitored survival via radio telemetry flights during each project and continued with a subset of bears with active collars in the areas through 1997. Information on non-anthropogenic mortalities was available only for bears with active radiocollars. Whenever practical, we visited death sites for radiocollared bears as soon as possible after deaths were detected, and we attempted to determine the timing and cause of mortality. Human-caused mortalities of marked bears were noted when their hides and skulls were presented for inspection from 1982 to 2004. During the project, only experienced individuals conducted those inspections, thereby giving us an excellent likelihood of detecting marked bears.

To determine the proportion of male bears achieving trophy size at various ages, we analyzed age and skull data from bears harvested on Kodiak from 1961 to 2004 (2-year age classes up to age 20+). We determined bear ages by counting cementum annuli from premolar teeth and used age estimates in our analyses when they had an accuracy of "high" or "moderate" ($\geq$80% within 1 year; Matson et al. 1993). Skull measurements were collected by experienced personnel using steel calipers when hunters brought in skinned skulls for inspection.

Brown bear density estimates were developed for 9 distinct survey areas that represented most of the habitats on Kodiak Island (Figure 2) using mark-resight (Miller et al. 1997) and intensive aerial surveys (Barnes and Smith 1998). We conducted flights in late May, prior to the time that leaf-out obscured sightability and after most bears had emerged from dens. One area was surveyed each year on a rotating basis. Survey areas were divided into several quadrats, and each quadrat was surveyed by experienced pilot/biologist teams flying in small fixed-winged aircraft (Piper Super Cub or equivalent) approximately 150 m above ground level at a speed of approximately 110 km/hour, yielding survey rates of about 1.6 km^2/minute. When we spotted bears, we plotted their location on 1:63,360 USGS topographic maps and noted the time, number of bears in the group, age and sex, habitat type, activity, and which observer saw the bear first. We attempted to fly ≥4 replicates of each quadrat during each survey, with rotating survey times (morning or evening) and pilot/biologist teams to minimize sampling bias. Survey results were multiplied by sightability correction factors that were derived for each survey area using radio-collared bears. Mean density estimates for independent bears (excluding dependent cubs) and total bears, and associated standard errors, were estimated by combining data from the multiple surveys of each area.

We used data from the aerial surveys, along with results from our population model and professional judgments from agency biologists and guides to extrapolate a Kodiak Archipelago-wide bear density and population estimate. Confidence intervals (90%) for extrapolated estimates were based on standard errors of density estimates from nearby survey units multiplied by $t_{2,0.10}$. 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 we had lower confidence in population estimates for those areas (Barnes et al. 1988).

We obtained estimates of adult survival for marked bears in each study area using Program MARK (White and Burnham 1999). Bears that died as a direct result of research were permanently censored. We calculated both comprehensive and study area-specific survival estimates for males and females, coding encounter histories with annual intervals. Our sample of radiocollared bears was biased toward adult females and harvest was biased toward adult males, so we used 2 alternate procedures for estimating survival rates for each: Burnham joint live /dead model (Burnham 1993) for radio telemetry data for both males and females, and the Brownie option in Program MARK for data from marked adult bears that were killed by hunters or found dead by researchers (Brownie et al. 1985, Cooch and White 2005). In all cases, we created several different models that considered combinations of different areas, and constraints on survival rates, recapture rates, fidelity rates, and reporting rates. We compared the models using Akaike's information criterion (AIC) to evaluate the candidate model set (Burnham and Anderson 2002).

We created a deterministic population model using Microsoft Excel® (Microsoft Corporation, Seattle, Washington, USA) software. We sought to develop a model that would operate with user inputs of either objective or subjective data for a variety of population parameters. Our goal was a deterministic model that would be parsimonious, transparent, easily understood by managers and the public, and could run on most conventional computers. Model outputs included estimates of the projected population (by sex) of independent bears in subsequent years, a calculation of the annual population change, and an estimate of the number of bears that would be in the trophy-size class.

We ran the model with a range of 10 variables within the 95% confidence interval for each study area and noted which variables had the greatest impact on the output (initial population, initial sex ratio, productivity, cub sex ratio, adolescent male survival, adult male survival, adolescent female survival, adult female survival, male harvest, female harvest). When we did not have objective estimates of parameters, we used a 10% confidence interval (90 – 110%) about the best guess. Confidence intervals about model estimates of population growth rate (λ) were calculated by analyzing the suite of results from the model runs. We compared model results to population changes (independent bears) noted in portions of each study area during consecutive intensive aerial surveys of those areas for similar time periods.

RESULTS

Survival Rates

We estimated survival rates from 33 adult male bears radiocollared over a 9-year period (individual tracking periods ranged from < 1 – 6 years). This resulted in an annual survival rate estimate of 0.72 (SE = 0.052) with a 95% confidence interval of 0.61 – 0.81. We also estimated annual adult male survival based on 108 bears permanently marked within all study areas and later recovered dead by hunters or researchers. These data yielded an estimated rate of 0.81 (95% CI = 0.75 – 0.85, SE = 0.026; Table 1). In both approaches, the best models were those that assumed a common survival rate for all males, with no differences among study areas, recapture, recovery, or fidelity rates (AICc = 329.7 and 459.0, respectively; Table 2).

Analysis of adult female survival included data from 181 radiocollared bears over an 11-year period (individual tracking periods ranged from < 1 – 7 years). The best model held survival and recovery rates the same, but had different reporting and fidelity rates (AICc = 967.6; Table 2). The comprehensive survival rate estimate for independent females in all study areas was 0.87 (95% CI = 0.82 - 0.91, SE = 0.022; Table 1).

Within the TLH data separately, we used data from 54 radiocollared adult females monitored for 7 consecutive years (1982-1988; individual tracking periods ranged from <1 – 7 years). The best model constrained survival, recovery, reporting, and fidelity parameters to be the same across re-encounter occasions (AICc = 258.6; Table 2a). It resulted in an annual survival rate estimate of 0.89 (SE = 0.022) with a 95% confidence interval of 0.84 – 0.92 (Table 1).

Within the ZSP area, we followed 45 radiocollared adult female bears for 9 consecutive years (1988-1996; individual tracking periods ranged from < 1 – 8 years). The best model constrained survival, recovery, reporting, and fidelity parameters to be the same across re-encounter occasions (AICc = 195.6; Table 2a). It resulted in an annual survival rate estimate of 0.88 (SE = 0.023) with a 95% confidence interval of 0.83 – 0.92 (Table 1).

Within the SWK, we monitored 53 radiocollared adult females for 6 consecutive years (1983-1988; individual tracking periods ranged from < 1 – 5 years). The best model constrained survival, recovery, reporting, and fidelity parameters to be the same across re-encounter occasions (AICc = 212.6; Table 2a). It resulted in an annual survival rate estimate of 0.80 (SE = 0.032) with a 95% confidence interval of 0.73 – 0.86 (Table 1).

Within the ALK, area survival rate estimates were derived from 29 radiocollared adult female bears we monitored for 5 consecutive years (1992-1996; individual tracking periods ranged from < 1 – 5 years). The best model constrained survival, recovery, reporting, and fidelity parameters to be the same across re-encounter occasions (AICc = 73.5; Table 2a). It resulted in an annual survival rate estimate of 0.91 (SE = 0.030) with a 95% confidence interval of 0.84 – 0.96 (Table 1).

When we used data from all bears that were permanently marked and later recovered dead by hunters or researchers, the estimated the annual adult female survival rate was 0.78 (95% CI = 0.73 – 0.82, SE = 0.022, *n* = 39). Once again, the best model constrained survival and recovery parameters to be the same across re-encounter occasions (AICc = 768.8; Table 2b). Study area specific adult female survival rates included smaller sample sizes, wider confidence intervals, and larger standard errors than models derived from radio telemetry data (TLH – 0.82 , 95% CI = 0.74 – 0.87, SE = 0.033, *n* = 9; ZSP – 0.75, 95% CI = 0.61 – 0.85, SE = 0.062, *n* = 8; SWK – 0.76, 95% CI = 0.67 – 0.83, SE = 0.040, *n* = 17; and, ALK – 0.80, 95% CI = 0.63 – 0.90, SE = 0.069, *n* = 5).

We collared 25 young bears (2- or 3- year olds; 16 males and 9 females) soon after they were weaned and monitored them through 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%).

We investigated the cause of deaths for all the radiocollared bears used for the survival rate analyses (Table 1). The major cause of death for males was hunter harvest (91%), whereas most females died of 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 in the causes of death between males and females ($x^2 = 148.4$, df = 3, $P<0.001$).

Harvest

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 3). The harvest rates of independent bears ranged from 6.7% in TLH to 10.3% on the ALK, and males dominated the harvest in all areas (68.4%), ranging from 63.7% in TLH to 72.2% in ALK. Archipelago-wide, the number of bears harvested remained relatively consistent during the study, but was higher than during the previous 20 years (Table 4). We detected an apparent increase in the number and percentage of the harvest that consisted of trophy-sized males (Figure 3), while the estimated harvest rate remained at about 5.6% of total bears (166.3 mean annual harvest / 2,980 estimated total bears) and 8.2% of independent bears (166.3/2,038).

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; 56.1% of the males in the oldest age class ($\geq$20 years) were trophy-sized ($\geq$71 cm). Bears in the >69 cm category (n = 710) also increased with age, including 91.2% of the males in the oldest age class (Figure 4). The relationship between male skull size and age was evident when we compared the average annual skull sizes and ages for bears harvested from 1982-2004 ($P < 0.001$; $r^2 = 0.77$; n = 22), especially for males with skulls >74 cm.

Model

Comparisons of several model runs revealed that changes in female survival rates had the greatest impact on the rate of population change (+3.4 to -4.8%) predicted by the model when we tested a range of inputs for each of the study areas. The second most influential parameter was annual productivity (+1.1 to -3.3%). Estimates of population growth rates (λ) within the study areas were: TLH - $\bar{x}$ = 1.010 (SE = 0.004; range = 0.947-1.054); ZSP - $\bar{x}$ = 1.021 (SE = 0.004; range = 0.963 – 1.068); SWK - $\bar{x}$ = 0.977 (SE = 0.007; range = 0.902 – 1.039); and, ALK - $\bar{x}$ = 0.994 (SE = 0.005; range = 0.923 – 1.029).

When we compared model predictions of independent bear population levels with the results of consecutive intensive aerial surveys of areas within each study area, results were similar 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 5). When the TLH model was run for a 10-year period, it predicted an increase of 16.6%. 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. In one study area (ALK) intensive aerial survey data did not agree with model predictions. 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 an increase of 340 (± 74.8) independent bears in the Archipelago-wide population from 1995 – 2005 (Table 6) with an estimated λ of 1.014.

DISCUSSION

This project provided the first comprehensive analysis of the population dynamics of a hunted population of coastal brown bears, including development of a model to estimate sustainable harvest rates that maintain trophy quality. A critical component of this analysis was estimation of survival rates. Although such metrics are essential considerations when managing coastal brown bear populations, they are often unobtainable due to the logistics and expense involved in collecting the necessary data. During this investigation we used 2 methods of estimating survival rates, one based on bears that were radio collared and tracked (live-dead encounter model; Burnham 1993) and the other based on bears that were permanently marked when they were captured and later recovered when they died (recovery model; Brownie et al. 1985, Cooch and White 2005). Both of these techniques were employed because of considerable biases in the sex ratios of the samples of radio collared bears (mostly female) and in the samples of harvested bears (mostly male). Each technique yielded lower survival estimates and greater standard errors when samples sizes were smaller. While it may be prudent in some situations to use the most conservative survival estimate possible when managing brown bears, we assumed the estimates derived from the recovery model were the most applicable for males and those generated from the live-dead encounter models were the most best for females on Kodiak.

In spite of considerable differences in available habitat and denning patterns (Van Daele 2007b), adult female bears on Kodiak had similar survival rates in 3 of our 4 study areas (TLH, ZSP, ALK). Adult females in the southwestern portion of Kodiak (SWK) did not follow a similar pattern, as their annual survival rate estimates were lower than anywhere else. 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-caused and natural mortalities. The sample of female bears in SWK had a similar age distribution to the radiocollared bears in the other areas, and the relative annual variation in food availability noted during the SWK study period was similar to other study areas and periods. Consequently, we believe the difference in survival was not due to sampling bias or habitat anomalies.

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 2007b). Female bears in that area moved farther than females in the other study areas as they sought out areas where spawning salmon were seasonally concentrated (Barnes 1990). Coincident with this movement pattern, the bears in SWK were more likely to interact with other bears concentrated at salmon spawning areas. Density data collected during radio tracking flights in late summer indicated that bears in SWK congregated at densities of up to 10,000 independent bears/1000 km^2 at Frazer and Thumb Rivers, and up to 16,200 independent bears/1000 km^2 at O'Malley River (Barnes 2006) for a couple months each year. Although adult female bears in SWK had similar causes of mortality to those on other parts of Kodiak, the magnitude of mortality factors seemed to be exacerbated by increased home ranges and intraspecific encounters at food concentration areas.

A comprehensive literature review by Schwartz et al. (2003) reported that annual survival rates of brown bears 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 (0.87 and 0.81, respectively) were lower than most noted in that publication, but their synopsis did not include any high-density coastal brown bear populations that were subjected to human harvest. Schwartz et al. (2003) also noted that subadult female survival was generally similar 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 were similar, with subadult females at 0.89 and subadult males at 0.56, reflecting a lower annual survival rate than in non-hunted and interior populations.

Our investigation was not designed to determine 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 nearly twice as likely to be killed by hunters as were adult females on Kodiak. This resulted from hunter selectivity, larger home ranges for males, and regulations that protected maternal females. Conversely, the adult females we radiotracked on Kodiak were over 10 times more likely to die of non-anthropogenic causes than were radiocollared males.

Productivity estimates are another critical factor when modeling a bear population. In a companion study (Barnes and Van Daele 2008), we found that females in the area with the lowest annual survival rate (SWK – 0.80) had the greatest reproductive rate (0.42 weaned cubs/female/year). Conversely, females in the area with the highest annual survival rate (ALK – 0.91) had the lowest reproductive rate (0.33 weaned cubs/female/year). The overall impact of these varying rates was a comparable population growth rate in each study area.

Our comparison of model results using area-specific survival, productivity and harvest information to data from intensive aerial surveys of portions of the study areas provided an evaluation of model accuracy (assuming the aerial surveys were unbiased). The only study area where estimates did not closely agree was ALK. In that case, we suspected that the model was more accurate than the intensive aerial survey. The second survey of ALK was plagued by poor weather conditions that prevented adequate coverage of the 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 of sex ratios and number of trophy males in the population.

Choosing the appropriate level of resolution for a population model is a pragmatic compromise between the complexity of the ecosystem and available data (Starfield and Bleloch 1986, Doak et al. 2005). Wildlife managers and the public are often skeptical of sophisticated models that invoke convoluted formulae, stochastic iterations, and immeasurable variables in a *black box* context, too often they respond by either avoiding using the models or by dismissing them as unrealistic or misleading.

The simplicity of our model was both its greatest asset and its greatest limitation. By using a deterministic model that employed data derived from long-term studies, impacts of interannual variation 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 is that if the model is only run once 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 results and the potential impacts of bias.

Managers using any deterministic model must clarify its constraints to the public and explain the link between unbiased inputs and unbiased outputs (Taylor et al. 2002). With this in mind, the model must be run several times using variables that are within confidence levels of each measured parameter (Jerina et al. 2003). This will provide bootstrapped confidence intervals about the results and clearly demonstrate 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, stochastic Excel spreadsheets (White and Lubow 2002), or by using a more refined program such as RISKMAN (Taylor et al. 2001), 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, even though the results were the same. This was especially true in our case because the target audience was interested in parameters not usually estimated by conventional population models (e.g. number of trophy-sized males available for harvest).

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

From the 1950s through 1970s, bear managers on Kodiak noted a decline in the harvest of trophy-sized bears, but found 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). In the mid-1970s, 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 within the harvest were stable to increasing Archipelago-wide, and the number and percentage of trophy-sized bears in the harvest steadily increased. Aerial survey data indicated that population densities were stable or 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 2007a).

Skull size-age data 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 (≥71 cm) if they live over 20 years. 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 were 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 5.6% of the total bear population on the Kodiak Archipelago was close to the suggested approximate maximum 5.7% exploitation rate from population simulation studies on brown bears in Southcentral Alaska (Miller 1990a). Other investigators have suggested that the 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). Another confusing factor in estimating sustainable harvest rates is that some calculations offered in the literature use only *independent bears* while others use *total bears*. In most jurisdictions, dependent cubs are not legal game and have higher natural mortality rates than independent bears. Consequently, we concluded that the best measure of sustainable harvest rate was based on independent bears.

The Kodiak bear management plan (ADF&G 2002) recommended we move beyond relying on harvest data and subjective judgments in making management decisions, and incorporate area-specific population data into exploring a suite of management strategies in open forums. This new paradigm encouraged us to more closely evaluate the data we had been collecting and seek the resources to improve our population monitoring techniques, obligated us to use more sophisticated analytical procedures and models to interpret our data, and required us to devise a simplified model that could be used to explain our data in a non-technical manner. All indicators suggested 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, but it was evident that we could not rely on a single harvest rate for all areas and that more information on trophy management was necessary.

Application of the model gave us an assessment of population status of each subunit and allowed us to develop a strategy to stabilize the bear population, while maintaining opportunities for high quality hunting. 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 complete agreement on harvest strategies was rarely possible, the model allowed exploration of potential biological ramifications of various management scenarios and assisted in framing a debate of pros and cons of different proposals. These deliberations also revealed areas needing further research.

It is well documented female survival and productivity are the most sensitive parameters driving most brown bear populations (Miller 1990b, this study); however, on Kodiak, we had an increasing bear population on many parts of the island, an increasing trend in the number of large males in the harvest, and a comprehensive bear plan that recommended a stable population. The increasing number of trophy males in the harvest during the past 30 years was encouraging, but our model suggested that it was reaching an asymptote, and higher levels would not be sustainable. To stabilize the population, maintain the current annual harvest of trophy-sized males, and avoid overcrowding of hunters, the model suggested slight increases in the harvest of adult females in some subunits while maintaining male harvests at existing levels in most areas. It also suggested that harvest rates ranging from 5.6 – 7.9 % of the estimated independent bear population would be appropriate in harvest subunits on Kodiak.

To refine harvest strategies brown bear 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. As a direct result of this project, we modified our bear permit allocations and hunter distribution for several areas on the Archipelago in 2007 and again in 2011, but more importantly we forged a much closer working relationship with the public and improved our understanding of the bear population and how to manage it.

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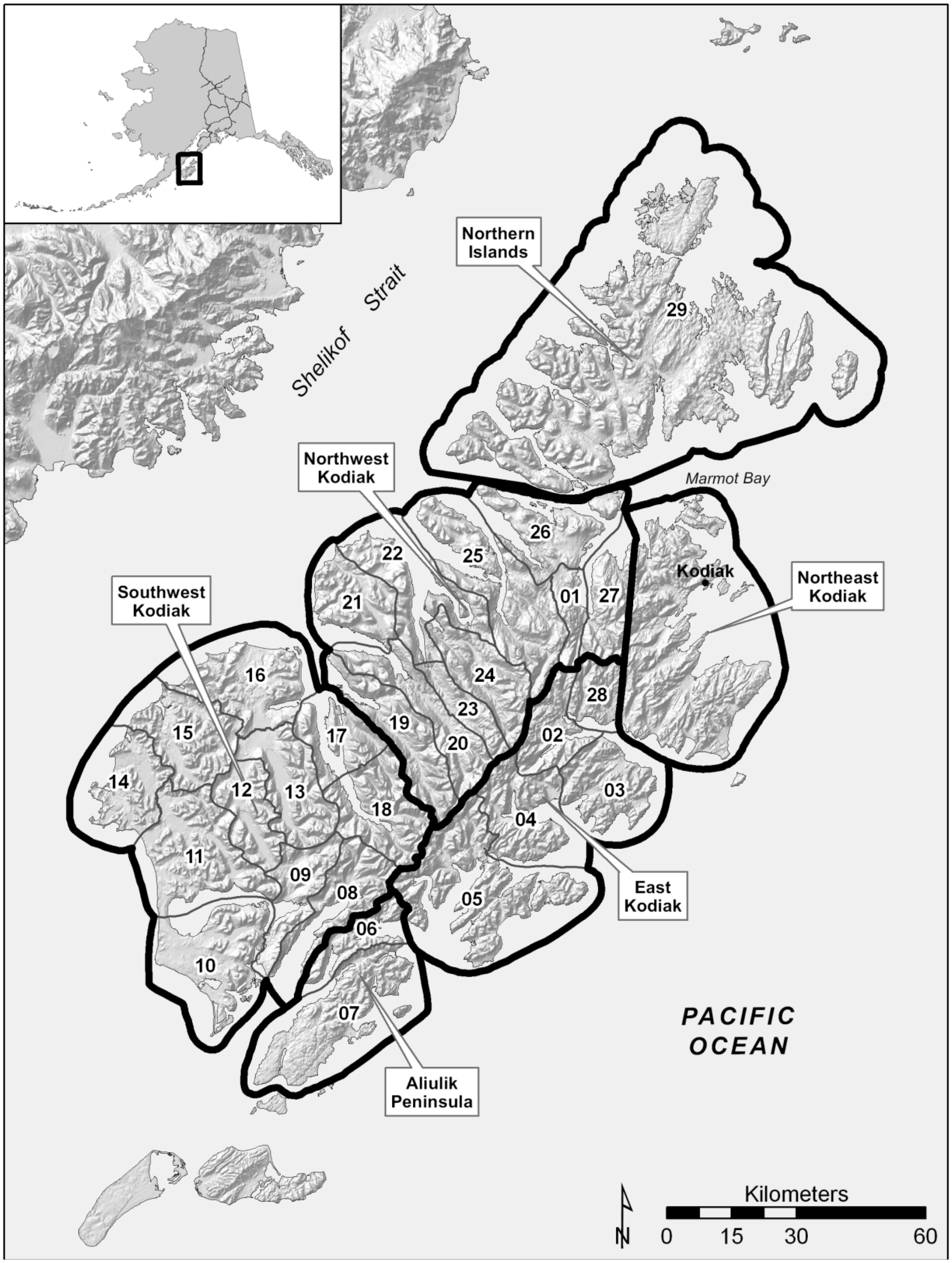

Figure 1. Brown bear hunt areas (Game Management Unit 8; bear hunt areas 01-29) and bear management subunits, Kodiak Archipelago, Alaska, 1982-2004.

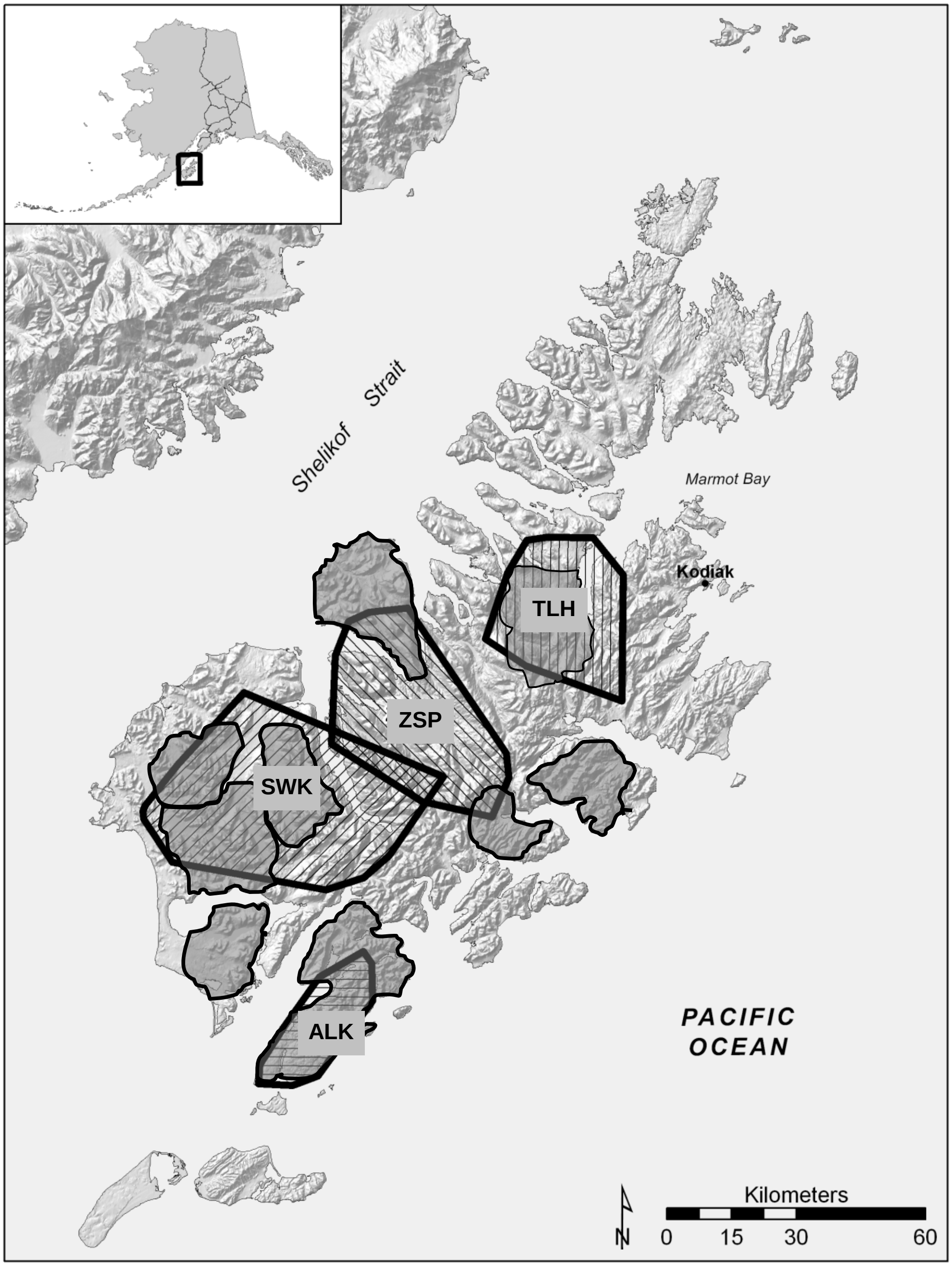

Figure 2. Kodiak Archipelago, Alaska, including the 4 brown bear study areas. (TLH – Terror Lake, ZSP – Zachar/Spiridon, SWK – southwest Kodiak, and ALK – Aliulik Peninsula), and intensive aerial survey areas (shaded), 1982 – 2004.

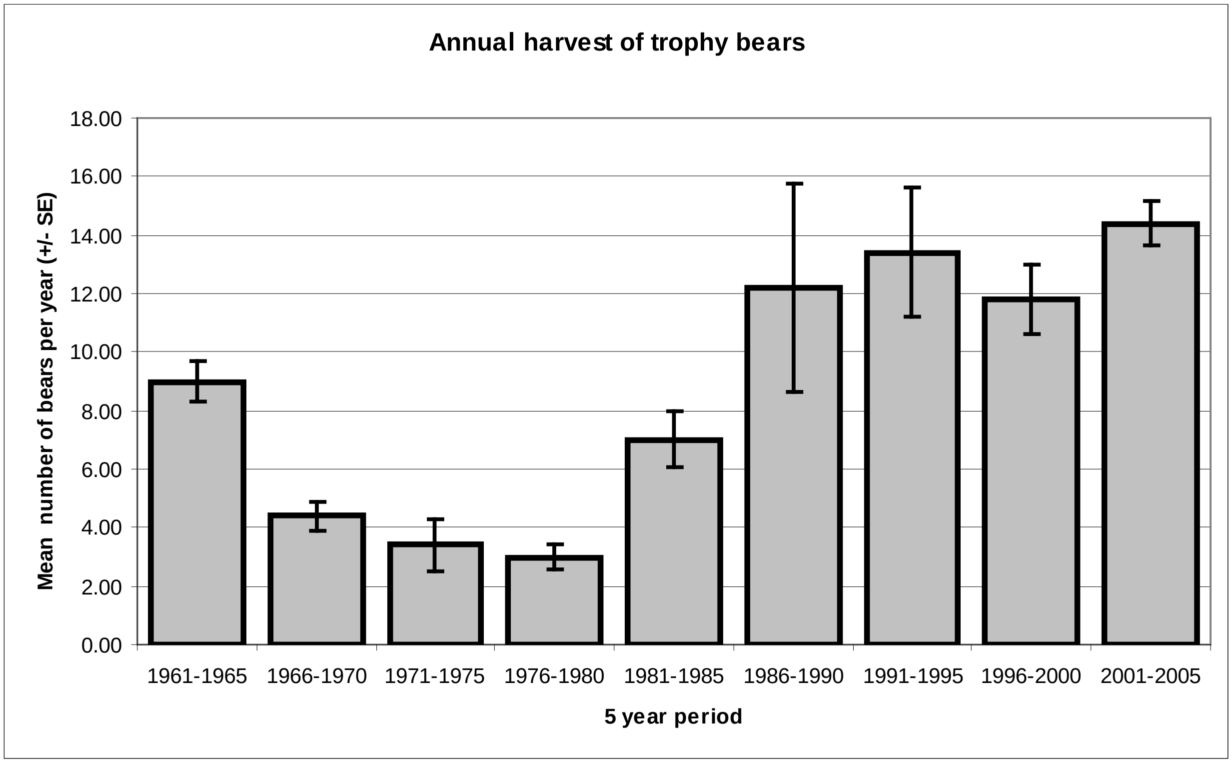

Figure 3. Mean number of brown bears with total skull sizes exceeding 71 cm (trophy-sized bears), by 5-year period, harvested on the Kodiak Archipelago, Alaska, 1961 – 2005.

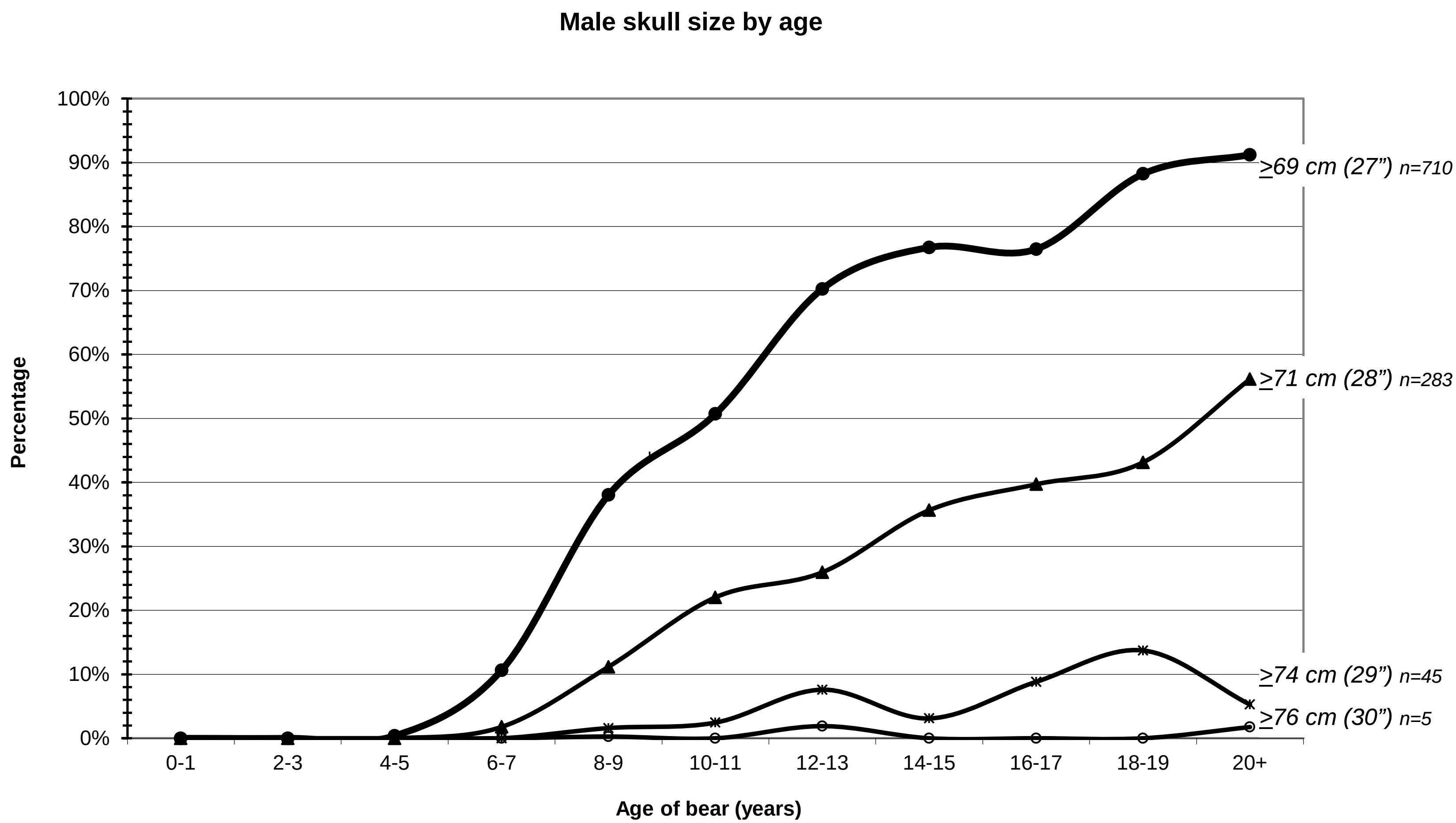

Figure 4. Proportion of male bears in various age classes with large total skull sizes (zygomatic breadth plus total length), Kodiak Archipelago, Alaska, 1961 – 2004.

Table 1. Annual survival rates and mortality factors for radiocollared adult bears, Kodiak Island, Alaska, 1982 – 2004.

Area / Sex	Estimated annual survival rate (95% CI)	Cause of death				
		Natural[a]	Hunter	DLP[b]	Illegal	Total
All males	0.81[c] (0.75 – 0.85)	1 (5%)	20 (91%)	1 (5%)	0 (----)	22
All females	0.87[d] (0.83 - 0.89)	21 (54%)	13 (33%)	4 (10%)	1 (3%)	39
Terror Lake females	0.89[d] (0.84 – 0.92)	5 (56%)	2 (22%)	2 (22%)	0 (----)	9
Zachar / Spiridon females	0.88[d] (0.83 – 0.92)	3 (38%)	4 (50%)	1 (12%)	0 (----)	8
Southwest Kodiak females	0.80[d] (0.73 – 0.86)	10 (59%)	6 (35%)	0 (----)	1 (6%)	17
Aliulik Peninsula females	0.91[d] (0.84 – 0.96)	3 (60%)	1 (20%)	1 (20%)	0 (----)	5

a – bears that appeared to have died of non-anthropogenic causes.
b – bears killed under defense of life or property provisions.
c – survival rates calculated using procedures outlined by Brownie et al. (1985) and Program MARK (White and Burnham 1999).
d – survival rates calculated using procedures outlined by Burnham (1993) and Program MARK (White and Burnham 1999).

Table 2a. Comparison of Burnham joint live /dead survival rate models (Burnham 1993) using radio-telemetry data from brown bears on Kodiak Island, 1982 -2004.

Model[a]	AICc[b]					
	TLH[c] females	ZSP[d] females	SWK[e] females	ALK[f] females	All females	All males
all same	258.6[g]	195.6[g]	212.6[g]	73.5[g]	1090.1	334.9
s,p,r same	266.0	207.6	220.0	79.6	984.2	339.6
s,r,f same	265.5	210.7	220.8	80.3	997.2	329.7[g]
p,r,f same	265.7	239.1	219.6	78.0	1120.8	330.2
s,p same	274.6	215.3	221.7	84.0	967.6[g]	346.9
s,r same	274.6	217.7	226.8	84.4	988.0	342.4
s,f same	272.9	213.4	221.7	85.0	978.9	334.0
p,r same	276.0	201.5	227.4	84.2	970.2	343.1
p,f same	271.3	202.4	220.2	81.2	967.7	331.4
r,f same	273.4	208.8	228.8	85.4	974.7	340.7
s same	280.3	230.4	228.9	89.1	973.9	348.8
p same	283.1	209.9	229.9	88.9	970.7	352.4
r same	281.2	219.0	234.6	89.4	976.6	358.5
f same	279.3	212.4	229.9	88.9	967.8	344.4
all different	291.6	228.1	240.1	97.2	977.4	368.7

a – “s” = survival; “p” = recapture; “r” = reporting; “f” = fidelity
b – Akaike’s information criterion with a correction for finite sample sizes
c – Terror Lake
d – Zachar-Sprirdon
e – Southwest Kodiak
f – Aliulik Peninsula
g – selected model

Table 2b. Comparison of Brownie survival rate models (Brownie et al. 1985) for brown bears on Kodiak Island, 1982 -2004.

Model	AICc[b]	
	All females	All males
all same	768.8 [b]	459.0[b]
survival same, recovery different	785.6	488.7
survival different, recovery same	786.6	489.7
all different	811.2	527.8

a – Akaike's information criterion with a correction for finite sample sizes
b – selected model

Table 3. Annual human harvest of brown bears within the 4 study areas, Kodiak Island, Alaska, 1982 – 2004.

Study area	Annual harvest				
	Independent bears / year/1000 km^2	Bears / year	Male	Female	% harvest of independent bears
Terror Lake	13.3	16.2	63.7 %	35.5%	6.7%
Zachar / Spiridon	16.5	24.6	70.7%	28.8%	7.4%
Southwest Kodiak	17.8	47.7	66.8%	32.9%	8.4%
Aliulik Peninsula	22.6	14.0	72.7%	26.7%	10.3%

Table 4. Mean annual harvest of brown bears, by 5-year period, on the Kodiak Archipelago, Alaska, 1961-2005.

Regulatory	Mean annual fall harvest			Mean annual spring harvest			Mean annual total harvest			Mean annual
Years	Bears	Male	Female	Bears	Male	Female	Bears	Male	Female	trophy[a] %
1961-65	32.0	62.5%	37.5%	103.6	60.4%	38.0%	135.6	60.8%	37.9%	7.0%
1966-70	44.8	61.2%	37.9%	81.2	59.1%	38.7%	126.0	59.8%	38.4%	3.5%
1971-75	54.2	52.0%	46.9%	87.2	63.1%	35.6%	141.4	58.8%	39.9%	2.4%
1976-80	35.6	59.0%	41.0%	96.6	63.6%	36.0%	132.2	62.3%	37.4%	2.3%
1981-85	50.0	58.0%	41.2%	112.4	71.4%	28.6%	162.4	67.2%	32.5%	4.3%
1986-90	60.0	52.7%	46.3%	108.8	67.6%	32.2%	168.4	62.2%	37.3%	7.3%
1991-95	53.4	64.0%	35.2%	106.6	67.2%	32.1%	160.0	66.1%	33.1%	8.4%
1996-2000	52.8	68.6%	31.4%	107.2	74.8%	25.0%	160.0	72.8%	27.1%	7.4%
2001–05	53.8	73.2%	26.8%	112.2	77.5%	22.5%	166.0	76.1%	23.9%	8.7%

a –“trophy” bears are those with a total skull size (maximum length + maximum width) >71 cm (28”).

Table 5. Results of intensive aerial brown bears surveys within specific study areas on Kodiak Island, Alaska, 1987-2002.

Study area	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	Terror Lake	1987	3	1.5	75	33%	234	29.8	355	83
	Terror Lake	1997	4	1.7	92	33%	276	31.7	355	98
Zachar / Spiridon	Spiridon Lake	1995	4	1.9	38	33%	118	24.4	287	34
	Spiridon Lake	2000	4	1.8	44	33%	134	23.3	287	38
Southwest Kodiak	Sturgeon River	1987	4	1.6	120	41%	293	22.3	264	77
	Sturgeon River	1998	4	1.9	94	41%	227	4.4	264	60
Aliulik Peninsula	Aliulik Peninsula	1992/93	8	1.6	108	53%	209	17.0	350	73
	Aliulik Peninsula	2002	5	1.4	92	53%	173	18.3	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 6. Estimates of brown bear numbers and density in each management subunit on the Kodiak Archipelago, Alaska, 1995 and 2005 (90% confidence intervals in parentheses).

Bear management subunit	Area (km²)	1995[a]						2005[b]					
		Density[c]		Independent bears[d]		Total bears[e]		Density[c]		Independent bears[d]		Total bears[e]	
Northern Islands	2,281	101	(±25)	231	(±58)	330	(±83)	132	(±33)	300	(±175)	430	(±108)
Northwest Kodiak	2,983	200	(±50)	596	(±149)	808	(±202)	224	(±56)	668	(±167)	908	(±227)
Northeast Kodiak	1,005	63	(±16)	63	(±16)	90	(±23)	70	(±18)	71	(±18)	101	(±25)
East Kodiak	1,738	146	(±30)	253	(±51)	471	(±94)	230	(±46)	400	(±80)	744	(±149)
Southwest Kodiak	3,498	204	(±41)	712	(±142)	1,019	(±204)	219	(±44)	765	(±44)	1,094	(±219)
Aliulik Peninsula	837	219	(±55)	183	(±46)	262	(±66)	208	(±52)	174	(±52)	249	(±62)
TOTAL	12,342	165	(±38)	2,038	(±462)	2,980	(±672)	193	(±42)	2,378	(±519)	3,526	(±790)

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).