

Effects of hunting on brown bear cub survival and litter size in Alaska

Sterling D. Miller^{1,4}, Richard A. Sellers², and Jeffrey A. Keay^{3,5}

¹Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518-1599, USA

²Alaska Department of Fish and Game, P.O. Box 37, King Salmon, AK 99613-0037, USA

³U.S. Geological Survey, Alaska Biological Science Center, 1011 East Tudor Road, Anchorage, AK 99503, USA

Abstract: We present data from 4 studies of radiomarked brown bears (*Ursus arctos*) in Alaska to evaluate the effects of hunting and differential removal of males on cub survival and litter size. In the Susitna area in southcentral Alaska, the proportion of males declined during a period of increasing hunting pressure (1980–96). Cub survivorship was higher in the heavily hunted Susitna population (0.67, $n = 167$ cubs) than in a nearby un hunted population in Denali National Park (0.34, $n = 88$ cubs). On the Alaska Peninsula, in coastal areas rich in salmon (*Oncorhynchus* spp.) and with higher brown bear densities, cub survivorship was significantly higher in the hunted Black Lake population (0.57, $n = 107$ cubs) than in an un hunted population in Katmai National Park (0.34, $n = 99$ cubs). The Black Lake population had alternate-year hunting, and cub survivorship was similar during years with and without hunting during the preceding fall and spring. In both coastal and interior comparisons, litter sizes were either larger or not significantly different in hunted areas than in nearby un hunted national parks. We found no evidence that removal of adult male bears by hunters reduced cub survival or litter size. For populations below carrying capacity, convincing evidence is lacking for density dependent effects on cub survivorship or litter size. In our studies, variations in cub survivorship and litter size were best explained by proximity to carrying capacity; local environmental factors and stochastic events probably also influence these parameters. We believe that cub survivorship in our national park study areas was lower than in nearby hunted areas because of density-dependent responses to proximity to carrying capacity.

Key words: Alaska, brown bear, compensatory mechanisms, density dependence, grizzly bear, hunting, infanticide, intraspecific mortality, sexually selected infanticide, survivorship, *Ursus arctos*

Ursus 14(2):130–152 (2003)

Brown bears are characterized by low rates of natural mortality in adult age classes and higher rates of natural mortality in newborns and subadults. In a review of North American brown bear studies, cub (defined here as bears in the first year of life) mortality rates were 30–40% (Bunnell and Tait 1985). Demographic models and calculated levels of sustainable harvest will be influenced

by factors that affect survival of cubs. However, few data are available on causes of cub mortality or on factors that may influence recruitment rates. In the absence of such data, there has been considerable speculation about relationships between adult bear abundance (especially adult males) and cub survivorship.

An inverse relationship between abundance of adult males and survivorship of cub and older dependent offspring was suggested by McCullough (1981) and Stringham (1980, 1983) based on data collected by Craighead et al. (1974) in Yellowstone National Park. The basis for this reported compensatory relationship was the suspicion that because male bears kill cubs, reductions in male abundance would increase cub survivorship. These interpretations of Craighead data

⁴Present address: National Wildlife Federation, 240 North Higgins, Suite 2, Missoula, MT 59802, USA, email: millerS@nwf.org

⁵Present address: Florida Integrated Science Center, 412 NE 16th Avenue, Room 250, Gainesville, Florida 32601-3701 USA, jeff_keay@usgs.gov

were challenged by Craighead et al. (1995) as well as McLellan (1994).

Most human hunting of bears is biased toward males for a variety of reasons (Bunnell and Tait 1981, 1985; Miller 1990a; McLellan 1994; Derocher et al. 1997). Based on the suggestions of McCullough (1981), a positive (compensatory) relationship between hunting and cub survivorship has been accepted by some managers of exploited bear populations. This was explicitly identified as a benefit of brown bear hunting in Montana by Dood et al. (1986). An early draft of the environmental impact statement for black bear hunting in California asserted, "The number of bears killed is expected to be replaced by increased survival of young," and included this relationship in a demographic model used to justify hunting bears (California Fish and Game 1999:64). This relationship was omitted from a revised version of the model (R. Barrett, 2000, The black bear population model—additive mortality, version 4-15-2000, University of California, Berkeley, California, USA).

Recent reviews found no evidence indicating increased cub survivorship resulted from reduced abundance of male bears for North American populations of brown bears (McLellan 1994), black bears (*U. americanus*; Ruff 1982, Garshelis 1994, Sargeant and Ruff 2001), and polar bears (*U. maritimus*; Derocher and Taylor 1994). Miller (1990b) and Taylor (1994) recommended that until studies adequately demonstrated such a relationship, managers should not include it in bear population or harvest models.

Studies in Scandinavia reported the opposite consequence of male biased hunting. These studies reported that selective removal of males decreased brown bear cub and yearling survivorship (Swenson et al. 1997; 2001a,b; Swenson 2003). These authors concluded that removing a male bear caused social disruptions that resulted in lower cub survivorship 0.5–1.5 years following male removal in the fall. This conclusion was based on (1) observed differences in cub survivorship between 2 areas with different rates of male removal, (2) rejection of alternative explanations for the differences and (3) male removal experiments reported by Swenson (2003). The Scandinavian authors concluded that the differences in cub survivorship were caused by sexually-selected infanticide (SSI) as has been observed in lions (*Panthera leo*), primates, and other species (Hrdy 1979, Hrdy and Hausfater 1984, Janson and van Schaik 2000, Van Noordwijk and van Schaik 2000). Sexually-selected infanticide can be advantageous to males who kill offspring fathered by

other males, breed with the mother, and father additional offspring. New findings in Scandinavia clarified that the SSI reported for the Scandinavian studies resulted primarily from increased predation by resident adult males and not from immigrant subadult males subsequent to the death of a resident male (Bellemain et al. reported in Swenson 2003). In Scandinavia, increased mortality of yearling females (but not yearling males) was also reported 2.5 years following the death of a resident male. This was attributed to intraspecific predation rather than SSI (Swenson et al. 2001a).

In southern Alberta, Canada, Wielgus and Bunnell (1994a,b; 1995; 2000) concluded that a small brown bear population at Kananaskis was destabilized when adult males were killed by hunters and replaced by immigrant subadult males (presumed to be more prone to infanticide). These subadult males were concluded to have displaced adult females from good foraging habitats, thereby compromising the females' physical condition and causing smaller litters. Wielgus and Bunnell (2000) also concluded that bears from an un-hunted population in the Selkirk Mountains of northern Idaho and southern British Columbia had larger litters than the Kananaskis population. They reported that the un-hunted Selkirk bears had higher survivorship of resident adult males, less immigration of young males, and less avoidance of prime foraging areas by adult females. All this resulted in better female condition and larger litter sizes compared to the hunted Kananaskis population (Wielgus and Bunnell 2000). This conclusion was used as the basis for a demographic model suggesting that, "... the effects of adult male mortality: increased immigration by new males, related sexual segregation, and reduced reproduction ... can result in lowered population growth and population declines and can even lead to rapid population extinctions when numbers are very small" (Wielgus et al. 2001:299).

In contrast to SSI arguments, Craighead et al. (1995:99) wrote that "[we view] infanticide in grizzly bears as an expression of a foraging strategy (conspecific predation) ... rather than as a genetically acquired mating strategy practiced by a subset of [socially dominant adult males]."

Authors of the studies in Canada and Scandinavia suggested their conclusions have management implications. Swenson et al. (2001b) and Swenson (2003) recommended that managers assume that loss of adult males has a compensatory relationship on cub survivorship; they estimated that male removal in their Scandinavian study area reduced the population growth rate by 4.5%.

Wielgus and Bunnell (2000:153) concluded “[our] studies do suggest that the commonly accepted hypothesis that increased reproduction derives from trophy hunting could contribute to further declines in some grizzly bear populations.” Janson and van Schaik (2000) and Boyce et al. (1999) cited Swenson et al. (1997) as an illustration that increased infanticide might be a consequence of male based hunting in mammal populations. Boyce et al. (2001) cited studies in Scandinavia (Swenson et al. 1997) and southern Canada (Wielgus 1993) as illustrating possible relationships meriting consideration in managing bear hunting. In contrast, a panel of 6 scientists reviewed brown bear hunting management in British Columbia and concluded: “that presently available data on [effects of selective removal of males by hunting] are equivocal, and therefore hunting-related changes in density or social structure should not be incorporated into [British Columbia] harvest management” (J. Peek, J. Beecham, D. Garshelis, F. Messier, S. Miller, and D. Strickland, 2003, Management of grizzly bears in British Columbia: A review by an independent scientific panel, Minister of Water, Land and Air Protection, Government of British Columbia, Victoria, British Columbia, Canada, page 53).

We examined data from Alaska for evidence of relationships between brown bear hunting biased toward males and cub survival and litter size. We report temporal comparisons in a population in southcentral Alaska exposed to increasing hunting pressure designed to reduce brown bear predation on moose (*Alces alces*) calves over a 16-year period. We compare cub survivorship and cub litter sizes in hunted and unhunted populations in southcentral Alaska. We also compare high-density hunted and unhunted populations in salmon-rich habitats on the Alaska Peninsula and cub survivorship following years with and without hunting on the Alaska Peninsula.

Study areas

Southcentral Alaska

Upper and Middle Susitna. Temporal changes in population density and composition in southcentral Alaska were measured in the 1,325 km² Middle Susitna study area (MidSu) during 1985 and 1995 (Miller et al. 1987, Miller 1990c; Fig. 1). MidSu was characterized by forests of spruce (*Picea glauca* and *P. mariana*), birch (*Betula papyrifera*), and alder (*Alnus* spp.) at lower elevations along the Susitna River. Above approximately 800 m elevation the vegetation graded into shrub



Fig. 1. Location of Alaskan study areas for unhunted (Denali and Katmai) and hunted (MidSu, UpSu, and Black Lake) populations of brown bears, 1980–1997.

tundra and then into mat and cushion tundra. In MidSu, only one stream (Prairie Creek) in the southwest corner had a run of salmon (*Oncorhynchus tshawytscha*); this run was exploited in July by a small proportion of the radiomarked bears in MidSu (Miller 1987).

Access to MidSu by bear, moose, and caribou (*Rangifer tarandus*) hunters was by aircraft, snow machines, or all-terrain vehicles, depending on season. MidSu was in a relatively remote portion of Alaska’s Game Management Unit (GMU) 13, Subunit 13E (17,555 km², Fig. 2), bordered on the north by the crest of the Alaska Range and on the south by the Talkeetna Mountains. Denali National Park overlapped the northwestern corner of Subunit 13E.

We also used reproductive and survival data from radiomarked bears in the Upper Susitna study area (UpSu) 40 km northeast of MidSu. Most of the UpSu was in Game Management Subunit 13E, but a small portion was in Subunit 13B (Fig. 2). UpSu surrounded the headwaters of the Susitna River, bordered on the east by the Clearwater Mountains and on the north by the crest of the Alaska Range. Bears in UpSu had no access to salmon, but moose density and vegetation were otherwise comparable to MidSu (Miller 1990c, Ballard et al. 1991). Moose densities in UpSu were 688–848/1,000 km² during 1980–83 (Miller and Ballard 1992). Hunting regulations were the same in UpSu and MidSu. UpSu was adjacent to the Denali Highway (Fig. 2) and was more easily accessed by bear hunters.

Although both UpSu and MidSu were heavily hunted for brown bears, bear hunting was earlier and more intense in UpSu because of easier hunter access (Miller and Ballard 1992). By 1987, UpSu had a reduced density of brown bears and a population skewed in favor of females (Miller 1990c). Black bears were rare in UpSu but were common in MidSu in forested habitats along the Susitna River. Hereafter, data collected in MidSu and UpSu areas are referred to as Susitna data.

Brown bear hunting regulations were liberalized by the Alaska Board of Game to increase brown bear harvests during 1980–2003 throughout GMU 13. The motive for these liberalizations was to reduce brown bear abundance and bear predation on moose (Miller and Ballard 1992). A spring season for brown bears was initiated in 1980. In 1979, brown bear hunting was open 1 September–10 October, the bag limit was 1 per 4 years, and residents needed a \$25 brown bear tag. By the end of our study in 1997, the season was open 10 August–31 May, the bag limit was 1 per year, and no tag was required for Alaska residents. The August season was authorized in 1995 to encourage caribou hunters to take bears incidental to caribou hunts. In 2003, the hunting season for brown bears was expanded to 365 days.

Denali National Park. We compared our data from Susitna studies to data collected in Denali National Park (hereafter “Denali”, Keay 2001 and J. Keay unpublished data). Denali overlaps the northwestern portion of Subunit 13E (Fig. 1), but Keay’s study area was in Subunit 20C on the opposite (north) side of the Alaska Range. The Denali study area included a similar mix of bear foods and habitat types, although typically at higher elevations (600–2,000 m) and with fewer trees than in Susitna. Moose densities in Keay’s study area were much lower (60/1,000 km² at elevations below 1,050 m, Adams et al. 1995) than in Susitna (600–1,000 moose/1,000 km², Miller and Ballard 1992). Like bears in the UpSu area and most bears in the MidSu area, bears in the Denali study area had no access to salmon.

There were no documented human-caused mortalities to brown bears in the Denali population. Keay (2001)

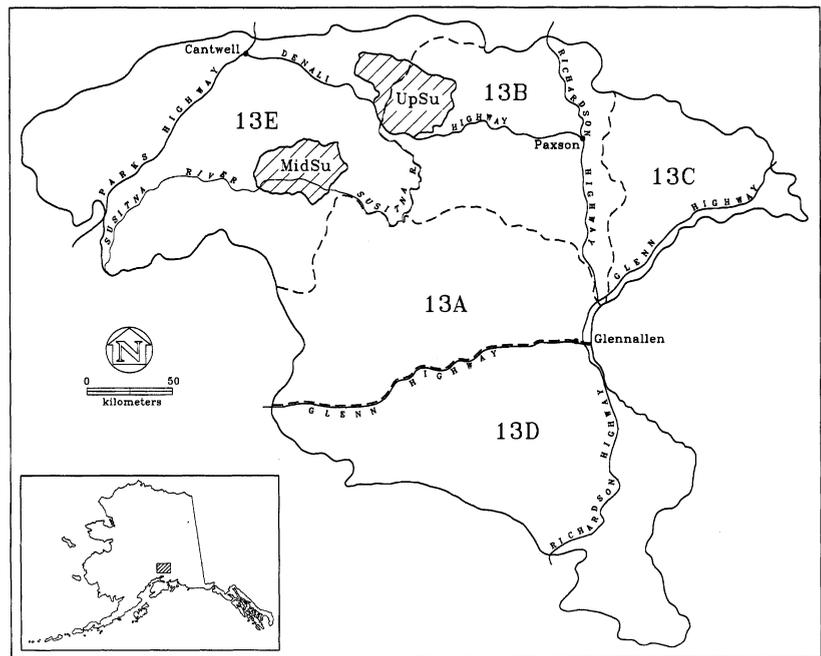


Fig. 2. Alaska’s Game Management Unit 13 in Southcentral Alaska, where a hunted population of brown bears was studied during 1980–97. A portion of Denali National Park overlaps the northwestern border of Subunit 13E. Population composition and density were estimated for 2 study areas in Subunit 13E (MidSu and UpSu).

found no evidence of poaching within the study area, and there were no management kills or translocations of nuisance bears. Keay (2001:4) concluded that “human activities have had virtually no impact on grizzly bear population dynamics in the study area for at least 80 years.” Thus, the comparisons of demographic parameters between Susitna and Denali represent comparisons between a population that has long been hunted, especially in the 1990s, and an unhunted population.

Habitat comparisons. Habitats were not identical in Denali and our Susitna study areas, but these areas shared the same primary sources of nutrition available to bears. Stable isotope analyses based on hair samples from the Susitna area and Denali study areas were conducted by Hilderbrand et al. (1999; samples for Susitna were provided by S.D. Miller and came from MidSu). Marine meat (salmon) constituted none of the diet in Denali compared to 4% ($\pm 6\%$) in Susitna. Terrestrial meat constituted 4% ($\pm 11\%$) in Denali Park compared to 9% ($\pm 13\%$) in Susitna. Plant matter constituted 96% ($\pm 11\%$) of the brown bear diet in Denali and 87% ($\pm 13\%$) in Susitna. Overall, both Denali and Susitna populations consumed among the

lowest proportions of dietary meat among the brown bear populations studied by Hildebrand et al. (1999).

Alaska Peninsula studies

Black Lake. The Black Lake study area was on the Alaska Peninsula 360 km southwest from Katmai (Fig. 1). Most bears were captured within a 1,215 km² area where we estimated bear density (Miller et al. 1997). The Black Lake study area was bordered on the southeast by the Pacific Ocean and on the northwest by Bristol Bay; it had a subarctic-maritime climate and vegetation pattern similar to that in the Katmai study area. All five species of Pacific salmon were found within the Black Lake area, but sockeye salmon (*O. nerka*) in the Chignik River provided the most reliable food source for bears.

The Black Lake study occurred in Subunit 9E (31,000 km²), which was the most popular brown bear hunting area in Alaska in which hunter participation was not limited by permits. There were no roads connecting the Alaska Peninsula with the rest of Alaska, but access by small aircraft was relatively easy for hunters. Subunit 9E was popular for brown bear hunting by both guided nonresident and unguided Alaska resident hunters.

Unlike Susitna, hunting regulations in the Black Lake study area were designed to maintain sustainable harvests and a population with large (trophy) males. Excessive harvests and reduced densities during the late 1960s and early 1970s prompted studies at Black Lake (Glenn 1980, Glenn and Miller 1980). Subsequently, bear populations on the Alaska Peninsula including Subunit 9E increased in response to conservative management based on alternate year hunting seasons (Sellers 1994, 1998). Counts of bears along salmon streams indicated that bear numbers have increased in recent decades (Sellers 1998 and unpublished data).

Katmai National Park. The Katmai National Park (hereafter Katmai) brown bear study (Fig. 1) was initiated shortly after the March 1989 *Exxon Valdez* oil spill to assess damage to bear populations. Brown bears were captured and radiomarked on the central portion of the Shelikof Strait coast of Katmai. The primary study area was bordered by Shelikof Strait on the east and the crest of the Aleutian Mountains (to 2,318 m) on the west. Brown bear density was estimated within a 901-km² area (Miller et al. 1997). Trees were sparse in the study area. Below the zone of alpine tundra, alder (*Alnus crispa*) and willow (*Salix* spp.) were abundant. Salmon (primarily pink [*O. gorbuscha*], chum [*O. keta*], and

coho [*O. kisutch*]) spawned in numerous streams distributed throughout the study area. Additional vegetative information was provided by Cahalane (1959). No influences from *Exxon Valdez* oil pollution on bear survival or reproduction were detected. Survival was 0.36 for cubs ($n = 26$) of females using polluted areas and 0.37 for cubs ($n = 37$) of females using unpolluted areas ($\chi^2 = 0.03$, 1 df, $P = 0.86$, Sellers and Miller 1999).

The Katmai study area was located centrally in an area closed to bear hunting since 1931. Subsequent additions to the park in 1942, 1969, and 1980 expanded the area closed to hunting. Additional closures during 1985–96 north of Katmai resulted in expanding the area closed to bear hunting to 14,500 km². Prior to the *Exxon Valdez* oil spill, human presence was limited primarily to commercial fishers and occasional guided sport anglers. There were no documented human-caused mortalities in Katmai since 1985, although 2 bears marked in Katmai were later shot outside park boundaries.

Habitat comparisons. Dietary composition of bears in Black Lake and Katmai study areas was analyzed by Hildebrand et al. (1999) using stable isotope analysis based on samples provided by R. Sellers. Marine meat (primarily salmon) constituted 79% ($\pm 14\%$) of the diet at Black Lake compared to 62% ($\pm 25\%$) at Katmai. Plant matter and terrestrial meat, respectively, represented 19% ($\pm 11\%$) and 2% ($\pm 5\%$) of the bears' diet at Black Lake compared to 31% ($\pm 19\%$) and 7% ($\pm 15\%$) at Katmai. Compared to the Denali and GMU 13 studies, bears on the Alaska Peninsula ate >15 times more salmon. Miller et al. (1997), Hildebrand et al. (1999), and others correlated the abundance of salmon with higher densities and larger body sizes in Alaskan brown bears.

Black bears did not occur in either of the Alaska Peninsula study areas.

Methods

One objective of the studies on the Alaska Peninsula and in GMU 13 was to examine the influence of harvest on survivorship of juvenile brown bears. In all areas data were obtained by periodically locating radiomarked bears and observing litter size. Density estimates were derived from capture–mark–resight estimates obtained using radiomarked individuals to establish geographic closure (Miller et al. 1997). We defined cubs as bears in their first year of life and yearlings as bears in their second year of life. Subadults were bears <5 years old no longer with their mother. Throughout most of Alaska,

including our study areas, brown bears typically separate from their mothers in the spring of their 3rd year of life (at age 2), infrequently in their 4th year of life or older, and rarely as yearlings (Sellers and Miller 1991, Miller 1993a).

During 1980–95, we captured and marked 175 different brown bears in Susitna (Miller 1997a). During 1988–94 we captured 112 different individuals in Black Lake, and during 1989–1993 we captured 122 in Katmai. During 1991–1998, we captured 74 different individuals in Denali. Bears were captured following searches with fixed-wing aircraft. Bears were darted from a helicopter (Miller et al. 1997) in and near areas used for density estimation. In all study areas, all captured adult females were fitted with radio transmitters. Where feasible, adult males and subadults of both sexes were also fitted with radio transmitters equipped with drop-off features. We periodically replaced radio transmitters on bears by recapturing them (up to 7 times during the 16 years, Miller 1997a, b).

Harvest data and hunter selectivity

Harvest data. Inspection was required of hides and skulls of bears shot by hunters in Alaska. During inspection, officials determined sex, recorded the location of kill, and extracted a premolar for aging by counting of cementum annuli (Matson et al. 1993). Evidence of gender, based on hide examination, was inconclusive in <2% of bears examined, and in such cases bears were allocated to a “sex unknown” category.

Hunter selectivity for males. Hunting provided an opportunity to test for responses to reduction in male abundance in bear populations because hunters bias kills toward males. In Alaska, this was a consequence of hunting regulations as well as bear behavior. Male bears were especially vulnerable to hunters during spring seasons because they exited their dens early when hunting conditions were more favorable than later during the spring (Miller 1990d, Van Daele et al. 1990). Male bears are also especially vulnerable during spring seasons because seasons for other species are not open and hunters afield are bear hunters mostly interested in larger (trophy) bears. In all seasons, male are more vulnerable than females because they have larger home ranges, which increases the likelihood that they will encounter hunters. Subadult males, unlike subadult females, emigrate from their maternal home ranges (Pasitschniak-Arts and Messier 2000, Schwartz et al. 2003). This movement of subadult males also increases the likelihood they will encounter hunters. In Alaska, regulations prohibited shooting females accompanied by

cub or yearling offspring. We believe this regulation additionally protected many females accompanied by 2-year old offspring during spring seasons because many hunters were unwilling to shoot females accompanied by offspring of any age. This further contributed to hunter selectivity for males during spring. The regulation protecting females accompanied by cub and yearling offspring functionally protected adult females from hunter harvests during approximately 83% of open hunting periods; such females were typically vulnerable only during autumn following weaning of their 2 year-olds (assuming a new litter was born the following spring).

Harvest rates and kill density

We estimated harvest rates as: (1) the proportion of marked bears killed by hunters and (2) reported kills in a subunit divided by the estimated population of bears in the portion of the subunit open to hunting. Population sizes were estimated by stratified extrapolation from density estimation areas (Miller et al. 1997) to the surrounding area. In southcentral Alaska, we developed upper and lower bounds for estimated harvest rate by making conservative and liberal assumptions about whether marked bears that disappeared during hunting season but were not reported in the harvest had been killed. Only bears ≥ 2 years old were included in harvest rate calculations.

In Katmai and Black Lake, we estimated the cumulative number of marked bears available for harvest in each of 4 categories (adult males, adult females, subadult males, and subadult females) by applying annual survival rates to the number of bears originally marked. The harvest rate was calculated by dividing the cumulative number of marked-bear years into the number of marked bears killed by hunters through 1996.

Kill density was defined as the number of bears reported killed per 1,000 km². Kill density for male bears ≥ 5 years old was calculated based on the harvest data and the entire area in the harvest management area (Game Management Subunit). Surface area was not corrected for areas of unacceptable bear habitat such as high elevations or lakes, so kill density based on occupied bear habitat would be slightly higher than values we report here.

Population composition

Standard techniques for measuring population composition in bears are not available. All available techniques, short of a complete census, have biases. Because

male bears have larger home ranges and greater daily movements than females, and because most methods of measuring composition are based on knowledge of which bears were present in an area during a period, male abundance will be overestimated relative to female abundance.

We used 3 approaches to estimate population composition. For the first estimate, we inferred composition from the sex and age composition of harvested bears. A predominance of males in the harvest of a heavily hunted bear population should reduce the proportion of living males compared to a less exploited population (Fraser et al. 1982). This should be especially notable in older cohorts. Harvest data were examined for such indicators in Susitna and Black Lake.

For the second estimate, we collected empirical data on population composition during density estimation procedures in MidSu and UpSu using capture–mark–resight (CMR) techniques (Miller et al. 1997). The CMR technique requires a series of replicated searches (typically 1 search/day) of a defined search area using 3–4 fixed-wing aircraft (PA 18). Both previously radiomarked bears and unmarked bears were in the search area. When unmarked bears were observed they were captured and radiomarked. At the end of the density estimate we had a total number of individuals of known sex and age that had been in the study area at least once. However, some individuals were in the study area more than others. To correct for this bias we calculated composition by weighting each individual known to have been present on the study area during at least one replication by the proportion of replications during which radio telemetry indicated that individual was present.

For our last estimate, teams of pilots (all of whom were experienced bear guides) and biologists assigned unmarked bears in Black Lake and Katmai into recognizable categories: adult males, medium-sized bears of unknown sex, subadults, and family groups. We have no test of the accuracy of these assignments and acknowledge that they should be interpreted cautiously. We divided the number of adult males (marked + visually classified unmarked adult males) by the number of bears seen during CMR flights to estimate the percentage of adult males in Black Lake and Katmai. Additionally, we estimated composition from bears captured during the first 2 years in each study area. Estimation of population composition based on data collected during CMR density estimates was not possible in Black Lake and Katmai because of the higher bear density in these coastal study areas.

Population density

Population density in MidSu, UpSu, Denali, Katmai, and Black Lake was estimated using the maximum likelihood estimator and CMR procedures described by Miller et al. (1997). No method was available to test for significance of differences in density estimates obtained using this estimator, so comparisons were based on overlapping confidence intervals (G. White, Colorado State University, Ft. Collins, Colorado, USA, personal communication, 2003). Separate density estimates were calculated for independent bears (offspring accompanying adult females were excluded) and for all bears (including dependent offspring, Miller et al. 1997). Density was reported for Denali in units of independent bears by Keay (2001). Here we also estimated density for bears of all ages in Denali using methods of Miller et al. (1997) for comparison with densities reported in Scandinavia and southern Canada.

Survival estimates

Cub survivorship. Survival rate for cubs accompanying radiomarked females was based on periodic observations from aircraft to count cubs. In most cases cubs were not radiocollared.

Monitoring to determine initial litter size occurred during the first 3 weeks of May (1 flight/week, weather permitting) when females accompanied by neonatal young emerged from dens (Miller 1990*d*). Subsequently, monitoring to determine survivorship was less intense (0.5–2 flights/month). During the period of den entrance (late September and early October in GMU 13; mid October to early November on the Alaska Peninsula), more frequent monitoring was resumed to count cubs before den entrance. The date midway between the last time a cub was seen with its mother and the first time it was missing from the litter was used as the date of mortality.

Cub survivorship was calculated using the staggered entry Kaplan-Meier technique (Pollock et al. 1989). Annual survivorship was calculated from emergence from dens as newborns to emergence as yearlings the following spring. Mortality of an entire litter was assumed when a female bear with cubs died. In cases where we lost contact with radiomarked females accompanied by cubs (possible radio failures, destruction of transmitters by hunters, dispersal, or other causes), the cubs were treated as censored data (Pollock et al. 1989). Tests of differences in survival rate between areas were conducted using the log rank test (Pollock et al. 1989). To compare survivorships between Susitna and Denali, data for Susitna were

collapsed into 6 monthly categories (May–Oct) to match data from Denali.

In Susitna, data on first year cub survivorship was calculated for 2 seven-year periods (1980–86, 1990–96). Each of these periods included the 5-year period before our density estimates in the MidSu area (1985 and 1995), the year of the density estimate, and the following year. Cub survivorship was also calculated for the intervening period (1987–89) and for the entire period (1980–96).

For data from Susitna, a logit log-linear model (Agresti 1990) was used to determine if survivorship in a litter of bear cubs was explained by 3 variables: (1) period (1980–1986, 1990–1996), (2) female age (≤ 8 years old or ≥ 9 years old), or (3) litter size (1, 2, or ≥ 3 ; 199 cubs in 94 litters, range 1–4 (Miller 1997a). We considered female age a surrogate for maternal experience; 98% of 72 radiomarked females produced a litter by age 8. Eleven females were in the sample for each period; these were older and presumably better mothers during the second period. For both pairs of study areas, multinomial tests (Analytical Software 2000) were used to test hypotheses that the number of cubs dying during the breeding season (May–Jun) and the non-breeding season (Jul–Oct) was the same as expected based on the length of these periods.

In the Black Lake study area, hunting seasons were open during alternate regulatory years (fall of odd-numbered years and spring of the following year). This permitted evaluation of cub survival within the same area during years following open hunting and following years after hunting was closed.

Adult survivorship. Survivorship for bears ≥ 5 was calculated for radiomarked bears using the staggered entry Kaplan-Meier procedure (Pollock et al. 1989). When a radiomarked bear was tracked for a number of years, each year's data were treated as independent.

Age and reproductive parameters

We calculated observed mean age of first litter based on the age at which radiomarked nulliparous females were first observed with a litter. This underestimates actual mean age for females because of a bias against females that are late in producing their first litter or those that die prior to producing a litter (Garshelis et al. 1998). We corrected for this bias by assuming that females that had not produced a litter at an age greater than the mean age produced a litter in the year following their loss through mortality or signal loss. This procedure generated a mean age at first litter less biased by premature

loss of females producing a litter at older ages. Litter size was calculated based on first observation out of the den. Because of small numbers of litters with 4 cubs, litters of 3 and 4 cubs were combined for χ^2 tests of independence. We also calculated the proportion of litters losing all cubs and the proportion of those losing some cubs that lost all cubs.

For the Alaska Peninsula studies, mean age was calculated based on age of captured bears. For studies in Susitna, mean age was based on marked bears present in the density estimation area during the density estimation study.

Biomass

For Alaska Peninsula studies, biomass was calculated separately for adult males, adult females, subadult males, subadult females, yearlings, and cubs based on mean weight at capture in mid-May–mid-June. For cubs and yearlings, we supplemented our limited data with weights reported by Glenn (1980) from captures in June. Mean weights were multiplied by the density of individuals in each category. Density of each sex and age group was calculated based on proportion in the population as estimated from population composition information described above. Biomass for UpSu in 1979 was previously reported as 1.3 kg/km² based on captures during May–early June (Miller and Ballard 1982). In Denali, bears were captured and weighed during May as well as September (Keay 2001); only May data were used to compare with weights from Susitna. In all study areas, we used a spring scale suspended from a helicopter or the helicopter's integrated digital scale to weigh large bears and a hand-held spring scale to weigh small bears. We used 2-way analysis of variance to evaluate the importance of location (coastal or interior) and treatment (hunted or unhunted) for captured and weighed female bears ≥ 5 years old (Analytical Software 2000).

Identity of infanticidal bears

Few attacks on litters have been observed, and the sex or residency status of the attacker is rarely known. In data presented here, we supplemented the data from McLellan (1994) for several protected and hunted populations in Alaska. We included nonlethal attacks that resulted in injury to dependent offspring or permanent separation of cubs that likely led to their deaths. Protected populations were at McNeil River State Game Sanctuary, Katmai, and Denali and included data reported by Glenn et al. (1976), Dean et al. (1986), Olson (1993), and Hessing and Aumiller (1994), plus more recent cases witnessed

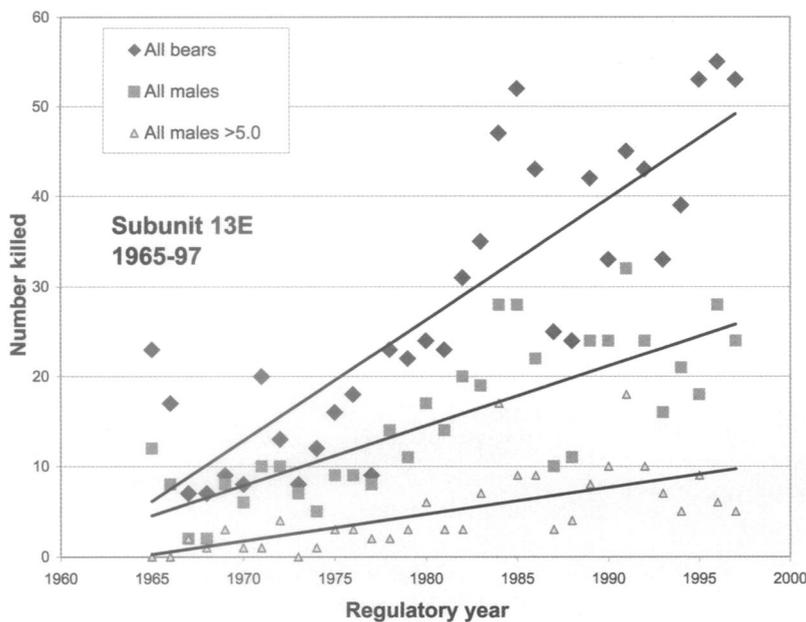


Fig. 3. Trends in brown bear harvests in south-central Alaska's Game Management Subunit 13E, 1965-97.

by agency personnel or documented during radiotelemetry flights in Katmai and Black Lake.

Results

South-central Alaska studies: changes in population composition in Subunit 13E

Inferences from harvest data. Numbers of bears harvested in Subunit 13E (including MidSu and UpSu) trended upward during 1965-97 (Fig. 3). Years of maximum harvest were 1982-86 and 1995-96, when the bag limit was 1 per year instead of 1 per 4 years (Fig. 3). During 1965-97, significant increases in kills occurred for all bears ($F = 78.9$; $\beta = 1.3$; 1, 31 df; $P < 0.001$), for males of all ages ($F = 48.3$; $\beta = 0.6$; 1, 31 df; $P < 0.001$), and for males ≥ 5 years old ($F = 22.2$; $\beta = 0.3$; 1, 31 df; $P < 0.001$; Fig. 3). The rate of increase in harvest during our study period was less dramatic; this suggested a preexisting harvest impact on bear abundance. During 1979-97, the kill of all bears increased ($F = 12.1$; $\beta = 1.3$; 1, 17 df; $P = 0.003$). Positive slopes occurred as well, for kills of males ≥ 5 years old and for kills of males of all ages, but these were not significant ($F = 0.6$; $\beta = 0.14$; 1, 17 df; $P = 0.46$ and $F = 2.7$; $\beta = 0.4$; 1, 17 df; $P = 0.12$, respectively).

A total of 912 bears of known sex and age were reported killed in Subunit 13E during 1965-97. Of

these, 55% were males. Males constituted 57% of 592 bears < 5 years old in the harvest and 51% of 321 bears ≥ 5 years old (Fig. 4). Males constituted 39-67% of the annual harvest (3-year running averages, Fig. 4). The sharp decline in the proportion males in the hunter kill of bears ≥ 5 years old during the early 1990s (Fig. 4) was consistent with an interpretation that adult males were less abundant in the population of adult bears than previously. This interpretation was consistent with data on population composition (see following section) that indicated reductions in abundance of adult males.

Harvest rate of marked males (17% based on 194 marked bear-years) was also higher than for marked females (8% based on 441 marked bear-years) during 1980-95 ($\chi^2 = 8.9$, $P = 0.003$). For both sexes combined, harvest rate of marked bears was 10.8%; this value is biased toward females because more

females were radiomarked than males. In Subunit 13E, harvest rate was calculated as 22% (possible range = 15-40%) based on known kills and the range of population estimates (Miller 1992, 1993b). Over the 16-year study in Subunit 13E, adult male kill density was 0.54 males ≥ 5 years old killed/year/1,000 km².

The harvest of more males than females did not reflect differences in sex ratio at birth. Sex ratio at exit from dens was not different from 50:50 for 19 male and 16 female neonatal cubs handled between 6 May and 5 June during 1979-93 ($\chi^2 = 0.61$, $P = 0.43$; Miller 1997a).

Measured changes in population composition. There were fewer males in the population of bears using MidSu during the 1995 density estimate than during the 1985 density estimate ($\chi^2 = 14.1$, $P < 0.001$; Table 1). There were also fewer older males (≥ 5 years old) in 1995 than in 1985 ($\chi^2 = 4.83$, $P = 0.02$; Table 1). Sex ratio for bears ≥ 5 years old at time of first capture was 70 males:100 females during 1980-85 ($n = 34$ bears captured) and 43 males:100 females during 1993-95 ($n = 30$ bears). This difference was not significant ($\chi^2 = 0.86$, $P = 0.35$).

Between 1985 and 1995, there were no significant differences in mean age of females present at least once in the density estimation area for females ≥ 2 (Wilcoxon rank sum test, $P = 0.81$) or for females ≥ 5 ($P = 0.86$).

Similarly, there were no significant differences in mean age of independent males ($P = 0.46$) or for males ≥ 5 ($P = 1.0$; Table 1).

South-central Alaska studies: Temporal changes in cub survivorship

The Susitna survival rate of cubs was similar during 1980–86 (0.67, 95% CI = 0.55–0.79) and 1990–96 (0.64, 95% CI = 0.52–0.77) ($\chi^2 = 0.08$, 1 df, $P = 0.78$; Table 2). Overall, mean cub survival 1980–96 was 0.67 (95% CI = 0.60–0.75, Table 2). Approximately half of the litters experienced no losses during both earlier and later periods (Table 2). There was also no change in the frequency of whole litter loss between periods ($\chi^2 = 0.02$, $P = 0.87$; Table 2). Over the whole study period, 28% of cub litters observed were completely lost between den exit and den entrance the following fall (Table 2).

None of the factors examined in the logit log-linear model influenced cub survivorship. Cub survivorship was not correlated with period ($\chi^2 = 0.08$, $P = 0.78$), female age ($\chi^2 = 0.03$, $P = 0.79$), or litter size ($\chi^2 = 0.96$, $P = 0.62$).

South-central Alaska studies: Spatial comparisons of cub survival rates

In hunted Susitna, cub survivorship was almost twice that in nearby un hunted Denali ($\chi^2 = 20.58$, 1 df, $P < 0.001$; Table 3). In Susitna, adult male survival and, by 1995, proportion of males in the adult population, was lower than in Denali (Table 3).

The rate of loss of entire litters was higher in un hunted Denali than in the hunted population in Susitna (Table 3; $\chi^2 = 12.2$, 1 df, $P < 0.001$). However, the proportion of litters experiencing loss of ≥ 1 cub where the entire litter was ultimately lost was higher in hunted Susitna (Table 3; $\chi^2 = 7.7$, 1 df, $P = 0.006$).

Alaska Peninsula studies: Changes in population composition

Inferences from harvest data. During 1987–96, guided nonresident hunters killed 72% of brown bears taken in Subunit 9E ($n = 1,520$), which encompasses the Black Lake study area; resident hunters killed 28%. Males composed 66% of the total harvest and 74% of



Fig. 4. Percent males in harvests of brown bears aged <5 years old and ≥ 5 years old in Alaska's Subunit 13E, 1967–2001 (3-year running average).

harvested bears ≥ 5 years old. Forty-nine percent of all males in the harvest were ≥ 5 years old, and these males averaged 11 years old. Sellers (1998) estimated a population of 3,200 brown bears in areas of Subunit 9E open to hunting. Based on this estimate, the overall annual harvest rate (known kills plus estimated unreported kills) was 5.0% during 1987–96.

Harvest rates of marked bears in Black Lake also indicated a hunter bias toward males. By 1999, 31% of all males marked in 1988–92 ($n = 35$) were taken by hunters compared to only 15% of females ($n = 45$). Minimum annual harvest rates of marked bears during 1988–92 were 9% for adult males and 2% for adult females. Including subadult bears, the harvest rates were 9% for males and 4% for females.

In contrast, only 2 bears marked in Katmai were killed by hunters during 1989–2000. Both of these were adult males killed outside the park boundary, at least 85 km south of their capture locations. Forty-eight adult males were marked throughout the entire study in Katmai, including bears originally marked when they were <5 years old that became ≥ 5 during the study. Based on radiotracking data, we estimated an annual survival rate for adult males in Katmai of 0.96 (95% CI = 0.72–1.0). Using this survival rate, we estimated a total of 225 marked adult male bear-years were available during 1989–96. This estimate and the kill of 2 adult males were used to calculate an annual harvest

Table 1. Temporal changes in brown bear populations in the Middle Susitna (MidSu) study area of southcentral Alaska during a period of increasing hunting pressure between 1985 and 1995 based on independent bears (excludes offspring still with their mothers).

	1985	1995
Replications in density and composition estimate	7	5
Density of independent bears, both sexes/1,000 km ² (95% CI)	18.8 (15.2–24.3)	23.3 (19.3–30.1)
Density of independent males/1,000 km ² (95% CI)	9.3 (7.0–14.4)	3.6 (2.4–14.7)
Independent bears		
Males	14	5
Females	17	20
Males (%)	45.2 ^a	20.0 ^a
Males ≥5 years old	10	4
Females ≥5 years old	13	14
Males (%) among bears ≥5 years old	43.5 ^a	22.2 ^a
Weighted number of independent bears		
Males	7.6	3.0
Females	10.9	14.6
Males (%)	41.1 ^a	17.1 ^a
Males ≥5 years old	5.0	2.6
Females ≥5 years old	8.3	10.2
Males (%) among bears ≥5 years old	37.6 ^a	20.3 ^a
Male survivorship based on radiomarked bears ≥2 years old (95%CI)	0.82 (0.6–0.95, <i>n</i> = 7 deaths during 1980–85)	0.71 (0.38–1.0, <i>n</i> = 2 deaths during 1991–95)
Female survivorship based on radiomarked bears ≥2 years old (95%CI)	0.90 (0.84–0.96, <i>n</i> = 9 deaths during 1980–85)	0.90 (0.85–0.97, <i>n</i> = 3 deaths during 1991–95)
Median age		
Independent males	9.2 (9)	11.0 (8)
Males ≥5 years old	12.4 (10)	12.4 (8)
Independent females	10.1 (8)	11.6 (8)
Females ≥5 years old	10.7 (15)	15.1 (12)

^aSignificant difference between 1985 and 1995 ($P < 0.05$).

rate for adult males of 0.9% in Katmai. Overall, 4% of all males marked at Katmai were killed by hunters by 2000, which was significantly fewer ($\chi^2 = 11.3$, $P = 0.001$) than at Black Lake. The harvest rate for all other marked cohorts at Katmai was 0% (315 adult female bear-years, 38 subadult male bear-years, and 25 subadult female bear-years). We inferred that the male-biased harvest in Black Lake resulted in fewer adult males in the Black Lake population than in the Katmai population.

Measured changes in population composition. During CMR density estimation flights, adult males made up a higher percentage of all bears seen in Katmai (20.0%, $n = 456$) than at Black Lake (10.9%, $n = 607$; $\chi^2 = 17.06$, $P < 0.001$). The sex ratio of bears captured during 1989–90 in Katmai (including uncaptured companions of consorting pairs) was 79 adult males:100 adult females compared to 39 adult males:100 adult females at Black Lake ($\chi^2 = 3.32$, $P = 0.07$). The sex ratios of captured subadult bears did not differ between the 2 areas: 122 males:100 females ($n = 38$) at

Katmai and 127 males:100 females ($n = 36$) at Black Lake ($\chi^2 = 0.06$, $P = 0.8$).

There were proportionally more subadults at Black Lake than at Katmai. Subadults made up a significantly smaller percent of all bears ≥2 years old in the capture sample from Katmai (16%) than Black Lake (44%; $\chi^2 = 14.95$, $P < 0.001$). Subadult males comprised 20% of all males ≥2 years old captured at Katmai, compared to 58% at Black Lake ($\chi^2 = 11.92$, $P = 0.001$). Subadult females comprised 12% of all females captured at Katmai, compared to 33% at Black Lake ($\chi^2 = 4.85$, $P = 0.03$).

The mean age of adult males at Katmai was 10.7 years ($n = 28$) and was 9.7 at Black Lake ($n = 15$; Wilcoxon Rank Sum, $P = 0.65$). The mean ages of adult females were 10.8 and 12.6 at Katmai and Black Lake, respectively (Wilcoxon Rank Sum, $P = 0.13$).

Alaska Peninsula studies: Spatial differences in cub survivorship

In the hunted brown bear population at Black Lake, cub survivorship was significantly higher ($\chi^2 = 7.7$, 1 df,

Table 2. Temporal comparisons of cub survivorships and litter loss (percent) in Alaska's Middle and Upper Susitna (MidSu and UpSu) study areas during periods of increasing hunting pressure (95% CI, n = number of cubs accompanying radiomarked females). Rates calculated from den exit as newborn cubs until den entrance the following fall.

	1980–86 (moderate hunting)	1990–96 (heavy hunting)	1980–96 ^a
Individual cub survivorship	0.67 (0.55–0.79, n = 64)	0.64 (0.53–0.77, n = 63)	0.67 (0.60–0.74, n = 167)
Litters without mortality	52.1% (n = 13)	51.9% (n = 14)	48.7% (n = 37)
Partial litter loss	24.0% (n = 6)	25.9% (n = 7)	23.7% (n = 18)
Whole litter loss	24.0% (n = 6)	22.2% (n = 6)	27.6% (n = 21)

^aIncludes 1987–89, not included in the previous columns.

$P = 0.006$) than in the un hunted population at Katmai (Table 4). Bear density and biomass was lower at Black Lake than in Katmai (Table 4). Biomass at Black Lake was about 19 times higher than in Susitna (1.3 kg/km², Miller and Ballard 1982). The limited data based on radiomarked males were consistent with an interpretation that adult male survivorship was lower in the hunted population at Black Lake than at Katmai (Table 4), but small sample sizes of marked males precluded detecting a significant difference ($\chi^2 = 0.08$, 1 df, $P = 0.78$).

The rate of loss of entire litters was higher in Katmai than Black Lake (Table 4; $\chi^2 = 4.8$, 1 df, $P = 0.02$). Unlike our Susitna studies, the proportion of litters experiencing loss of >1 cub that were completely lost was higher in un hunted Katmai than in Black Lake (Table 4; $\chi^2 = 9.6$, 1 df, $P = 0.002$).

Alaska Peninsula studies: Temporal differences in cub survivorship

On the Alaska Peninsula, cub survival rates were compared following seasons when bear hunting was open and closed during the preceding spring and autumn. In the Black Lake study area during 1988–95, survivorship of cubs accompanying radiomarked females (to den entrance) was 0.60 (95% CI = 0.44–0.67) following open hunting seasons. Following closed hunting seasons, cub survivorship was 0.65 (95% CI: 0.51–0.79). These differences were not significant ($\chi^2 = 0.03$, 1 df, $P = 0.86$). Similar comparisons for cub survivorship data only during the period from den emergence through June 30 (the primary breeding season) were also not significant ($\chi^2 = 0.63$, 1 df, $P = 0.43$).

Additional comparisons

Density and kill density. Based on overlapping 95% confidence intervals, bear density in MidSu was not different between 1985 and 1995 (Table 1). In spite of intensive harvests, during 1980–1997 population growth (λ) calculated from survivorship and reproduc-

tive data from radiomarked bears was 1.02. Measured density of independent males was not significantly different between 1985 and 1995 (Table 1). Both measurements of density had large confidence intervals (Table 1). Preliminary results based on surveys conducted in 2003 suggest that bear populations may have declined in GMU 13 since our Susitna studies ended in 1997 (E. Becker, Alaska Department of Fish and Game, Anchorage, Alaska, personal communication 2003).

Based on non-overlapping confidence intervals, independent bear density was higher in Denali than in MidSu (Table 3). Bear density was higher in Katmai than at Black Lake (Table 4).

In Subunit 13E (which includes our Susitna study areas), average annual adult kill density was 0.54 males and 0.45 females per 1,000 km². Kill density in 13E (1961–91) was higher than in any other management area in interior Alaska (Miller 1993b).

We know of no bears killed within the Denali and Katmai study areas during our studies. Annual adult male kill density at Black Lake was 3.1/1,000 km² (annual range 2.1–3.7). Adult female kill density at Black Lake was 1.1/1,000 km² (annual range 0.9–1.3). Reflecting the higher bear density at Black Lake, adult male kill density was about 6 times higher and adult female kill density about double that in Subunit 13E.

Bear body mass. In both Susitna and the Alaska Peninsula samples, bears were heavier in the hunted populations than in the nearby un hunted population. Mean weights for adult females were about a third higher in the hunted populations in Susitna than in the un hunted Denali population (Table 3). Similarly, mean adult female weights were about 20% higher in the hunted Black Lake population than in the un hunted Katmai population (Table 4). Two-way analysis of variance on weight of females ≥ 5 years old revealed that the most significant determinant of weight was whether bears were coastal or interior ($F = 561$; 3,157 df; $P < 0.001$) followed by whether they were in a hunted area ($F = 170$; 3,157 df; $P < 0.001$). The

Table 3. Demographic comparisons between a heavily hunted brown bear population in south-central Alaska (Susitna study areas in Subunit 13E), 1980–97, and an un hunted population in nearby Denali National Park and Preserve, 1991–98.

Parameter	Susitna		Denali National Park	
	Value	<i>n</i>	Value	<i>n</i>
Cub survival (95% CI)	0.67 (0.60–0.75)	167	0.34 (0.24–0.44)	88
Adult (≥5 yr) female survival (1980–95) (95% CI)	0.92 ^a (0.68–0.92) ^a	257 ^b	0.97	125 ^b
Adult (≥5 yr) male survival (1980–95) (95% CI)	0.80 ^a (0.68–0.92) ^a	63 ^a	0.98 (0.95–1.0)	59 ^b
Males (%) among bears ≥5 yr old	35 (1985) 21 (1995)	—	36	—
Litters lost (%)	26	74	59	41
Litters (%) losing ≥1 cub that lose all cubs	50	38	17	29
Density (independent bears/1000 km ²) in 1985 (95% CI)	18.8 (spring) (15.2–24.3)	—	—	—
Density (independent bears/1000 km ²) in 1995 (95% CI)	23.3 (spring) (19.3–30.1)	—	34.7 (fall) (32.2–38.7)	—
Mass (in spring) of females (kg) ≥5 yr old	133	50	98	65
SD	17.9	—	13.7	—
Mean age of independent males	9.2 (1985) 11.0 (1995)	14 (1985) 5 (1995)	9.5	21
Mean age at weaning ^c	2.1 ^d	54	2.9 ^d	19
Mean age at first litter ^c	5.6 ^d	37	10.3 ^d	15

^aData from 1980–95.^bBear-years.^cCalculated based on age in whole numbers (2.5 yrs-old = 2).^dData from Miller (1997a).

interaction term between area and hunting was not significant ($F = 0.19$; 1 df; $P = 0.67$). Mean age of the adult female bears weighed in each area was 15.3 years in Denali ($n = 65$), 14.1 in Black Lake ($n = 34$), 12.8 in Katmai ($n = 11$), and 12.5 in Susitna ($n = 50$). Ages of weighed adult female bears did not differ among the 4 areas (Kruskal-Wallis one-way analysis of variance = 5.3; 3, 157 df; $P = 0.15$).

Cub survivorship in Denali and Katmai. Bears in Katmai rely on salmon consumption to maintain high densities while diets of Denali bears do not include salmon. Regardless, cub survivorship did not differ between these 2 un hunted populations (0.34; Tables 3 and 4).

Timing of cub mortality. In Katmai, 62% of the cubs lost ($n = 50$) were lost during breeding season compared to 35% at Black Lake ($n = 37$ cubs lost). In Denali, 54% of cubs lost ($n = 58$) were lost during breeding season compared to 67% ($n = 51$ cubs lost) in Susitna. Based on expected values calculated from the length of these periods, these differences were significant at Katmai ($\chi^2 = 18.5$, $P < 0.001$), Denali ($\chi^2 = 10.6$, $P = 0.001$), and Susitna ($\chi^2 = 25.5$, $P < 0.001$), but not at Black Lake ($\chi^2 = 0.05$, $P = 0.8$).

Litter sizes. The distribution of litter sizes differed between Black Lake and Katmai ($\chi^2 = 11.3$, 2 df, $P = 0.003$). Mean litter size at emergence from dens was smaller in Katmai than at Black Lake (Wilcoxon rank sum test, $P < 0.001$; Table 5).

Mean litter size at emergence from dens was 2.1 in both un hunted Denali and in heavily hunted Susitna (Wilcoxon rank sum, $P = 0.47$), and the distribution of litter sizes was not different ($\chi^2 = 1.75$, 2 df, $P = 0.41$; Table 5). The distribution of litter sizes in Susitna differed between early in the period of heavy hunting (1980–86) and later (1990–96; $\chi^2 = 6.9$, 2 df, $P = 0.03$). This resulted from decreased proportion of litters of 2 cubs and increased proportion of litters of 3 cubs later in the period of heavy hunting. There was a significant difference between numbers of litters ≤2 cubs and litters of ≥3 cubs between 1980–86 and 1990–96 ($\chi^2 = 6.32$, 1 df, $P = 0.01$). However, mean litter sizes were not significantly different between these periods (Wilcoxon rank sum test, $P = 0.12$).

Bears attacking family groups. Cases from hunted populations on the Alaska Peninsula and Kodiak Island include published accounts by Troyer and Hensel (1962), observations made during radio-telemetry flights

Table 4. Demographic comparisons on the Alaska Peninsula between a moderately hunted brown bear population at Black Lake and an un hunted population in Katmai National Park and Preserve.

Parameter	Black Lake (1988–96)		Katmai (1989–96)	
	Value	<i>n</i>	Value	<i>n</i>
Cub survival (95% CI)	0.57 (0.48–0.67)	107	0.34 (0.26–0.42)	99
Adult (≥5 yr) female survival (1980–95) (95% CI)	0.90 (0.86–1.00)	229 ^a	0.91 0.87–0.95	210 ^a
Adult (≥5 yr) male survival (1980–95) (95% CI)	0.75 (0.33–1.00)	9 ^a	0.96 (0.72–1.0)	25 ^a
Males (%) among bears ≥5 yr old	28 ^b	—	43 ^b	—
Adult males (%) among all bears	11 ^c	456 ^c	20 ^c	607 ^c
Litters lost (%)	14	37	35	43
Litters (%) losing ≥1 cub that lose all cubs ^d	24	21	69	26
Density (independent bears/1000 km ²) (95% CI)	122 ^e (108–139)	—	412 ^e (325–545)	—
Mass (in spring) of females (kg) ≥5 yr old	200 ^f	34	162	12
SD	34.7	—	31.8	—
Bear biomass (kg/km ²)	24	—	82	—
Mean age of independent males	6.9	32	9.2	35
Mean age at weaning ^g	2.4	33	2.7	25
Mean age at first litter ^g	6.3	8	7.2	12

^aBear-years.^bBased on sample of bears captured.^cBased on aerial classification of bears observed during capture–mark–resight survey flights.^dExcludes litters lost when mother died.^eData from Miller (1997a).^fIncludes 4 males weighed during this study and 21 weighed by L. Glenn (Alaska Department of Fish and Game, Anchorage, Alaska, USA, unpublished data collected at Black Lake during 1970–77).^gCalculated based on age in whole numbers (2.5 yrs-old = 2).

and accounts by experienced hunting guides. In total, 19 attacks were documented, and in all cases the attackers were adult males. In 8 cases the age of the males involved was known and averaged 9.4 years (range 5–15). Most documented attacks in hunted areas occurred during the breeding season, but this may reflect the large number of hunting guides in the field during the spring bear season. In only 1 case was the killer known, and this was a 14-year-old resident male bear.

In un hunted areas on the Alaska Peninsula, adult males were identified as the attackers in all 4 cases that occurred during the breeding season. Because most eyewitness accounts occur when bears are congregated at Brooks River in Katmai and McNeil River during the peak of salmon availability, the timing of these incidents is biased toward mid- to late-summer. Adult males were identified either directly or by circumstantial evidence to have been the attacker in 10 of the 13 cases where the identity of the killer was known. Adult females were the attackers in the other cases (Hessing and Aumiller 1994). In at least 8 adult male cases, the perpetrator was classified by observers to be a resident based on his presence during previous years.

Discussion

Information on population regulation mechanisms in bears is difficult to obtain, and it is not surprising that information gaps are sometimes filled by inference and speculation. Comparisons between study areas may be confounded by habitat differences that are poorly documented or understood. Comparisons within an area subjected to different treatments over time may be confounded by small sample sizes that yield estimates with low precision or biased key parameters.

Further, it is difficult to obtain unbiased data on population composition. Carrying capacity as well as vital rates for bears may vary stochastically between years and this variability may confound studies of density dependence. Our studies in Alaska are not immune to these problems but are nevertheless instructive regarding effects of hunting on hypothesized changes in vital rates of bears. We summarize key characteristics of our 4 Alaska study areas in Table 6.

Our studies in Alaska do not support earlier suggestions that hunting biased toward male brown bears increased cub survivorship. Similarly, other reviews (Miller 1990b, Derocher and Taylor 1994,

Garshelis 1994, McLellan 1994, Taylor 1994) found inconclusive evidence for such compensatory effects.

Our studies included spatial comparisons between hunted areas and unhunted areas. We also made temporal comparisons of cub survivorship within a period of increased harvests during which male abundance declined in a portion of interior Alaska. For a portion of coastal Alaska, we also contrasted cub survivorship following years in which hunting was open and closed. We examined both low density interior populations and high density coastal populations where salmon was a significant component of diets. Cub survivorship was higher in the hunted Alaskan populations than in the unhunted populations. This finding is consistent with a decline in cub survivorship in bear populations living near carrying capacity in unhunted parks compared to populations in similar habitats with hunting-induced reductions in density to levels below carrying capacity.

We found no differences in cub litter sizes between hunted and nearby unhunted areas in southcentral Alaska (Denali and Susitna). In contrast, on the Alaska Peninsula, litter sizes were larger in a hunted area (Black Lake) than in nearby, unhunted Katmai National Park.

In Susitna, with increasing hunter harvest and a declining proportion of adult males in the population, we found no significant differences between mean cub litter sizes early and late in the period of increased hunting. However, we did find a significant increase in the proportion of 3-cub litters and decline in proportion of 2 cub litters later in the period of intense hunting compared to the earlier period. Although we do not conclude this, our litter size data from Susitna were more consistent with an increase in litter size correlated with hunting rather than with a decline, as would be expected from the hypothesis advanced by Wielgus and Bunnell (2000). Wielgus and Bunnell (2000) and Wielgus et al. (2001) were careful to clarify that their conclusions might apply only to very small populations at the edge of the species' range.

Our results from Alaska differed from the predictions of Swenson et al. (2001b) and Swenson (2003) in Scandinavia and Wielgus and Bunnell (2000) in Canada. Although these authors proposed different mechanisms for their findings, both of these studies concluded that removal of males through hunting had negative effects on brown bear populations. The disparity between their results and ours merit an examination of their studies and the factors that may help explain our different conclusions.

Table 5. Litter sizes for litters of newborn cubs in south-central and coastal study areas in Alaska. Litter size is based on first observation subsequent to emergence from dens. Data for Denali from Keay (2001 and unpublished data).

Study area	Number of litters				Mean litter size
	1 cub	2 cubs	3 cubs	4 cubs	
Black Lake	4	14	26	2	2.57
Katmai	11	26	14	0	2.06
Susitna (1980–86)	8	26	4	1	1.95
Susitna (1990–96)	7	14	13	0	2.18
Susitna (1980–96) ¹	17	50	23	1	2.09
Denali	5	28	9	0	2.1

¹Includes data from 1987–89 not included in other rows.

Comparisons between Alaskan, Scandinavian, and Canadian studies

Proportion males removed in Scandinavian studies. The rate of male removal in the hunted areas in Susitna in Alaska was approximately twice that in Scandinavia. In hunted southern Scandinavia, 11 adult males were killed during the 12-year period ($\bar{x} = 0.92/\text{year}$, range 0–4; Swenson et al. 2001b). Based on an average size (4,108 km²) of cub areas as defined by Swenson et al. (2001b), approximately 0.22 adult males were killed annually per 1,000 km² of cub area. Adult male kill density in Subunit13E was 0.54/1,000 km².

Density for bears of all ages was similar in the hunted Susitna area and in the hunted area in southern Scandinavia. In southern Scandinavian, density varied between 8 and 20 bears of all ages/1,000 km² (J. Swenson, Norwegian Institute for Nature Research, Trondheim, Norway, personal communication, 2003) based on methods described by Swenson et al. (1994). In Susitna, density was 27 bears of all ages/1,000 km² in the MidSu area (in 1985) and 11 bears of all ages/1,000 km² in the UpSu area (Miller et al. 1997).

Swenson et al. (2001b) estimated that a 20% kill of adult males in southern Scandinavian resulted in their reduced cub survival. This was not an annual rate but a rate “for the years in which adult males died” (Swenson 2001b:76). In Susitna, we estimated a 17% annual harvest of males based on marked males of all ages.

These comparisons suggested that a decrease in cub survivorship from adult male removal by hunters similar to that suggested by Swenson et al. (2001b) should have been evident in our hunted area in Susitna in south-central Alaska. Because we did not detect this effect, we

Table 6. Summary of characteristics of Alaska study areas. K represents carrying capacity.

Southcentral Alaska	Alaska Peninsula
Hunted populations	
Susitna	Black Lake
Studied 1980–97	Studied 1988–96
Heavy harvest approximately 9.5%	Moderate harvest, approximately 5%
Declining proportion males in population	Proportion males prob- ably stable
Population below K	Population below K
Density (all bears, UpSu & MidSu, respectively) = 10.7–27.1/1,000 km ²	Density (all bears) = 191/1,000 km ²
Unhunted populations	
Denali National Park	Katmai National Park
Studied 1991–98	Studied 1989–96
Human kill negligible	Human kill negligible
Population at K	Population at K
Density (all bears) = 37.1/1,000 km ²	Density (all bears) = 551/1,000 km ²

conclude that the conclusions of Swenson et al. (2001b) are not generally applicable.

More recently, Swenson (2003) reported on a management experiment in Sweden during which large numbers of male bears were killed by hunters. This experiment was conducted on a rapidly growing population believed to be below carrying capacity. A dramatic 35-fold increase in annual adult male mortality and a 6-fold increase in annual mortality to all bears resulted in a reported doubling of cub mortality (Swenson 2003). This experiment was similar in design to our temporal MidSu comparisons but yielded different results with a much higher degree of male reduction in the Swedish study.

Proportion males removed in Kananaskis and Selkirk studies. In southern Canada, bear density (all ages) was reported as 16.1/1,000 km² in Kananaskis area of southwestern Alberta and 16.8/1,000 km² in the Selkirks of British Columbia, northern Idaho and northeastern Washington (Wielgus and Bunnell 2000). Density was calculated based on home range overlap techniques for 5 radiocollared adult bears in Kananaskis and 9 in the Selkirks (Wielgus and Bunnell 2000). In the 6,300-km² Kananaskis study area, 5 male bears were reported shot during 1980–84, an average of 1/year for an annual adult male kill density of approximately 0.16 adult males/1,000 km², about the same as in southern Scandinavia. Based on the (probably generous) assumption that a quarter of the pop-

ulation density was adult male, we calculated an annual adult male removal rate in Kananaskis of approximately 4%. This calculated removal rate was less than for Scandinavia and Susitna. These rough calculations suggested that any compensatory effect from male removal in Kananaskis should also have been evident in southcentral Alaska, if the pattern suggested by Wielgus and Bunnell (2000) was a general consequence of male-biased hunting.

Alaska Peninsula comparisons. Bear densities in our hunted and unhunted areas in Susitna and Denali were similar to densities in Scandinavia and southern Canada. Density for bears of all ages for the Denali study area was 37.1/1,000 km² (95% CI = 34.4–41.1). Densities in both hunted and unhunted areas on the Alaska Peninsula were much higher: 191/1,000 km² at Black Lake and 551/1,000 km² at Katmai (Miller et al. 1997; these density estimates vary from Tables 3 and 4 because they include bears of all ages). The high density in our Alaska Peninsula areas probably reflects more abundant food, notably salmon, in coastal Alaska compared to interior areas (Miller et al. 1997). This conclusion was also indicated by the heavier weight of adults in the coastal study areas (Glenn 1980) compared to the interior Alaska (Hilderbrand et al. 1999).

Katmai has the highest density currently documented for a brown bear population (Miller et al. 1997). The annual harvest rate for adult males at Black Lake ($\geq 9\%$, roughly) was lower than Susitna and the Scandinavian studies (Swenson et al. 2001b) but higher than southern Canada (Wielgus and Bunnell 2000).

Proximity to carrying capacity in Alaskan, Canadian, and Scandinavian studies

Proximity to carrying capacity in our studies was inferred. Our inferences were supported by the higher densities, higher biomass, lower mortality, and lower bear weights in the national park populations.

We lack data on bear habitat quality that could suggest that differences in bear weights were caused solely or primarily by availability or quality of bear foods. However, we believe a more persuasive case can be made that differences in density and biomass of the bears reflecting proximity to carrying capacity is a more parsimonious explanation for the weight differences. We believe the relatively low cub survivorships in Katmai and Denali compared to hunted populations in Black Lake and Susitna, respectively, resulted because the populations in the unhunted parks were at carrying capacity. It is accepted ecological theory that at carrying capacity, density dependent competition for food and

intraspecific predation would be expected to increase mortality rates for dependent offspring and subadults, decrease reproductive rates, or both (Andrewartha and Birch 1954; Caughley 1966, 1977).

Cub survivorships in hunted populations thought to be below carrying capacity in southern Scandinavia (Swenson et al. 2001*b*), central Alaska, and the Alaska Peninsula were remarkably similar (0.65, 0.67, and 0.57, respectively). Cub survivorship in the northern Scandinavian population (0.96) was the highest ever reported and occurred in a very low density population (16.4 bears/1,000 km², J. Swenson personal communication, 2003). Swenson et al. (2001*b*) and Sæther et al. (1998) thought both Scandinavian populations were below carrying capacity. The characteristics of the northern Scandinavian population described by Swenson et al. (2001*b*) appear to be rare (unhunted but below carrying capacity and surrounded by a hunted population producing few emigrants).

We offer no explanation for the high cub survivorship observed in the northern study area in Scandinavia (Swenson et al. 2001*b*). However, we suggest that circumstances described for this area indicate it was atypical for naturally-occurring brown bear populations. If so, this would make the northern Scandinavian area an inappropriate model from which to draw general conclusions about bear demographics.

Sample size constraints

The southern Canada study (Wielgus and Bunnell 2000) was constrained by small sample sizes. This study claimed hunting of adult males caused females to avoid preferred foraging habitats, resulting in reduced litter sizes (Wielgus and Bunnell 2000). Litter size ($\bar{x} = 1.4$, $SE = 0.24$) for marked females in the hunted Kananaskis area of southwestern Alberta came from 5 litters over a 4-year period. In the Selkirk area, mean litter size ($\bar{x} = 2.2$, $SE = 0.13$) was based on 10 litters observed during a 6-year period (Wielgus and Bunnell 2000). The mean litter size in Kananaskis was the smallest reported for brown bears in North America and was based on the smallest sample size. This, along with the absence of differences in other vital rates, suggested that the reported low mean litter size for Kananaskis should be interpreted cautiously. Vital rates for adult females during the period of hunting in Kananaskis were based on monitoring only 5 female bears for a total of 11 adult female bear-years (Wielgus and Bunnell 1995: Table 3).

SSI in Scandinavia and Alaska

In Scandinavia, available data indicated that infanticidal males were not fathers of the cubs they killed (E. Bellemain et al. unpublished data cited by Swenson 2003). The ability of a male to recognize females with whom he may have fathered cubs and to forego infanticide on such cubs would clearly be advantageous. Realization of this benefit by males does not require removal of males and resulting increases in SSI.

Swenson et al. (1997, 2001*b*:69) originally reported that the decreased cub survivorship he reported was caused by immigrating males: "We suggest that immigrating males kill cubs, as predicted by the sexually selected infanticide hypothesis." More recently, Swenson (2003) indicated that resident adult males kill most of these cubs, and noted: "... SSI increases the fitness of a resident male as much, or more, than an immigrating male, and nothing in the SSI hypothesis requires that the species be territorial or social."

Our observations agree with the more recent view by Swenson (2003); immigrant males need not be invoked to explain infanticide in bears. Resident male bears were infanticidal in 2 cases documented during the breeding season on the Alaska Peninsula. One of these cases occurred in a hunted area and the other in an unhunted area. Although anecdotal, these observations indicated that resident males, not just immigrant males, were infanticidal. Adult females are also sometimes infanticidal (e.g. Hessing and Aumiller 1994).

Comparisons of reproductive intervals between Alaska and Scandinavia suggest that if SSI occurs in brown bears, it would be more likely to be selected for in Alaska than in Scandinavia. In the southern Scandinavian study area, 89% of females separate from their offspring as yearlings (Swenson et al. 2001*a*). In all Alaskan study areas, separation from offspring as yearlings was extremely rare; separation usually occurred when offspring were 2 years old (in their 3rd year of life). If SSI exists in bears, selection for it should be strongest in populations, like Alaska, where it would generate the greatest benefit by hastening estrous in females with longer intervals between litters. In contrast, Swenson (2003) suggested that the longer period of coexistence between humans and bears in Scandinavia compared to North American may have resulted in the evolution of different behaviors.

Swenson et al. (2001*b*) suggested that the prevalence of cub mortality in the spring, during the breeding season, supported their SSI explanation. We also found higher than expected incidence of mortality of cubs in the spring in 3 of our 4 Alaskan studies. We suspect this

pattern reflected relatively high vulnerability of young, small, inexperienced cubs following their emergence from dens. High mortality rates for young individuals is common in many mammals (Andrewartha and Birch 1954, Caughley 1966).

Breeding opportunities for males are not enhanced unless the whole litter is ultimately lost. Therefore, insights into the likelihood of the SSI hypothesis may be gained by examination of the frequency with which entire litters are lost in bear populations exposed to different levels of male removal. From Swenson's (2001*b*) data for southern Scandinavia, we calculated a rate of whole litter loss of 42% (23 of 55 litters). Among our study sites, this is most comparable to the rate of whole litter loss in un hunted Katmai (35%) and un hunted Denali (59% of 41 litters; J. Keay, unpublished data). The two national parks in Alaska as well as the hunted population in southern Scandinavia all had higher rates of whole litter loss than in the hunted populations at Black Lake and Susitna (14% and 26%, respectively). These comparisons suggest that hunted populations do not universally have higher rates of loss of entire litters.

The frequency with which entire litters are lost may be influenced by the frequency of 1-cub litters. In the Alaska studies, litters of a single cub were most common in Katmai (22% of litters) and least common in Black Lake (9%). In Denali and Susitna, single cub litters occurred in 12% and 19% of litters respectively (Table 5).

Similarly, we found no consistent pattern among our hunted and un hunted areas of the likelihood that litters experiencing loss of ≥ 1 cub were completely lost. Complete loss for such litters was higher in the un hunted area on the Alaska Peninsula (Katmai compared to Black Lake) but lower in the un hunted area in southcentral Alaska (Denali compared to Susitna).

The decrease in cub survival in Sweden following the intentional increase in male bear killing appeared consistent with the SSI explanation offered by Swenson (2003). These recent results appear to support the suggestion of Swenson (2003) that brown bears in Europe may respond to hunting pressure differently than North American brown bears.

Female avoidance of immigrant males

We believe that Wielgus and Bunnell (1994*a*) did not present persuasive evidence of increased male immigration following hunting in Kananaskis. Immigration was inferred based on increased number of captures during 1982–83 compared to 1980–81, although trap-nights were roughly equal. Carr (1989:7) offered another

explanation for this difference in capture rates: "The major increase in both total and individual captures after 1981 was likely due to the crew's added experience and enhanced efficiency, along with increased availability of bait."

We suspect that there is typically a flux of immigrant males through both hunted and un hunted areas (Glenn and Miller 1980; Reynolds 1997; R. Sellers, unpublished data for Katmai). Correspondingly, we suggest that avoidance of the best habitats of the type posited by Wielgus and Bunnell (2000) should occur in both hunted and un hunted populations if it occurs in either.

In other studies, adult females, with or without young, routinely dominated subadult males in using the most favored sites at concentrated food resources, such as salmon streams or dumps (Hornocker 1962, Stonorov and Stokes 1972, Egbert and Stokes 1976, Bledsoe 1987, Walker 1993, Craighead et al. 1995). Adult females, including those with cubs, seldom completely avoided these feeding aggregations (Sellers and Aumiller 1994). We suspect that adult females with offspring foraging at widely dispersed food resources such as berries (which constituted the prime feeding areas in Kananaskis) would be less likely than those at concentrated food sources to be socially displaced by males to the point they are nutritionally disadvantaged. We believe displacement of adult females is even less likely to be caused by subadult males.

Infanticide in brown bears

Brown bears have some characteristics consistent, but others that are inconsistent, with the evolution of SSI by males. Unlike lions or primates, for which SSI has been demonstrated (Pusey and Packer 1994, Van Noordwijk and van Schaik 2000), bears do not defend territories or form family groups; a single male does not dominate a group of adult females; infanticidal males do not necessarily gain breeding opportunities to the newly-available females; and females are polyandrous during a single breeding season. In our view, these characteristics are impediments to the evolution of SSI in bears, although we acknowledge that polyandry has been suggested as a female counterstrategy to SSI by males (van Schaik et al. 2000). Even in lions, where SSI is well demonstrated to occur when a dominant male dies, male-biased hunting may in some cases increase population growth rate if it reduces takeover attempts by non-harem males (Greene et al. 1998).

Predation and reduced competition may be motives for some infanticide in brown bears. Bears are large

predatory carnivores that will readily kill and consume other mammals when they can. Adult female brown bears sometimes also kill cubs of other females (Hessing and Aumiller 1994). This may increase a female's fitness by reducing competition her cubs would otherwise confront or through nutritional gains by consumption of conspecifics.

The evolutionary history of bears appears to be one where populations were seldom reduced below environmental carrying capacity by high levels of adult mortality. Densities in excess of carrying capacities were avoided through high offspring mortality mediated by food competition, maternal nutritional constraints, and predation by conspecifics. For brown bears, few predators other than larger conspecifics can penetrate a female's formidable ability to defend her cubs. It would be expected that these evolved mechanisms and behaviors would persist in modern bear populations at densities below carrying capacity.

Our results are consistent with general ecological theory that suggest reduced recruitment or survivorship occurs as populations approach carrying capacity and increases occur as populations decline from carrying capacity densities (Andrewartha and Birch 1954, Caughley 1977). Because animals are removed, hunting tends to drive populations below carrying capacity.

Cub survivorship: other North American studies

Like our Susitna studies, high cub survivorship was also found in other hunted brown bear populations in interior Alaska. Survivorship was 87% ($n = 76$ cubs) in the Noatak region of northwestern Alaska subjected to moderate male-biased hunting pressure (Ballard et al. 1993). High cub survivorship (72%, $n = 137$ cubs) was also found in a heavily hunted populations in the northcentral Alaska range (Reynolds 1997). The hunted Noatak and northcentral Alaska Range populations both had higher cub survivorship than the unhunted Denali population (34%). This suggests that the high survivorship in heavily hunted Susitna (67%) relative to Denali was not atypical of comparisons between hunted and unhunted brown bear populations in interior Alaska.

Similar results were obtained in other Alaskan studies of high-density populations sustained by salmon. We combined data from 4 hunted areas on Kodiak Island (Smith and Van Daele 1991, V. Barnes, U.S. Geological Survey [retired], Kodiak, Alaska, USA, unpublished data). In these high-density salmon-rich areas, lumped cub survivorship was 65% (range = 56–70%, 468 cubs

in 196 litters). High cub survivorship (79%, 43 cubs in 24 litters) was also found in a high-density hunted population in a salmon-rich habitat on Admiralty Island in southeastern Alaska (Schoen and Beier 1990). The high cub survivorship on Kodiak and Admiralty Islands indicate that there are additional hunted populations occurring in salmon-rich habitats that, like Black Lake, have higher rates of cub survivorship than the unhunted population in Katmai (34%).

Results similar to ours in Alaska were evident in the United States–Canada border region. Cub survivorship was slightly higher in a hunted population on the North Fork of the Flathead River in southeastern British Columbia, Canada (0.87; Hovey and McLellan 1996) than in an unhunted population 100 km southeast in the Swan Mountains, Montana (0.79; Mace and Waller 1998). Unlike our Alaskan national park populations (Denali and Katmai), the unhunted Swan Mountain population was probably below carrying capacity because of management kills. Regardless, this comparison suggests that our results showing high cub survivorship in hunted areas relative to ecologically similar unhunted areas are not unique to Alaska.

Throughout the range of the brown bear in North America, there are areas with both high and low survivorship of cubs in hunted and unhunted conditions. We suspect that survivorship of cubs and natality rates in bear populations below carrying capacity in North America varies because of factors largely unrelated to the harvest of males. In populations at carrying capacity, our data indicate reduced cub survivorship relative to nearby hunted areas. This appears to be a density-dependent response resulting from proximity to carrying capacity in bears.

Management implications

Bear hunters and some managers of hunted bear populations have eagerly embraced reports purporting to show that hunting of bears increases survival of young. More recently, other studies have suggested that killing of male bears resulted in smaller litter sizes or decreased survivorship of young. These studies have been embraced by groups opposed to bear hunting. When applied to populations below carrying capacity, we believe that both of these suggestions are inadequately supported by available data. The latter hypotheses were also inconsistent with the results we report here for hunted populations in Alaska. In Alaska, increased hunting pressure did not decrease cub survivorship. Cub survivorship also did not vary subsequent to years with and without hunting seasons.

A different pattern was evident for the unhunted populations in 2 Alaskan national parks where bear densities are likely at carrying capacity. Compared to nearby hunted areas, cub survivorship was lower in nearby national parks. This was the reverse of what would be expected if male-biased hunting disrupted social structures leading to increased infanticide. In Alaska, litter size was not lower in hunted populations than in unhunted populations. These findings are inconsistent with studies on small populations of bears that claimed hunting reduced litter size by restricting female access to the best foraging areas.

Managers of exploited bear populations should be cautious and explicit about including density dependent relationships in their demographic models for bear populations below carrying capacity. Our results support the inclusion of density-dependent reductions in cub survivorship as bear populations reach carrying capacity. Harvests of brown bears should be conservative because available techniques to estimate population size are imprecise and expensive, and because brown bears have low and variable reproductive and survivorships (Miller 1990a). At least in North American hunted populations below carrying capacity, inclusion of functional relationships between male removal and cub survivorship or litter size cannot be justified based on currently available information. We suspect this is true for very small as well as larger populations.

Acknowledgments

We thank V. Barnes for allowing us to cite his unpublished cub survivorship data for Kodiak Island. J. Swenson made many helpful comments and clarifications of his data during preparation of this manuscript. We further appreciate comments made by referees J. Swenson, D. Garshelis, and R. Wielgus during their review of this manuscript and comments made by B. McLellan on an early draft. Studies in southcentral Alaska were funded by the Alaska Power Authority (1980–86) and as Federal Aid in Wildlife Restoration projects (most recently Grant W-24-4, Study 4.26). Studies on the Alaska Peninsula were funded by the National Park Service, the U.S. Fish and Wildlife Service, the Exxon Valdez Trustee Council, the Alaska Fish and Game Department, and numerous Federal Aid in Wildlife Restoration Projects (most recently Grant W-24-4, Study 4.0). Many people from state and federal agencies participated in these projects. Special recognition for their work on all these projects goes to D. McAllister and B. Taylor (Alaska Department of Fish

and Game). Many pilots of fixed-wing aircraft and helicopters contributed to the safety, efficiency, and accuracy of our studies; these pilots are the unsung heroes of our studies in Alaska. We thank our supervisors at the Alaska Department of Fish and Game for their support of this work and the National Wildlife Federation for support during the preparation of the manuscript.

Literature cited

- ADAMS, L.G., B.W. DALE, AND L.D. MECH. 1995. Wolf predation on caribou calves in Denali National Park, Alaska. Pages 245–260 in L.N. Carbyn, S.H. Fritts, and D.R. Seip. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication No. 35.
- AGRESTI, A. 1990. Categorical data analysis. John Wiley and Sons, New York, New York, USA.
- ANALYTICAL SOFTWARE. 2000. Statistix 7 User's Manual. Analytical Software, Tallahassee, Florida, USA.
- ANDREWARTHA, H.G., AND L.C. BIRCH. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.
- BALLARD, W.B., J.S. WHITMAN, AND D. REED. 1991. Population dynamics of moose in south-central Alaska. *Wildlife Monograph* 114.
- , L.A. AYRES, D.J. REED, S.G. FANCY, AND K.E. RONEY. 1993. Demography of grizzly bears in relation to hunting and mining development in Northwestern Alaska. Scientific Monograph NPS/NRRO/NRSM-93/23, U.S. Department of Interior, National Park Service.
- BLED SOE, W.T. 1987. Brown bear summer. Dutton, New York, New York, USA.
- BOYCE, M.S., A.R.E. SINCLAIR, AND G.C. WHITE. 1999. Seasonal compensation of predation and harvesting. *Oikos* 87:419–426.
- , B.M. BLANCHARD, R.R. KNIGHT, AND C. SERVHEEN. 2001. Population viability for grizzly bears: a critical review. International Association for Bear Research and Management Monograph Series 4.
- BUNNELL, F.L., AND D.E.N. TAIT. 1981. Population dynamics of bears—implications. Pages 75–98 in C.W. Fowler and T.D. Smith, editors. Dynamics of large mammal populations. John Wiley & Sons, New York, New York, USA.
- , AND ———. 1985. Mortality rates of North American bears. *Arctic* 38:316–323.
- CAHALANE, V.H. 1959. A biological survey of Katmai National Monument. Smithsonian Institute Publication 4376.
- CALIFORNIA FISH AND GAME. 1999. Bear hunting, final environmental document Section 265, 365, 366, 367, 367.6, Title 14 California Code of Regulations. California Fish and Game, Sacramento, California, USA.
- CARR, H.D. 1989. Distribution, numbers, and mortality of grizzly bears in and around Kananaskis Country, Alberta.

- Wildlife Research Services No. 3, Alberta Forestry, Lands and Wildlife. Fish and Wildlife Division, Edmonton, Alberta, Canada.
- CAUGHLEY, G. 1966. Mortality patterns in mammals. *Ecology* 47:906–918.
- . 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, New York, USA.
- CRAIGHEAD, J.J., J.R. VARNEY, AND F.C. CRAIGHEAD, JR. 1974. A population analysis of the Yellowstone grizzly bears. Montana Forest and Conservation Experimental Station Bulletin 40. University of Montana, Missoula, Montana, USA.
- , D.J. CRAIGHEAD, S. SUMNER, AND J.A. MITCHELL. 1995. The grizzly bears of Yellowstone; their ecology in the Yellowstone ecosystem, 1959–1992. Island Press, Washington, D.C., USA.
- DEAN, F.C., L.M. DARLING, AND A.G. LIERHAUS. 1986. Observations of intraspecific killing by brown bears, *Ursus arctos*. *Canadian Field-Naturalist* 100:208–211.
- DEROCHER, A.E., AND M.K. TAYLOR. 1994. Density-dependent population regulation of polar bears. Pages 25–30 in M. Taylor, editor. Density-dependent population regulation in black, brown and polar bears. International Conference on Bear Research and Management. Monograph Series 3.
- , I. STIRLING, AND W. CALVERT. 1997. Male-biased harvesting of polar bears in western Hudson Bay. *Journal of Wildlife Management* 61:1075–1082.
- DOOD, A.E., R.D. BRANNON, AND R.D. MACE. 1986. Final programmatic environmental impact statement: the grizzly bear in northwestern Montana. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.
- EGBERT, A.L., AND A.W. STOKES. 1976. The social behavior of brown bears on an Alaskan salmon stream. *International Conference on Bear Research and Management* 3:41–56.
- FRASER, D., J. GARDNER, G. KOLENOSKY, AND S. STRATHERN. 1982. Estimation of harvest rate of black bears from age and sex data. *Ursus* 10:53–57.
- GARSHELIS, D.L. 1994. Density-dependent population regulation of black bears. Pages 3–14 in M. Taylor, editor. Density-dependent population regulation in black, brown and polar bears. International Conference on Bear Research and Management. Monograph Series 3.
- , K.V. NOYCE, AND P.L. COY. 1998. Calculating average age of first reproduction free of the biases prevalent in bear studies. *Ursus* 10:437–447.
- GLENN, L.P. 1980. Morphometric characteristics of brown bears on the Central Alaska Peninsula. International Conference on Bear Research and Management 4:313–319.
- , AND L.H. MILLER. 1980. Seasonal movements of an Alaska Peninsula brown bear population. *International Conference on Bear Research and Management* 4:307–312.
- , J.W. LENTFER, J.B. FARO, AND L.H. MILLER. 1976. Reproductive biology of female brown bears (*Ursus arctos*), McNeil River, Alaska. *International Conference Bear Research and Management* 3:381–390.
- GREENE, G., J. UMBANHOWAR, M. MANGEL, AND T. CARO. 1998. Animal breeding systems, hunter selectivity, and consumptive use in wildlife conservation. Pages 271–305 in T. Caro, editor. Behavioral ecology and conservation biology. Oxford University Press, New York, New York, USA.
- HESSING, P., AND L. AUMILLER. 1994. Observations of conspecific predation by brown bears, *Ursus arctos*, in Alaska. *Canadian Field-Naturalist* 108:332–336.
- HILDERBRAND, G.V., C.C. SCHWARTZ, C.T. ROBBINS, M.E. JACOBY, T.A. HANLEY, S.M. ARTHUR, AND S. SERVHEEN. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- HORNOCKER, M. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. Thesis, University of Montana, Missoula, Montana, USA.
- HOVEY, F.W., AND B.N. McLELLAN. 1996. Estimating population growth of grizzly bears from Flathead River drainage using computer simulations of reproductive and survival rates. *Canadian Journal Zoology* 74:1409–1416.
- HRDY, S.B. 1979. Infanticide among animals: a review, classification and examination of the implications for the reproductive strategies of females. *Ethnology and Sociobiology* 1:13–40.
- , AND G. HAUSFATER. 1984. Comparative and evolutionary perspectives on infanticide: introduction and overview. Pages xiii–xxxv in G. Hausfater and S.B. Hrdy, editors. Infanticide—comparative and evolutionary perspectives. Aldine Publication Company, New York, New York, USA.
- JANSON, C.H., AND C.P. VAN SCHAIK. 2000. The behavioral ecology of infanticide by males. Pages 469–494 in C.P. Van Schaik and C.H. Janson, editors. Infanticide by males and its implications. Cambridge University Press, New York, New York, USA.
- KEAY, J.A. 2001. Grizzly bear population ecology and monitoring, Denali National Park and Preserve, Alaska. U.S. Department of Interior, U.S. Geological Survey, Alaska Biological Science Center, Anchorage, Alaska, USA.
- MACE, R.D., AND J.S. WALLER. 1998. Demography and population trend of grizzly bears in the Swan Mountains, Montana. *Conservation Biology* 12:1005–1016.
- MATSON, G., L. VAN DAELE, E. GOODWIN, L. AUMILLER, H. REYNOLDS, AND H. HRISTIENKO. 1993. A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth. Matson's Laboratory, Milltown, Montana, USA.
- MCCULLOUGH, D.R. 1981. Population dynamics of the Yellowstone grizzly. Pages 173–196 in C.W. Fowler and T.D. Smith, editors. Dynamics of large mammal populations. John Wiley & Sons, New York, New York, USA.

- McLELLAN, B. 1994. Density-dependent population regulation of brown bears. Pages 15–24 in M. Taylor, editor. Density-dependent population regulation in black, brown and polar bears. International Conference on Bear Research and Management. Monograph Series 3.
- MILLER S.D. 1987. Susitna hydroelectric project final report. Big game studies, Volume VI, black and brown bear. Alaska Department of Fish and Game, Anchorage, Alaska, USA.
- . 1990a. Population management of bears in North America. International Conference on Bear Research and Management 8:357–373.
- . 1990b. Impact of increased bear hunting on survivorship of young bears. Wildlife Society Bulletin 18:462–467.
- . 1990c. Detection of differences in brown bear density and population composition caused by hunting. International Conference on Bear Research and Management 8:393–404.
- . 1990d. Denning ecology of brown bears in south-central Alaska and comparisons with a sympatric black bear population. International Conference on Bear Research and Management 8:279–287.
- . 1992. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Alaska Department of Fish and Game, Federal Aid In Wildlife Restoration Progress Report on Project W-23-4, Study 4.21. Juneau, Alaska, USA.
- . 1993a. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Alaska Department of and Fish and Game, Federal Aid In Wildlife Restoration Final Report on Project W-23-6, W-23-1, W-23-2, W-23-3, W-23-4 and W-23-5, Study 4.21. Juneau, Alaska, USA.
- . 1993b. Brown bears in Alaska: A statewide management overview. Alaska Department of Fish and Game, Division of Wildlife Conservation Wildlife Technical Bulletin 11. Juneau, Alaska, USA.
- . 1997a. Impacts of increased hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration. Final Report on Study 4.26 (June). Juneau, Alaska, USA.
- . 1997b. Impacts of increased hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Alaska Department of Fish and Game, Federal Aid In Wildlife Restoration Progress Report on Study 4.26 (December). Juneau, Alaska, USA.
- , AND W.B. BALLARD. 1982. Density and biomass estimates for an interior Alaskan brown bear, *Ursus arctos*, population. Canadian Field Naturalist 96:448–454.
- , AND ———. 1992. Analysis of an effort to increase moose calf survivorship by increased hunting of brown bears in south-central Alaska. Wildlife Society Bulletin 20:445–454.
- , E.F. BECKER, AND W.B. BALLARD. 1987. Black and brown bear density estimates using modified capture–recapture techniques in Alaska. International Conference on Bear Research and Management 7:23–35.
- , G.C. WHITE, R.A. SELLERS, H.V. REYNOLDS, J.W. SCHOEN, K. TITUS, V.G. BARNES, JR., R.B. SMITH, R.R. NELSON, W.B. BALLARD, AND C.C. SCHWARTZ. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark–resight techniques. Wildlife Monograph No. 133.
- OLSEN T.L. 1993. Infanticide in brown bears, *Ursus arctos*, at Brooks River, Alaska. Canadian Field-Naturalist 107:92–94.
- PASITSCHNIAK-ARTS, M., AND F. MESSIER. 2000. Brown (grizzly) and polar bears. Pages 409–428 in S. Demarais, and P.R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.
- POLLOCK, K.H., S.R. WINTERSTEIN, C.M. BUNCK, AND P.D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.
- PUSEY, A.E., AND C. PACKER. 1994. Infanticide in lions: consequences and counterstrategies. Pages 277–299 in S. Parmigiani and F.S. vom Saal, editors. Infanticide and parental care. Harwood Academic, London, England, U.K.
- REYNOLDS, H.V. 1997. Effects of harvest on grizzly bear population dynamics in the northcentral Alaska Range. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration Research Final Report. Juneau, Alaska, USA.
- RUFF, R.L. 1982. Dynamics of black bear populations (low to no human exploitation). Pages 87–103 in F.G. Lindzey, editor. Western Black Bear Workshop 2:87–103.
- SÆTHER, B.E., S. ENGREN, J.E. SWENSON, Ø. BAKKE, AND F. SANDEGREN. 1998. Viability of Scandinavian brown bear *Ursus arctos* populations: the effects of uncertain parameter estimates. Oikos 83:403–416.
- SARGEANT, G.A., AND R.L. RUFF. 2001. Demographic response of black bears at Cold Lake, Alberta, to the removal of adult males: a re-evaluation. Ursus 12:59–68.
- SCHOEN, J.W., AND V. BEIER. 1990. Brown bear habitat preferences and brown bear logging and mining relationships in southeaster Alaska. Final Report, Federal Aid in Wildlife Restoration Project No. W-22 and W-23, Study 4.17. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- SCHWARTZ, C.S., S.D. MILLER, AND M.A. HAROLDSON. 2003. Grizzly/brown bear. Pages 556–586 in G. Feldhamer, B. Thompson, and J. Chapman, editors. Wild mammals of North America. John Hopkins University Press, Baltimore, Maryland, USA.
- SELLERS, R.A. 1994. Dynamics of a hunted brown bear population at Black Lake, Alaska. 1993 Annual Progress

- Report, December 1994. Alaska Department of Fish and Game, King Salmon, Alaska, USA.
- . 1998. Game Management Unit 9. Pages 89–100 in M. Hicks, editor. Brown bear. Federal Aid in Wildlife Restoration Management Report, Survey-Inventory Activities. Federal Aid in Wildlife Restoration Grants W-24-3 and W-24-4, Study 4.0. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- , AND S.D. MILLER. 1991. Dynamics of a hunted brown bear population at Black Lake, Alaska. Third Annual Progress Report, 1990. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- , AND L.D. AUMILLER. 1994. Brown bear population characteristics at McNeil River, Alaska. International Conference on Bear Research and Management 9(1):283–293.
- , AND S.D. MILLER. 1999. Population dynamics of brown bears after the *Exxon Valdez* oil spill. *Ursus* 11:73–78.
- SMITH, R.B., AND L.J. VAN DAELE. 1991. Terror Lake Hydroelectric Project, Kodiak Island, Alaska. Final report on brown bear studies (1982–1986). Alaska Department of Fish and Game, Kodiak, Alaska, USA.
- STONOROV, D., AND A.W. STOKES. 1972. Social behavior of the Alaskan brown bear. International Conference on Bear Research and Management 2:232–242.
- STRINGHAM, S.F. 1980. Possible impacts of hunting on the grizzly/brown bear, a threatened species. International Conference on Bear Research and Management 4:337–349.
- . 1983. Roles of adult males in grizzly bear population biology. International Conference on Bear Research and Management 5:140–151.
- SWENSON, J.E. 2003. Implications of sexually selected infanticide for hunting of large carnivores. In M. Festa-Bianchet and M. Apollonio, editors. Animal behavior and wildlife management. Island Press, Covelo, California, USA.
- , F. SANDEGREN, A. BJÄRVALL, A. SÖDERBERG, P. WABAKKEN, AND R. FRANZÉN. 1994. Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation* 70:9–17.
- , F. SANDEGREN, A. SÖDERBERG, A. BJÄRVALL, R. FRANZÉN, AND P. WABAKKEN. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450–451.
- , B. DAHLE, AND F. SANDEGREN. 2001a. Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. *Ursus* 12:81–92.
- , F. SANDEGREN, S. BRUNBERG, AND P. SEGERSTRÖM. 2001b. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80.
- TAYLOR, M. 1994. Density-dependent population regulation of black, brown, and polar bears. Pages 1–2 in M. Taylor, editor. Density-dependent population regulation in black, brown and polar bears. International Conference on Bear Research and Management Monograph Series 3.
- TROYER, W., AND R. HENSEL. 1962. Cannibalism in brown bears. *Animal Behavior* 10:231.
- VAN DAELE, L.J., V.G. BARNES, JR., AND R.B. SMITH. 1990. Denning characteristics of brown bears on Kodiak Island. International Conference on Bear Research and Management 8:257–268.
- VAN NOORDWIJK, M.A., AND C.P. VAN SCHAIK. 2000. Reproductive patterns in eutherian mammals: adaptations against infanticide? Pages 322–360 in C.P. Van Schaik and C.H. Janson, editors. Infanticide by males and its implications. Cambridge University Press, New York, New York, USA.
- VAN SCHAIK, C.P., J.K. HODGES, AND C.L. NUNN. 2000. Paternity confusion and the ovarian cycles of female primates. Pages 361–387 in C.P. Van Schaik and C.H. Janson, editors. Infanticide by males and its implications. Cambridge University Press, New York, New York, USA.
- WALKER, T. 1993. River of bears. Voyageur Press, Stillwater, Minnesota, USA.
- WIELGUS, R.B. 1993. Causes and consequences of sexual habitat segregation in grizzly bears. Dissertation, University of British Columbia, Vancouver, British Columbia, Canada.
- , AND F.L. BUNNELL. 1994a. Sexual segregation and female grizzly bear avoidance of males. *Journal of Wildlife Management* 58:405–413.
- , AND ———. 1994b. Dynamics of a small, hunted brown bear *Ursus arctos* population in southwestern Alberta, Canada. *Biological Conservation* 67:161–166.
- , AND ———. 1995. Tests of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management* 59:552–560.
- , AND ———. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation* 93:145–154.
- , F. SARRAZIN, R. FERRIERE, AND J. CLOBERT. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* 98:293–303.

Received: 18 May 2001

Accepted: 10 February 2003

Associate Editor: A.E. Derocher