Population Dynamics of a Naturally Regulated Brown Bear Population on the Coast of Katmai National Park and Preserve

Final Report

Resource Report NPS/AR/NRTR – 99/36

Richard A. Sellers
Alaska Department of Fish and Game
Sterling Miller
Alaska Department of Fish and Game
Tom Smith
Biological Resource Division, USGS
Rick Potts
National Park Service

A cooperative interagency study funded by

National Park Service, Alaska Region
and
Alaska Department of Fish and Game

1999

The National Park Service, Alaska Region
Natural Resource Reports

The Alaska Region of the National Park Service manages 16 areas in Alaska. The diversity of areas and of their resources is reflected in their designation as national parks, monuments, preserves, and historical parks. These 16 areas represent more than 50 percent of the total acreage the National Park Service administers. The Alaska Region's Resource Management Program directs scientific research and resource management programs in a wide range of biological, physical, and social science disciplines.

The National Park Service disseminates reports on high priority, current resource management information, with managerial application, through the Alaska Region's Natural Resource Report Series. Technologies and resource management methods; resource management papers; proceedings of conferences and resource management workshops; and natural resource management plans are also disseminated through this series. Documents in this series usually contain information prepared primarily for internal use by the National Park Service.

To order a copy from the National Park Service, use the reference number on the report's title page. Copies of this report are available from the following:

National Park Service
Alaska Support Office, Biological Resources Team
2525 Gambell Street, Rm. 107
Anchorage, AK 99503-2892

SUMMARY

Research on brown bears (*Ursus arctos*) along the Katmai coast began in response to the March 24, 1989, *Exxon Valdez* oil spill (EVOS). Original study objectives focused on testing for population-level effects of the EVOS. Although some bears did ingest crude oil and one yearling apparently died from exposure to oil, there was no difference in survival rates or recruitment between a group of bears whose multiannual locations suggested use of oiled coastline and another group of bears that used unoiled areas (Sellers and Miller 1999). Consequently, this study evolved into Phase II of the interagency study to allow comparisons of population parameters between an unhunted population (Katmai) and a population (Black Lake) that has been subjected to different harvest levels through time (Sellers 1994).

The research hypothesis addressed by the study of comparative population dynamics of three brown bear populations (Black Lake -1970s; Black Lake - current; and Katmai) is that different rates of harvest will result in different population structure, density, survival rates and recruitment. We hypothesize that higher rates of harvest will result in:

> (1) lower proportion of adult males, (2) higher proportion of family groups, (3) younger age structure, (4) overall lower survival rates for independent bears, but proportionally less natural mortality, (5) lower population density and (6) higher recruitment rates as a result of larger litters, higher survival rates of offspring and shorter reproductive interval.

An ancillary hypothesis is that higher population density and higher proportion of adult males (which are expected to result from lower harvests) will increase competition for food and will result in:

> (1) smaller body size (particularly for subdominant sex/age cohorts), (2) lower reproductive rates, (3) larger home ranges, (4) higher rates of subadult dispersal and (5) more conspecific predation.

Statistical testing of these hypotheses will be addressed in the final report on the Black Lake study.

Here we report on the dynamics of a naturally regulated population along the coast of Katmai National Park during the period of 1989-1996. The study area is centrally located in a 14,500-km2 area of national park and state lands closed to brown bear hunting. The core study area was closed to hunting in 1931. During 1989-1996, two marked males were legally harvested outside the closed area. This is an annual harvest rate of 0.9% for males and 0.18% for the total population. This low harvest rate and the relative absence of other human-induced mortality are believed to have had minimal effects on population density and structure.

We used a capture-mark-resight (CMR) technique in 1990 to estimate the bear density in a 901-km2 area from Hallo Bay to Amalik Bay. The estimated density was 551 bears of all ages/1,000 km^2 (95% CI = 451-694) or 479 bears ≥2 years old/1,000 km^2 (95% CI = 384-619). To our knowledge, this density of brown bears was the highest that has been reported anywhere using reliable and replicable methods.

Surveys of Katmai National Preserve were conducted at about the same intensity as used for the park's coastal density estimate, but without the presence of any radiocollared bears. Using sightability factors between that documented on the Katmai coast and at Black Lake, we estimated a population of 131-184 bears and a density of 120-168 bears: 1000 km^2.

Estimates of sex and age composition from several sources showed a high percentage of adult males (20% of all bears), a low proportion of the population in family groups (38%) and a low proportion of subadults (22%). The brown bear population composition in the preserve was similar to that found on the coast, where 20% were adult males and 36% were in family groups.

Survival rates of bears >1 year old were within the range reported for other populations, but the cub survival rate of 0.342 was lower than reported for all other populations in North America except for Denali National Park (Keay 1999). Initial cub litter size (2.06), age at first reproduction (7.2 years), average age of offspring at weaning (3.2 years), interval between successful weaning (5.76 years) and overall recruitment (0.25 two-year-olds/adult female-bear-year) are on the low end of the range for brown/grizzly bears in North America. The low reproductive performance results in an estimated rate of population growth ($\lambda = 0.98$), which suggests population stability.

Mean weight (164 kg, SE = 8.57) and total skull size (582 mm, SE = 10.4) of adult females were lower than at Black Lake. The interplay between habitat productivity and bear population density may be responsible for smaller body size and low reproductive performance, but additional investigation will be needed to test this hypothesis.

Since 1989, a total of 3,386 locations of marked bears has been digitized and attribute data for each location entered into a computer database. Further analysis of these locations will be done by T. Smith using GIS technology and reported under separate cover.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

Population Dynamics of a Naturally Regulated Brown bear Population on the Coast of Katmai National Park and Preserve

BACKGROUND

Katmai National Park and Preserve supports one of the largest and highest density, protected brown bear populations in the world. As such, it offers unmatched opportunities to learn about natural processes of population regulation and habitat selection, which have important implications for managing brown bears in unhunted and hunted environments. Both exploited and unexploited brown bear populations are difficult to manage. This is because there are few techniques available by which to document population trends directly and because the species is highly sensitive to disturbances related to human development and activity. Also, brown bears have one of the lowest reproductive rates of North American mammals and can endure only low rates of human-caused mortality. As a result, bear populations are slow to recover from excessive reductions.

An interagency (National Park Service [NPS], Fish and Wildlife Service [FWS] and Alaska Department of Fish and Game [ADFG]) brown bear research project began in 1988 at Black Lake on the Alaska Peninsula. The central focus of the study was to measure the effects of hunting on the population dynamics of brown bears in prime habitat (Sellers 1994). This project involved assessing the current status of the bear population (density, composition, exploitation rates, survival rates, movements and so on.) and making comparisons with population parameters collected from the same area in the early 1970s when the population was subjected to much higher harvests. Fieldwork on the Black Lake study was completed in 1996.

A second phase of the Black Lake project was envisioned to be a comparison study of an unhunted population in the core of Katmai National Park and Preserve. Before approval of a final study proposal for the Katmai phase of the interagency study, in March 1989 the *Exxon Valdez* oil spill occurred in Prince William Sound, spilling 11 million gallons of crude oil. Within two weeks it became apparent that ocean currents would deposit oil on the beaches of the Alaska Peninsula. The coast of Katmai National Park and Preserve was the first to be fouled. Brown bears, as the top level omnivore, were vulnerable to ingesting crude oil from scavenging carcasses of oiled birds and marine mammals, from consuming contaminated marine invertebrates (particularly clams and mussels), or from ingesting oil directly (grooming or eating oil mousse). ADFG was appointed lead agency for assessing the effects of the oil spill on brown bears. Funding during 1989-1991 was provided by ADFG's damage assessment program; in 1992 funding was provided by the NPS.

The original objectives of the EVOS brown bear study on the Katmai coast were:

1. Test the hypothesis that brown bears in an oil contaminated area of the Alaska Peninsula ingested hydrocarbons (as measured from fecal and blood samples) at higher concentrations than did bears captured in an area that was not contaminated (Black Lake).

2. Test the hypothesis that natural mortality rates of female brown bears near oiled areas of the Katmai coast were higher than for females in other coastal populations that were not oiled.

3. Test the hypothesis that some of the natural mortality of brown bears near the Katmai coast could be attributed to physiological effects of ingested hydrocarbons.

4. Estimate the brown bear population density in a representative study area along the Katmai coast using a modified capture-mark-resight (CMR) technique.

5. Identify potential alternative methods and strategies for restoration of lost use, populations, or habitat if injury is identified.

The Katmai coast was chosen as the study area because of early exposure to oil, the high density of brown bears and observations that bears rely on intertidal resources. The timing and location of the EVOS suggested that the Black Lake brown bear project could serve as a control area against which to compare data from oil-fouled areas. However, it soon became apparent that differences in population density and structure between Katmai and Black Lake would affect vital rates independent of any impacts from the oil spill. Thus, we only relied on Black Lake bears to verify that hydrocarbons were not present in fecal samples from a population that had no exposure to crude oil from the EVOS.

Although brown bears did ingest oil and one unmarked yearling, whose mother had hydrocarbons in her feces, was believed to have died from ingestion of crude oil, we did not detect differences in survival or reproductive rates between radiocollared adult females (n = 12) whose movements indicated possible use of oiled shorelines compared to those (n = 21) whose multiannual locations did not include oiled beaches (Sellers and Miller, submitted). We did not detect a significant difference in these vital rates during 1989-1991 compared to 1992-1995 (when toxicity and availability of oil from the EVOS was considered negligible). Therefore, we concluded that the EVOS did not have measurable impacts on the Katmai brown bear population.

Beginning in 1993, a Natural Resource Preservation Project grant provided funding to further document the dynamics of a high density, protected brown bear population regulated by natural conditions. Consequently, this study evolved into Phase II of the interagency Black Lake study to allow comparisons of population parameters between an unhunted population (Katmai) and a population (Black Lake) that has been subjected to different harvest levels through time (Sellers 1994).

STUDY OBJECTIVES

The primary objective of this study is to test the hypothesis that the brown bear population on the central coast of Katmai National Park and Preserve has different population attributes and is regulated by mechanisms different from those found at Black Lake or other hunted populations in Alaska. Specific predictions implicit to this hypothesis include:

1. The exploitation rate for Katmai coastal bears, based on marked bears being sealed in the legal harvest, is lower than at Black Lake.

2. The population density at Katmai is higher than at Black Lake.

3. The population sex and age structure of the Katmai coastal population contains a higher ratio of males:females, has an older age structure including a smaller proportion of subadult bears and a lower percentage of family groups than exists at Black Lake and other hunted populations.

4. Natural mortality rates of adult females, cubs and yearlings is higher in Katmai National Park and Preserve than in hunted populations of brown bears at Black Lake and other hunted coastal populations.

5. Productivity (including such parameters as litter size, age at first successful weaning, reproductive interval and average recruitment) is lower in Katmai than at Black Lake and other hunted populations in coastal areas.

Additional objectives of this study were to: (1) evaluate the usefulness of aerial composition surveys to provide trend information between and within areas; (2) estimate the total bear population in Katmai National Park and Preserve, using the 1990 population estimate and data derived from composition surveys; (3) identify locations and document the timing and intensity of use by bears of habitats of special importance (e.g., sedge flats, clam beds, salmon streams, and so on) both inside and outside the park; (4) calculate adult female home range size and compare with home range size at Black Lake as a measure of habitat quality; and (5) document subadult male and female dispersal patterns and survival rates and analyze habitat components of subadult selected ranges.

Hypotheses and further discussion of results related to comparisons of vital rates between the Katmai population and the two studies at Black Lake will be addressed in the Black Lake final report (Sellers et al. In prep.). Objectives related to spatial analysis and habitat selection will be addressed separately by T. Smith.

STUDY AREA

We captured brown bears on the central portion of the Shelikof Strait coast of Katmai National Park and Preserve (58° 04' - 58° 10'N, 153° 40 - 154° 35'W). The study area, from Swikshak Bay to Amalik Bay, contained 482 km of shoreline. Brown bear density was estimated within a 901-km2 area from Hallo Bay to Amalik Bay. 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.

Grass/forb meadows dominated by blue stem (*Calamagrostis canadensis*) are interspersed with shrub alder (*Alnus crispa sinuata*) and willows (*Salix* spp.) communities on most slopes below 500 m. Trees are sparse: but scattered stands of cottonwood (*Populus balsamifera*), paper birch (*Betula papyrifera kenaica*) and Sitka spruce (*Picea sitchensis*) are found at low elevations. Bears forage on coastal sedge (*Carex* spp.) flats at Swikshak, Chiniak, Hallo and Kukak Bays. Salmon (primarily pink [*Oncorhynchus gorbuscha*], chum [*O. keta*] and coho [*O. kisutch*]) spawn in numerous streams distributed throughout the study area. Snow and ice fields dominate above 1,000-m elevation. Additional descriptions of the study area are provided by Griggs (1936) and Cahalane (1959).

The study area was closed to hunting in 1931 when the original Katmai National Monument was first enlarged. Subsequent additions to the monument in 1942 and 1969 and ANILCA in 1980 expanded the area closed to hunting. Actions by the Alaska Board of Game and state legislature during 1985-1996 closed additional coastal drainages as far north as the Paint River. Currently the study area is centrally located in a 14,500-km2 area closed to bear hunting (figure 1). Before the *Exxon Valdez* oil spill in March 1989, human presence in the study area was limited to commercial fishing boats, guided sport fishing, primarily at Big River and Swikshak River, and occasional brief use of a cabin at Amalik Bay by ADFG fisheries biologists and seasonal park rangers. During the course of this study, tourism, primarily in the form of bear viewing, increased dramatically. In 1994 a lodge was constructed on private land in Kukak Bay and a seasonal camp was established at Kaguyak.

We conducted aerial surveys in the 3,865 km^2 Katmai National Preserve, which adjoins the park on the northwest side. This area was open to bear hunting under normal state regulations.

METHODS

We captured bears during spring 1989, 1990, 1992 and 1993 by darting them from a helicopter (Glenn and Miller 1980), using a mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol) (Taylor et al. 1989). A premolar tooth was extracted for age determination. Bears were marked with lip tattoos and ear tags. Skull measurements, weights (either estimated or obtained from a scale) and body condition ratings were recorded. Blood was collected and processed to determine percent hemoglobin and packed cell volume; sera was separated and stored for later use in genetics work and testing for pathogens. Hair samples were collected from most bears and subsamples were supplied to Grant Hilderbrand at Washington State University for isotopic analysis to compare dietary components of brown bear populations throughout North America.

Standard radio collars (Telonics) were attached to adult females. Due to rapid growth of subadults and males, standard collars of fixed circumference can become too tight and were not used. On such bears a non-permanent transmitter was attached by inserting a canvas spacer, designed to rot through within 18 months, into a regular collar (Hellgren et al. 1988) or by gluing a small transmitter to the fur on the bear's back. In 1993 T. Smith designed an experimental expandable collar for use on subadults. This collar consisted of tubular PVC material in 2 diameters. The smaller tube fit inside the larger one and was attached to it with elastic belting. A canvas spacer held the collar in a fixed circumference until the canvas rotted, at which time the two PVC tubes were free to pull apart to the extent allowed by the elastic.

Bear density was estimated using the procedure described by Miller et al. (1997). In brief, this procedure involved replicated searches of the area in fixed-wing aircraft (PA-18). When bears were seen, telemetry equipment was activated to determine whether the bear was marked (with a functioning radio-transmitter) or unmarked. If a bear was marked, its identity, association and location were recorded. Unmarked bears were not captured, but estimated sex/age (adult male, medium-sized adult, family group and subadult) and location were recorded. The estimated age of offspring was also recorded. The number of radio-marked bears in the area searched was determined using radio-tracking gear in a manner that did not influence normal search patterns. Radio-marked bears were not located, but their presence was verified by telemetry signals during the searches.

Following the period of marking, five fixed-wing aircraft were available to conduct the searches. Unfortunately, bad weather prevented any searches during the period of 23-31 May 1990. It was considered important to accomplish these searches before leaf emergence restricted seeing the bears. By 31 May leaves were well developed, especially on lower, south facing slopes, so the density estimate was canceled. Weather improved on June 3 and one replicate was accomplished using a single airplane. Based on that flight, it appeared possible that acceptable results might be obtained even with the high level of leaf emergence and lower than ideal sightability. Consequently, three more replicates were flown during 5-7 June, each with two aircraft. Density was estimated based on these four replicate searches. Total times spent looking for bears during these four searches were 459, 547, 665 and 593 minutes, respectively.

Surveys done in May 1993 in Katmai National Preserve were conducted with the same procedure and intensity as the CMR density estimate flights, except no bears were marked. The preserve was divided into four blocks to distribute the search effort.

Telemetry flights were conducted primarily with fixed winged aircraft (Piper PA18, Cessna 185 and Cessna 206), but occasionally we used a Robinson R22 helicopter during spring and late fall to ensure visual observations of marked females to determine family status. In 1989 flights were made twice a week and thereafter approximately twice per month during the non-denning period. For each relocation, we recorded the date, time, precision of the relocation, denning period. For each relocation, we recorded the date, time, precision of the relocation, habitat type, activity of the radio-marked bear and whether any other bears were associated with the marked bear. We plotted locations on 1:63,360 scale topographic maps or recorded coordinates from aircraft GPS receivers. Wildlife Conservation Division staff in Anchorage digitized locations and merged the database file containing all the attributes associated with each relocation. When a radio collar was detected on the mortality mode, we inspected the site as soon as feasible to investigate the circumstances, i.e., whether the bear was dead or the collar had been shed.

In addition to capture samples, three types of aerial observations by experienced biologists provided population composition data: (1) 1989 and 1990 capture samples plus bears seen during the operation, but not captured (R. Sellers, S. Miller, R. Smith and D. McAllister) (2) observations made during the 1990 density estimate (R. Sellers and S. Miller) and (3) observations of unmarked bears made during routine telemetry flights in summer 1989 (R. Sellers). Bears observed from the air were classified into the following categories: females accompanied by cubs; females with ≥1-year-olds; breeding pairs; lone adult males; subadults; and other "single bears" (i.e., not in family groups). Aerial surveys were repetitive, and consequently we undoubtedly counted some individual bears more than once. Capture samples and aerial observations have associated biases and practical limitations (Sellers 1994), but collectively they provide insights into population composition that permit evaluation of eventual changes in population composition or comparisons with other populations, such as at Black Lake, where similar techniques were used.

Survival rates of radiocollared bears and dependent offspring were determined by Kaplan-Meier procedures (Pollock et al. 1989). We investigated bear mortalities to determine cause of death based on evidence at the scene. In cases where intraspecific predation was determined, the most common evidence was damage to the skull, often involving puncture wounds to the top of the cranium and/or damage to the zygomatic arch.

Hunters must have their bear hides sealed by ADFG representatives who inspect the hides for lip tattoos and ear tags. We estimated the cumulative number of marked bears available for harvest in each of four 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 during 1989-1996.

Differences among means, ranks and survival rates were determined by t-tests, one-way ANOVA, Kruskal-Wallis or Mann-Whitney tests. Chi-squared tests were used on proportional data sets.

RESULTS AND DISCUSSION

Captures

During the 1989-1993 period, 122 bears were captured a total of 145 times (table 1). In 1989, we captured 36 bears and deployed 30 radio-transmitters (including 20 regular collars and 10 collars with canvas spacers). In 1990, we captured 43 bears (including 2 recaptures); and deployed 42 transmitters (14 regular collars, 14 with canvas spacers and 14 glue-on radios). In October 1991, we captured 4 bears to remove break-away collars that had not yet dropped off. In 1992, we captured 31 bears (including 15 recaptures) and fitted 28 regular collars. In 1993, we captured 31 bears (including 2 recaptures) and deployed 10 regular collars and 19 expandable collars.

Five bears (3 adult females and 2 subadult males) died during capture operations. Although this rate of capture mortality (3.4%) is not exceptionally high, it is bothersome. One capture mortality occurred in October 1991 when a misplaced dart fitted with a 6 cm needle (used to penetrate accumulated subcutaneous fat deposits) penetrated the rib cage, causing internal injuries. Bears killed the other four before they fully recovered from being tranquilized. Two of these (an adult female and a juvenile male) were killed by an adult male; and in the other two cases the identity of the attacker was unknown. These deaths occurred despite periodical monitoring of recovery (which typically takes two to three hours with Telazol) and a policy of airlifting estrus females to safe recovery sites so their scent trails could not be followed by courting males. In Southeast Alaska, Schoen and Beier (1990) reported a male bear killing an estrous female while she was still sedated; but at Black Lake (Sellers 1994) and on Kodiak Island (V. Barnes, Biological Resource Div., Kodiak, pers. comm.), no case has been documented of a tranquilized bear being killed by another bear in 140 and approximately 600 captures, respectively. Two possible factors in the deaths at Katmai are: (1) the exceptionally high bear density and high proportion of adult males and (2) Black Lake and Kodiak bears (particularly adult males) are hunted and may have more fear of human scent lingering on sedated bears.

Population Size and Density Estimates

At the time density estimation began, there were 44 radio-marked bears in the study area (33 females and 11 males). Eighteen of these females were accompanied by a total of 28 offspring (ages 0-3). Four other bears radio-marked in 1989 did not enter the study area during the density estimate in 1990. During the density estimate, the population of marked bears was naturally closed because all of the radio-marked bears present at least once were present during all four replicate searches and no radio-marked bears moved onto the search area during the search period. This means that the value for T_i (total number of individual marked bears present at some time during the density estimation phase) was the same as M_i (number of marked bears in the search area during each replicate search. These values were 62, 44 and 52, respectively, for the estimates of all bears, independent bears and bears > 2.0 years old. One glue-on radio was shed between replicate 2 and 3, reducing the number of radio-marked bears from 44 to 43.

For each replication, information on the association with other bears, presence in the search area and whether or not the bear was seen is provided in table 2. For each replication, summary information on presence and sightings of both marked and unmarked bears is presented in table 3. The group size of marked females with 2- or 3-year-old offspring is not precisely known if these bears were not seen during or shortly after the search period because these offspring may have separated from their mothers. To bracket the feasible range caused by this uncertainty, the maximum and minimum number of marks present were calculated. This uncertainty does not affect the estimated number of "independent" bears (excluding offspring still with their mothers), but does affect estimates of all bears and bears >2.0 years old.

Minimum Population and Density Estimate

A minimum number of bears known to be present was calculated as the sum of marked bears present and unmarked bears seen. For bears of all ages, this minimum number was 142, 162, 182 and 159 for replications 1-4, respectively (table 3). Based on at least 182 bears present in the study area, the minimum density would be 202 bears/1,000 km^2 (523/1,000 mi^2, 1.9 mi^2/bear). The minimum number of independent bears was largest during replication 3, with 131 bears seen or known present.

In both cases, the minimum number of bears estimated in this way was significantly less than the lower limit of the 95% CI calculated below. This means that it would not be helpful to truncate the confidence interval at this minimum value.

Capture-Recapture Estimates

Capture-recapture estimates were calculated in three ways. The first way utilized the bear-days estimator described by Miller et al. (1987). The second method utilized the mean of the Lincoln-Petersen estimates calculated for each of the four replications. The third method utilized the maximum likelihood estimator described by White (1993). Results from all three of these estimators are presented here.

In comparison with the Katmai estimate, the density estimate obtained at Black Lake the year before was more precise because of more replications (6 instead of 4), higher visibility of bears (43% of independent bears, instead of 21%), more intensive search effort (0.9 min/km^2 instead of 0.6) and higher percentage of marked bears in the population (28% of independent bears, instead of 12%). These problems with the Katmai estimate would not have existed if weather had permitted the estimate to be conducted as originally planned, before leaves emerged and before temporary, glue-on transmitters were shed (n = 12).

Bear-days Estimates. Using the bear-days estimator, 493 bears (all ages) were in the Katmai study area during the search period. The calculated 95% CI around this estimate, based on the binomial approximation to the hypergeometric distribution, was 394-651. The corresponding density estimate was 547 bears/1,000 km^2 (95% CI = 437-722 bears/1,000 km^2) (table 4). For independent bears, the estimated density was 407 bears/1,000 km^2 (95% CI = 311-571 independent bears/1,000 km^2) (table 4). For bears >2.0 the estimated density was 474 bears/1,000 km^2 (95% CI = 368-647 bears >2.0/1,000 km^2). To accommodate the uncertainty of weaning dates for families of marked bears, calculations were made for the maximum and minimum number of offspring still with their mothers (table 5).

Mean Lincoln-Petersen Estimates. Estimates and confidence intervals based on the mean Lincoln-Petersen estimator (Eberhardt 1990) are presented in table 6. The mean Lincoln-Petersen density estimate for all bears was 537 bears/1,000 km^2 (95% CI = 454-621 bears/1,000 km^2), just 2% less than the bear-days estimate of density. For independent bears the mean Lincoln-Petersen estimate was 396 bears/1,000 km^2 (95% CI = 314-479 bears/1,000 km^2), just 3% less than the bear-days estimate.

The entire range of the 95% CI can be expressed as a percentage of the estimate to compare the relative size of the CIs associated with different estimators. For the estimate of all bears, the CI of the mean Lincoln-Petersen was 31% of the estimate, compared to 52% for the bear-days estimator. For the estimate of independent bears, the CI of the mean Lincoln-Petersen was 42% of the estimate, compared to 50% with the bear-days estimator. Even though the bear-days CI was asymmetric (larger above than below the estimate) and the mean Lincoln-Petersen estimate was symmetric, the entire range of the mean Lincoln-Petersen CI was contained in the bear-days CI. These results suggest that for the Katmai data, the bear-days CI was more conservative than that calculated using the mean Lincoln-Petersen.

Maximum Likelihood Estimates. Estimates using the immigration-emigration, joint-hypergeometric, maximum likelihood estimator and CI (Miller et al. 1997) are presented in table 7. These density estimates were similar to the other estimators used, but are considered the most appropriate model based on the characteristics of the sampling scheme and assumptions (see Miller et al. 1997).

Potential Errors Due to Time of Weaning. Because leaves were out during the density estimate period, it was difficult to verify whether 2- and 3-year old offspring were still with their radio-marked mothers. This influences the number of "marked" bears available to be resighted in the estimates for bears of all ages and bears >2.0. An attempt was made to verify the family status of radio-marked females immediately following the density estimate, but not all bears were seen then. Some bears were not seen until mid-summer. The range of error introduced by uncertainty over family status was estimated by (1) assuming that all families were still together (the "maximum" estimate) and (2) assuming that all family groups had separated (the "minimum" estimate) (table 6). A subjective estimate, or "best" estimate, was also made of whether or not they were together. The "best" estimate was based both on the estimated age of the young (large or probable 3-year old offspring were assumed more likely to have separated and smaller or 2-year old offspring less likely to have separated at the time the density estimate was conducted) and on the elapsed time between the last observation of the intact family and the density estimate period. The range of result is reported in table 8. For the bear-days estimator, the minimum estimate was <4% smaller than the best estimate for both all bears and bears older than 2.0 years; the maximum estimate was about 15% higher. Similar results were found for the mean Lincoln-Petersen estimate, except the maximum estimate was 38% higher than the best estimate for bears older than 2.0 years.

The bear density estimates from this study were higher than any reported in North America (McLellan 1994, Miller et al. 1997). The closest densities (bears of all ages/1000 km^2) were in southeast Alaska (399-440 at Admiralty Island and 318 at Chichagof Island) and on Kodiak Island (342 at Terror Lake and 323 at Karluk Lake) (Miller et al. 1997). All these areas are hunted, and some have had significant habitat alterations; so these brown bear populations may be held below carrying capacity.

Extrapolated Population Estimate

Using the CMR estimate of 551 bears:1,000 km^2, we extrapolated to the entire Katmai National Park and Preserve to arrive at an estimate of 1,500-2,000 bears. This estimate was based on subjective impressions of densities in various portions of the park and will be refined upon completion of GIS vegetation mapping and more objective habitat evaluation. From surveys done in late May 1993 (see below, "Composition/Trend Surveys of Katmai National Preserve"), we estimated an additional 131-184 bears in Katmai National Preserve. The estimated density in the preserve was similar to previous subjective density estimates based on extrapolation from the 1989 CMR estimate at Black Lake (Sellers and Miller 1991).

Population Composition

The sex and age composition of bears in Katmai is of considerable interest because the population has been relatively undisturbed by humans, either from hunter kills (see Harvest Rates, below), bear-human conflicts or habitat alteration.

Analysis of the sex and age composition of the Katmai coastal bear population is based on capture samples and three data sets from aerial observations. Information obtained from aerial observations is necessarily less detailed than obtained from captured bears. Nevertheless, the larger sample sizes and similar methodology to surveys conducted at Black Lake make these data useful for comparative purposes.

Sex Ratios

The adult (≥5 years old) sex ratio of bears captured during 1989-1990 was 43% males and 57% females (*n* = 60). Occasionally members of consorting pairs escaped capture. Including uncaptured companions, the adult sex ratio was 45% males and 55% females (*n* = 69). Adult males composed 23% of the 1989-1990-capture sample. During CMR density estimate flights, adult males composed 20.0% of all bears seen (*n* = 456). At McNeil River State Game Sanctuary (MRSGS) during 1976-1991, the adult sex ratio averaged 54.5% males and 45.5% females (range 37.8-53.2% males, SE = 1.04), and adult males composed an average of 31.6% (range 26.1-38.6%, SE = 0.89) of all bears classified at MRSGS (Sellers and Aumiller 1994). The higher proportion of adult males at McNeil Falls may have resulted from more males having the falls in their larger home ranges, as compared to females having falls in their home ranges. Also, some females, especially those with cub litters, may have avoided the social stress associated with the large bear aggregation at this concentrated food source, although the "absentee" rate was only 7% for females with cub litters (Sellers and Aumiller 1994).

In Alaska coastal brown bear populations subjected to hunting, adult males represent a smaller proportion of the population. At Black Lake during the early 1970s, the overall harvest rate for bears ≥2 years old was estimated at 11%, and adult males were harvested at 20%. There the adult sex ratio was 17% males and 83% females (Sellers 1994). By 1988-1989, the harvest rate at Black Lake had dropped to 6.2% for bears ≥2 years old, and the adult sex ratio had increased to 28% males and to 72% females. On a portion of Kodiak Island, recent harvest rates have been estimated at 5%, and the adult sex ratio of captured bears was 31% males and 69% females (Barnes and Smith 1997).

Maternal females composed 14, 14.9 and 13.2% of bears seen during capture operations ($n = 258$), CMR surveys ($n = 456$) and telemetry flights ($n = 1{,}426$), respectively (table 9); but the age composition of litters differed among samples. There was no difference in the proportion of cubs seen during capture observations and CMR surveys ($\chi^2 = 0.52$, $P = 0.47$) which both occurred during spring, but both these samples had a lower percentage of cubs than did the summer telemetry flights ($\chi^2 = 5.52$, $P = 0.019$; $\chi^2 = 4.70$, $P = 0.03$, respectively). The higher percentage of cubs seen during summer, especially considering the high cub mortality occurring during May and June (see below, "Composition/Trend Surveys of Katmai National Preserve"), illustrates the bias against capturing and observing females with cubs in the spring. Females with cubs tend to remain at higher elevations (Miller et al. 1987) where terrain and weather combine to hamper search efforts (Glenn and Miller 1980). Additionally, some of these families remain in dens as late as the second week of June. The percentage of dependent offspring ≥1 year old dropped between early June CMR surveys and summer telemetry flights ($\chi^2 = 3.56$, $P = 0.067$), by which time some older litters were weaned.

Bears in family groups composed 37.6, 39.7 and 36.6% of the bears seen during these three aerial surveys (table 9). From 1976 to 1991, 39% of bears using MRSGS were in family groups (Sellers and Aumiller 1994). In contrast, at Black Lake, family groups composed an average of 76.7% of bears counted during 1965-1976 when hunting pressure was highest and 64% during 1982-1992 when harvest rates were reduced (Sellers 1994). Hunting regulations protect cubs, yearlings and their mothers. Thus in intensively hunted populations, the proportion of single bears is likely to be reduced (Sellers 1994).

The sex ratio of subadults (2-4 years old) captured during 1989-1993 in Katmai (21 males and 17 females) was not significantly different from even ($\chi^2 = 0.42$, $P = 0.50$).

Age Structure

The age structure of adult males and females captured during 1989-1990 was the same (mean age: males = 10.7, females = 10.8; median age: 10 for both sexes). For all independent bears captured in 1989 and 1990, the mean age was 9.2 for males and 10.0 for females. The median age for all independent bears was 8 for males and 10 for females.

Subadult males comprised 26% of all independent males captured, and subadult females comprised 19% of all independent females captured. Subadults made up 22% of all independent bears in the capture sample.

The maximum age documented in this study was 23 for males (bear no. 156) and 25 for females (bear no. 325, which successfully weaned a litter at age 24).

Composition/Trend Surveys of Katmai National Preserve

Brown bear surveys were flown in Katmai National Preserve during 22-30 May 1993. The original study design called for up to five replicate surveys; but because of the advanced stage of leaf phenology and the single survey team, only two complete surveys were done. In more than 30 hours of surveying 103 bears were seen. The average of 3.41 bears seen per hour was lower than at Black Lake (5.45 bears/hr) and the Katmai Coast (12.3 bears/hr). Survey intensity in the preserve averaged 1.74 minutes/mi^2. This intensity was lower than during the Black Lake density estimate (2.38 minutes/mi^2) and was similar to the search effort during the Katmai Coast density estimate (1.63 minutes/mi^2).

The preserve was divided into four count areas (Moraine Creek, Nanuktuk Creek, Nonvianuk River and Kukaklek), based on the need to break up the area into manageable-sized quadrants and to examine some preconceived ideas about bear densities. Two complete surveys were made in each of the four areas. Additional partial surveys were done on Nanuktuk Creek on 22 May and Moraine Creek on 24 May; but these were aborted due to poor conditions (low clouds and turbulence) (table 10). The two complete surveys of the preserve yielded counts of 39 and 46 bears. Because no radiocollared bears were present, we could not directly calculate a sightability correction factor to estimate the total bear population of the preserve. During the 1989 CMR density estimate at Black Lake, we saw an average of 43% of the marked bears known to be present. This work had ideal timing regarding phenological development and had among the highest sightability of all spring density estimate work done in Alaska (Miller et. al 1997). In contrast, the 1990 Katmai coastal CMR density estimate was done after leaf emergence (similar phenology to what was encountered in the preserve), and only 21% of marked bears were seen. We are confident that the sightability during surveys in the preserve fell within these values. Habitat in the preserve included more area of open tundra and flat barren snow/rock than encountered in the Katmai coastal area, so we believe we had a higher sightability than the 21% recorded there. On the other hand, bears seem to prefer slopes with thicker brush, suggesting the sightability was lower than the 43% achieved under near-perfect conditions at Black Lake. The rate of repeat sightings of the same family groups or very distinctive individuals was low, further suggesting that sightability was relatively low. Using the best single count of 46 bears and sightability rates of 25%, 30% and 35%, total population estimates for the preserve were 184, 153 and 131 bears, respectively. Unfortunately, a tremendous amount of work and expense would be required to narrow this range of estimated population size. However, for the purposes of bear management, these estimates are useful. For example, when a harvest rate of 5% (the rate currently used for Unit 9) is applied to the extremes of the population estimates, the allowable sport harvest for the preserve is 7-9 bears per season. Harvests in the preserve from 1989-1996 averaged 7 bears (range 2-11), and there appears to be no reason to alter the management system now.

Converting the range of population estimates to density figures, the preserve has between 120 and 168 bears: 1,000 km^2 (i.e., one bear: 2.3-3.2mi^2). The two western count areas had a lower density (one bear: 6.6-9.1 mi^2) than did the Nanuktuk area (one bear: 1.4-2.0 mi^2). If the density estimate for the western areas is extrapolated to the remainder of the Alagnak drainage (a reasonable procedure based on similarity of habitat types and early summer bear distribution), there would be roughly 50 additional bears downstream of the preserve. Thus, the population estimate of 195 bears for the entire drainage made in 1990 by extrapolation (Sellers and Miller 1991) appears reasonable.

The second major objective of these surveys was to estimate composition of the brown bear population to evaluate if current harvest levels are affecting sex and age structure. Based on the number of breeding pairs and single bears of obviously large size, 21 (20%) of the 103 bears seen were adult males. This is virtually identical with the findings of the Katmai Coast density estimate. Of all bears seen, 64% were not in family groups, another indication that the population is under relatively light harvest pressure. Two points require emphasis: (1) the composition data are based on a relatively small sample size (probably less than 80 different individuals) and (2) reported harvests during 1980-1988 averaged three bears per year and were considerably below the calculated sustainable harvest level.

Reproductive Biology

Breeding Season

The breeding season extended from early May through 22 July based on observations of non-maternal, radiocollared females associated with males. During each of 11 periods between 24 April and 31 July, the percentage of non-maternal, radiocollared females consorting ($n = 101$) as opposed to being alone ($n = 343$) was used to describe the progression of the breeding season. Breeding appeared to peak the first week of June when 59% of the females were associated with males (figure 2). During the first half of July, only 6% of females were with males.

Age at First Production of Young

The mean age at first parturition, using the methodology of Garshelis et al. (1999), was 7.2 years (4 bears at 6 yrs, 5 at 7 yrs, 2 at 8 yrs and 1 at 11 yrs). The mean age at which females produced first litters of cubs that survived to weaning (2.5 years old) was 8.0 years ($n = 12$). These 12 bears lost at least 8 litters before weaning their first cubs. Because most earlier studies used different and usually less rigorous methods to calculate the age at first reproduction, comparisons may be misleading. However, it appears that reproductive maturation may be delayed at Katmai in that no 4-year-old ($n = 6$) or 5-year-old ($n = 9$) females produced cubs.

Reproductive Senility

We did not detect evidence of reproductive failure in females due to old age. Seven of 8 females followed past age 20 remained fertile, with 1 producing cubs at age 20, 3 at age 21 and 3 at age 23. The only nonproductive female failed to produce a litter between ages 18 and 20, after which contact was lost.

Litter Size

Mean litter size for cubs of radiocollared females first seen when captured or at den emergence (May or early June) was 2.06 ($n = 52$ litters). Cub litter size at den emergence has been suggested as one parameter that may reflect nutritional condition of the mother and thereby indirectly measure habitat quality (e.g., Craighead et al. 1995). Coastal Alaska has generally been assumed to represent some of the best brown bear habitat in North America, based primarily on bear densities and large body size. However, while cub litter sizes on Kodiak Island (2.48, Smith and VanDaele 1991) and Black Lake (2.54, Sellers 1994) are among the largest reported in North America, two study areas in Southeast Alaska had small average cub litter sizes: Admiralty Island - 1.8 (Schoen and Beier 1990) and Chichagof Island - 2.05 (Beier et al. 1996). Without objective measures of habitat quality, it will be difficult to complete further analysis of the influence of food availability on cub litter size.

For comparisons with some other study areas (e.g., McNeil River), we also determined the mean cub litter size at mid-summer to be 2.11 ($n = 19$). The mean litter size of unmarked females seen during summer telemetry flights was 2.2 ($n = 41$). By fall, the mean cub litter size of radiocollared females was 1.83 ($n = 23$), but this does not include 23 other litters that had no survivors by 10 months of age. If all 46 litters are used, the average litter size in fall is reduced to 0.91. Many past studies presented average litter sizes only for litters having at least one survivor, and then estimated cub mortality based on the change in average litter size. This procedure grossly underestimates mortality of cubs because the loss of entire litters is not included.

At MRSGS during 1963-1991, the mean cub litter size determined when families first arrived at the river (mean date of 14 July) was 2.15 ($n = 137$) (Sellers and Aumiller 1994). Cub litter sizes at MRSGS tended to be smaller ($\bar{x} = 2.11$, $n = 47$) during 1973-1984, when the population was stable, than during 1985-1991 ($\bar{x} = 2.24$, $n = 49$), when the population was growing, although the difference was insignificant ($0.30 < P > 0.20$) (Sellers and Aumiller 1994).

The mean litter size for yearlings at capture or den emergence was 1.71 ($n = 34$). The mean yearling litter size in mid-summer was 1.71 ($n = 19$), and by fall was 1.61 ($n = 18$). Three entire yearling litters (not including the litter of bear 136, which was believed lost because of ingestion of oil from EVOS, [Sellers and Miller 1999]) were known to be lost between spring and fall. The mean yearling litter size at MRSGS was 1.85 ($n = 139$)(Sellers and Aumiller 1994).

Mean spring litter size for 2-year-olds and 3-year-olds was 1.67 ($n = 36$) and 2.0 ($n = 14$), respectively. Average size of litters ≥ 1-year-old seen during mid-summer tracking flights (which may include some duplicate sightings) was 1.70 ($n = 174$).

Age at Family Separation

Radiocollared females weaned litters at an average age of 3.2 years (10 litters at 2.5 years, 13 litters at 3.5 years and 2 litters at 4.5 years). There was no difference in the mean age of females weaning litters at 2 years old ($\bar{x} = 14.9$ years, range 9-22), 3 years old ($\bar{x} = 14.5$ years, range 9-24), or 4 years old ($\bar{x} = 15.5$ years).

Reproductive Interval and Recruitment

During 1989-1996, only seven radiocollared bears successfully weaned two litters. These were weaned at a mean interval of 4 years; but by virtue of their very success, these bears form a highly biased sample. We used the most optimistic scenarios for all adult females observed for at least 4 years ($n = 33$) to calculate a minimum weaning interval of 5.76 years.

Because different methods were used in several studies on the Alaska Peninsula, we also used the cumulative summary of production based on the number of 2-year-old litters produced for all adult female bear-years. Only adult females captured in 1989-1990 were used because capture samples after 1990 were biased toward females with litters composed of offspring ≥1 year old. An annual recruitment rate of 0.25 2.5-year-olds/adult female/year was calculated from 21 litters totaling 36 2.5-year-olds produced during 143 bear-years. The average interval between successful weanings was 6.8 years.

At MRSGS the average annual recruitment was 0.34 yearlings/adult female/year (Sellers and Aumiller 1994). If this rate is adjusted to account for yearling mortality from summer through to the next spring, as estimated in Katmai (see below) and Black Lake (Sellers 1994), the average annual recruitment at McNeil would be approximately 0.31 2.5-year-olds/adult female.

Annual Production of Cubs

The percentage of available radiocollared adult females (i.e., that were unaccompanied by offspring during at least part of the previous breeding season [$n = 7$-20 females per year]) that subsequently produced cub litters varied annually during 1990-1996 from 32% to 65% (table 11). Cub production per available female appeared higher in 1992 and 1994 than in 1991 and 1993 (table 11).

We were unable to test for the effects of food supplies on subsequent productivity because several complicating factors exceeded the scope of this study, including: (1) the diverse diet of bears along the Katmai coast; (2) the numerous small salmon runs used by radiocollared females, which complicated both estimating annual salmon availability and documenting bear use of individual streams; and (3) movements of some females to distant salmon systems (e.g., Becharof and Ugashik). Bears at Black Lake appear to be more dependent on the run of sockeye salmon, which is enumerated annually by counts at the Chignik weir. We will explore the correlation between sockeye escapements and subsequent cub production in the Black Lake study final report (Sellers et al. In prep., "Dynamics of a hunted brown bear population at Black Lake, Alaska"). However, the complexity of this issue was summarized by Craighead et al. (1995): "There is little doubt that food abundance plays a major role in ursine reproduction, but the subject is extremely complex and difficult to assess, partly because of the grizzly's extremely varied diet and its physiological responses to a wide range of environmental and population factors."

Adoption

In 1991 Female 135 was seen on 22 May, 8 August and 10 September with 3 cubs. On 4 October she was seen on Kaflia Creek with 4 cubs. She weaned all 4 cubs as 3-year-olds between 2 May and 23 May 1994.

Another possible adoption or whelping of litters in consecutive years was observed in July 1991 when an unmarked female was observed twice on the Douglas River sedge flats with 2 cubs and 2 probable yearlings (Dean et al. 1992).

Body Size and Physical Condition

Several reproductive parameters (age at first reproduction, litter size, cub survival and age at weaning) may be influenced by nutritional condition. Nutritional condition is a result of several factors, including overall habitat quality, annual variations in food production (e.g., the size of annual salmon escapements or berry crops), the number of bears competing for available food (i.e., bear density) and the social status of individual bears. Unfortunately the complexity of the issue is confounded by difficulty in assessing body condition of bears in the wild. Hilderbrand et al. (1998) reported on the use of biological impedance analysis (BIA) and isotopic water dilution, which both produced good results under laboratory conditions, but have practical limitations for use under typical field conditions. Stephenson et al. (1997) used ultrasonography to measure the thickness of rump fat deposits on moose with good results, and this technique may have potential for use on bears.

Lacking more sophisticated techniques, body mass and other morphological measurements have been used most often to assess physical condition. In Katmai, the mean weight of adult females was 164 kg (SE = 8.57, *n* = 14).

Body measurements have proven unreliable in estimating body mass of polar bears (Cattet et al. 1997), and probably are no more predictive for brown bears. Several researchers have identified error in taking various body measurements as one key problem in linking morphometrics to body mass. We recognized the subjectivity in taking many body measurements, and consequently only measured skull length and width. Skull size was selected because the use of calipers and standardized technique reduced error among biologists taking the measurements and permitted comparisons with bears captured in other areas or taken by hunters. Total skull size (length plus width) for 59 adult females captured at Katmai averaged 582 mm (SE = 10.4).

Franzmann and Schwartz (1988) used discriminant analysis of blood parameters to evaluate seasonal body condition of black bears and found that for males packed cell volume (PCV), among several other parameters, was useful in differentiating poor (spring and early summer) versus good (fall and winter) physical condition. For females, hemoglobin (Hb) was among the best parameters. However, Schwartz and Franzmann (1991) could not demonstrate any difference in blood parameters collected during the spring from black bears in two study areas that appeared to differ in habitat quality, based in part on body weights. Hb and PCV values for bears in Katmai averaged 14.64 (SE = 0.282, $n = 43$) and 43.16 (SE = 0.777, $n = 42$) for males and 14.69 (SE = 0.219, $n = 62$) and 44.02 (SE = 0.56, $n = 82$) for females.

Hair samples from 18 bears captured in 1989 were provided to Grant Hilderbrand, of Washington State University, for isotopic analysis as part of his doctoral research into dietary components of brown bear populations throughout North America. The source of nutrients in summer and fall diets (the period of hair growth when nitrogen and carbon were incorporated into hair tissue) was estimated to be 31.1% (SE = 4.4) vegetation, 62.3% (SE = 5.8) marine meat and 6.6% (SE = 3.5) terrestrial meat (G. Hilderbrand, Washington State University, unpublished data).

Harvest Rates

Only two bears marked in Katmai have been killed by hunters during 1989-1996 (Male 150 in Oct. 1991; and Male 318 in Oct. 1993). Both adult males were killed outside the park boundary near Becharof Lake, at least 85 km south of their capture locations. Including recruitment of subadults, a maximum of 48 adult males was marked. We applied the annual survival rate of 0.955 for adult males (see below, "Survival Rates and Causes of Mortality") to estimate a total of 225 adult male bear-years available and a harvest rate of 0.9% per year. The harvest rate for all other marked cohorts was 0% based on 315 adult female bear-years, 38 subadult male bear-years and 25 subadult female bear-years. If adult males comprised 20% of the population (see above, "Composition/Trend Surveys of Katmai National Preserve"), the estimated harvest rate for the entire population was 0.18% per year. Most coastal brown bear populations in Alaska are managed for a sustainable harvest rate of 5% to 6% (Miller 1993).

Survival Rates and Causes of Mortality

No radiocollared bears were killed by humans, so the Kaplan-Meier estimates in table 12 are natural survival rates for the various categories.

We followed 61 adult females during 210 bear-years and recorded 17 natural mortalities. The annual survival rate for adult females during 1989-1996 was 0.909 (table 12). During individual years, adult female survival ranged from 0.86 in 1992 and 1994 to 1.00 in 1989 (table 13). Of 14 females whose reproductive status was known just before their deaths, 11 had offspring (6 with cubs, 2 with yearlings and 3 with 2-year-olds) and 3 were alone. The survival rate for maternal females (0.864) was lower than for single females (0.937) ($\chi^2 = 4.17$, $P = 0.04$).

Eight adult females were killed by other bears, and in two cases we identified the killers as adult males. Six females died during spring, three of which were killed and fed upon by other bears; one apparently died in a spring avalanche; and the cause of death was undetermined for the other two. Three of six adult females that died during the summer were killed by other bears, and the rest died of unknown causes. Four bears died during the fall, and the only one for which we could determine the circumstances was killed by another bear. Another female, which was last seen with two cubs in October, was emaciated when found dead on 11 April. She died of starvation that was attributed to injuries to her muzzle and tongue that were apparently sustained earlier in a fight with another bear. Sample sizes for adult males, subadult males, and subadult females are too small for extensive evaluation. Only one adult male and one subadult male were found dead and both appeared to have been killed during the spring by other bears.

We followed 99 cubs from 48 litters of 35 different radiocollared females, and documented the loss of 61 cubs, including 11 whose mothers ($n = 5$) died. The survival rate for cubs was 0.342 (table 12). To our knowledge, this is the lowest survival rate reported in North America except for Denali National Park (Keay 1998). The inaccuracy of using the change in average-cub-litter size to estimate mortality is demonstrated by following the survival of individual litters of radiocollared females. The average initial cub litter size at den emergence (mean date 24 May) was 2.06 (n = 49). By mid summer, 34% of the cubs were lost/no longer seen, but the mean litter size had been reduced only 1.2% (2.04) because 13 entire litters were lost.

Several researchers have speculated about the role of "sexually selective" motivation for infanticide by immigrant, subadult males (LeCount 1987, Weilgus 1994 and Swenson et al. 1997). This theory points to removal of resident adult males by hunters as leading to immigration by subadult males. These subadult males have no genetic investment in cubs and thus realize a selective advantage by killing cubs if this subsequently causes the mother to come into estrus and provide a breeding opportunity. This theory has gained some acceptance despite the lack of a single documented case of an immigrant, subadult male killing cubs or yearlings. This is obviously a difficult theory to prove or refute, but it may be useful to examine circumstances in an unhunted, naturally regulated population where male immigration presumably would be minimal. During 1989-1996, 61% of cub deaths not associated with the death of their radiocollared mother occurred during May and June, and 39% occurred after the primary breeding season. This could be interpreted as supportive of the sexually selective infanticide theory; but alternatively, it could be related to the greater vulnerability of cubs to all types of mortality factors during their first month out of the den. Spring is also the period of greatest food shortage, and infanticide could be simple food-seeking predation. Of six incidents of infanticide in Katmai National Park and Preserve (Appendix A) where the killer was known, five were caused by adult males and one by an adult female. In another incident, two cubs were orphaned, and undoubtedly later died or were killed, when their mother was killed by an adult male during a fight that started at the den.

Population Growth Rate

Using the methods of Eberhardt et al. (1994) and a computer model developed by Ward Testa (Alaska Department of Fish and Game, Anchorage), we estimated the rate of population growth (λ) from cumulative data on female survival and reproductive rates. The model estimated λ at 0.979, which equates to a relatively stable population.

Status of Marked Bears

During 1989-1996, approximately 3,411 locations of marked bears were recorded. Most bears captured in 1993 were fitted with "Mod 500" transmitters which had a shorter battery life than the "Mod 600" transmitters used earlier. As of October 1996, only eight adult females had functioning radio collars. Because of the difficulty of keeping radio collars on males without risking neck injury, only temporary radio attachment designs have been used. Consequently, only nine males have been relocated ≥20 times. During May 1993, 18 subadults (2- to 4-year-olds still accompanying their mothers were captured and fitted with expandable collars. By October 1993, only seven of these collars were still on. Another bear killed one subadult, and the other 10 collars fell off prematurely because of failure of the PVC tubing material. The status of radio collared bears is listed in table 14.

Population Regulation

Most populations of brown bears in North America are subjected to some level of human-induced mortality, or at the least are impacted by human activities that affect their habitats or behavior. Consequently, it is difficult to assess the mechanisms that regulate populations that are near carrying capacity and primarily influenced by natural processes, especially density-related changes in vital rates. Inquiry into the presence and effects of density-dependent mechanisms may be exacerbated if they come into play only near carrying capacity, or if carrying capacity is subject to fluctuations caused by environmental change (e.g., human-caused disturbance, fire, extreme weather fluctuations or major, long-term changes in staple food resources). Several researchers (Bunnell and Tait 1980, 1981; McLellan 1994; Taylor 1994) have postulated that overt intraspecific aggression (directly resulting in conspecific predation or increased dispersal) or simple competitions for limited high quality foods (affecting reproductive parameters and survival rates of dependent offspring and subadults) may contribute to density-dependent regulation of bear populations. Unfortunately, exploring these ecological mechanisms in bear populations is constrained by the difficulty in applying controlled experimental design and the slow rate in population change intrinsic to bears. Furthermore, as Taylor (1994, p. 1) points out: "Cub production and cub survival.... are the most likely parameters to be reduced by density effects because these parameters affect population growth rate (evolutionary fitness) less than adult survival rate. The parameters most likely to be affected by density are also those most likely to be affected by environmental variation."

Given the constraints on controlled manipulation of brown bear populations, one approach is to study a population for an extended period of time during which population density changes and vital rates can be monitored. Counts of brown bears using McNeil River State Game Sanctuary were stable during 1969-1984, then increased during 1985-1989 (Sellers and Aumiller 1994) and have apparently stabilized during 1989-1996 (unpublished ADFG annual reports). During the period when the total number of bears using McNeil increased, all segments of the population except subadults increased, leading Sellers and Aumiller (1994) to speculate the subadult mortality and/or dispersal may have been influenced by overall population density at the Sanctuary. They found no correlation between the number of adult males or total number of adults and cub production or survival. However, all reproductive parameters for bears at McNeil were relatively low.

Results from this study, as listed below, support the contention that the Katmai coastal brown bear population is naturally regulated near carrying capacity and that density-dependent population regulation mechanisms may be involved.

1.) The estimated density of 551 bears (479 bears ≥2 years old)/1,000 km^2 is the highest ever measured in North America.

2.) The level of human disturbance and the amount of habitat alteration are undoubtedly among the lowest in the world.

3.) The nutritional condition of adult females, as measured by reproductive parameters, (mean age at first reproduction, average cub litter size, average age at weaning and percent of available females producing litters), body weight and skull size is lower than in a nearby coastal population.

4.) Cub survival is among the lowest ever reported.

5.) Based on a model using population parameters from this study, the population appears stable.

MANAGEMENT AND RESEARCH IMPLICATIONS

Based on data on population composition and density from this study, it appears that the brown bear population along the coast of Katmai National Park and Preserve meets the legislative mandate of being "natural and healthy." It appears to be at carrying capacity, is subject to minimum human harvests and is regulated by natural mechanisms. Data in this report provide a good baseline against which to measure suspected changes in the future.

The importance of the Katmai bear population for scientific understanding of natural population regulation would be hard to overstate. This study provided much baseline information, but future advances in technology may enable researchers to explore some of the more elusive questions we were unable to address. New methods to assess nutritional condition (e.g., ultra sound and assay of various body chemicals) may provide insights into factors affecting productivity. The ability to monitor movements and habitat use on a daily basis with GPS telemetry holds great promise to refine habitat preferences and to evaluate the effects of human activities on bears. Improvements in the design of expandable collars, ear transmitter attachments and implanted transmitters may allow researchers to affix radio transmitters to sex/age cohorts (e.g., cubs, subadults and adult males) that have been difficult to monitor. Questions such as what causes most cub mortality, and if it is infanticide, which bears are responsible and what is their motivation (i.e., potential reproductive advantage versus acquisition of food) may become feasible to address at Katmai.

Population fluctuations would be expected to be rather small in a naturally regulated brown bear population such as at Katmai. However, changes in human activities or a catastrophic event (e.g., an oil spill in Shelikof Straits in late spring) might precipitate the need for updated information on population size or vital rates. It is impossible at this time to speculate when such a disturbance might occur and thus trigger the need for another density estimate. In the mean time, refinement of less intrusive population estimates such as use of DNA finger printing or remote sensing techniques (e.g., thermal imaging) may reduce the cost and invasiveness of estimating bear numbers. A line transect sampling procedure has been tested on Kodiak Island with encouraging results, compared to estimated density derived from the CMR technique. This procedure will undergo further application during May 1999 in Lake Clark National Park and Preserve. Pending analysis of results achieved at Lake Clark, the line transect method might be used in Katmai National Preserve on a regular schedule to monitor population density and composition. Unless there is an increase in hunting pressure, the number of "defense of life an property" kills or some major change in habitat in the preserve, a 10-year schedule for monitoring surveys should be adequate. However, the NPS should be prepared to increase survey efforts in the preserve to address suspected change in the brown bear population from any major disturbance.

Monitoring other aspects of population dynamics, either in the park or preserve, will likely continue to require capturing bears, both to assess physiological status and monitor long-term reproductive and survival rates.

Acknowledgments: We thank all those who participated in various aspects of this project during 1989-1996 and regret that space does not permit a full listing. Field assistance was provided by J. Meldrum, S. Mills, R. Squibb and B. Holms (NPS); J. Faro, T. Boudreau, D. Johnson, D. McAllister, J. Lewis, R. Smith, L. VanDaele, M. McNay and C. Gardner (ADFG); and G. Wilker (FWS). G. Windell, C. Soloy, C. McMahan, H. McMahan, J. Lee, J. Collins, J. Tudor, S. Egli, J. McPhearson, L. Larrivee, J. Larrivee, B. Smoke and C. Bent provided safe and efficient aircraft operation. D. Caulkins, K. Pitcher, D. Anderson and K. Schneider (ADFG) and D. Stevens, K. Kunkel and T. Smith (NPS) provided administrative support.

LITERATURE CITED

BARNES, V.G., AND R.B. SMITH. 1997. Population Ecology of brown bears on Aliulik Peninsula, Kodiak Island, Alaska. Final Report, Project 94-237.

BEIER, L., K. TITUS AND J.R. FARO. 1996. Population and habitat ecology of brown bears on Admiralty and Chichagof Islands. Study 4.22. Alaska Department of Fish and Game. Juneau. 37pp.

BUNNELL, F.E., AND D.E.N. TAIT. 1980. Bears in models and reality – implications to management. Intl. Conf. Bear Res. and Manage. 3:15-23.

BUNNELL, F.E., AND D.E.N. TAIT. 1981. Population dynamics of bears – implications. Pages 75-98 *in* C.W. Fowler and T.D. Smith, eds. Dynamics of large mammal populations. John Wiley and Sons. New York, N.Y.

CAHALANE, V.H. 1959. A biological survey of Katmai National Monument. Smithsonian Institute Publication 4376.

CATTET, M.R. L., S.N. ATKINSON, S.C. POLISCHUK AND M.A. RAMSAY. 1997. Predicting body mass in polar bears: is morphometry useful? Journal of Wildlife Management. 61:1083-1090.

CRAIGHEAD, J.J., J.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.

DEAN, F.C., R. MCINTYRE AND R.A. SELLERS. 1992. Additional mixed-aged brown bear, *Ursus arctos*, associations in Alaska. Canadian Field-Naturalist. 106(2):257-259.

EBERHARDT, L.L. 1990. Using radio-telemetry for mark-recapture studies with edge effects. J. Applied Ecology 27:259-271.

EBERHARDT, L.L., B.M. BLANCHARD AND R.R. KNIGHT. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology. 72:360-363.

FRANZMANN, A.W., AND C.C. SCHWARTZ. 1988. Evaluating condition of Alaskan black bears with blood profiles. Journal of Wildlife Management. 52:63-70.

GARSHELIS, D.L., K.V. NOYCE AND P.L. COY. 1998. Calculating average age of first reproduction free of the biases prevalent in bear studies. International Conference on Bear Research and Management. *Ursus* 10:437-447.

GLENN, L.P., AND L.H. MILLER. 1980. Seasonal movements of an Alaska Peninsula brown bear population. International Conference on Bear Research and Management. 4:307-312.

GRIGGS, R.F. 1936. The vegetation of the Katmai district. Ecology 17 (3).

HELLGREN, E.C., D.D. CARNEY, N.P. GARNER AND M.R. VAUGHN. 1988. Use of breakaway cotton spacers on radio-collars. Wildlife Society Bulletin. 16: 216-218.

HILDERBRAND, G.V., S.D. FARLEY AND C.T. ROBBINS. 1998. Predicting body condition of bears via two field methods. Journal of Wildlife Management. 62:406-409.

KEAY, J.A. 1999. Grizzly bear population ecology and monitoring in Denali National Park and Preserve, Alaska. Final report of project development and findings. US Geological Survey-Biological Resources Division, Alaska Biological Science Center. Anchorage. Forthcoming.

LECOUNT, A.L. 1987. Causes of black bear cub mortality. International Conference on Bear Research and Management. 7:75-82.

MCLELLAN, B. 1994. Density-dependent population regulation of brown bears. Pages 15-24 *in* M. Taylor, ed. . Density-dependent population regulation in black, brown and polar bears. International Conference on Bear Research and Management. Monograph Series Number 3.

MILLER, S.D. 1993. Brown bears in Alaska: A statewide management overview. Wildlife Technical Bulletin 11. Alaska Department of Fish and Game. Juneau. 40pp.

MILLER, S.D., 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.

MILLER, S.D., G.C. WHITE, R.A. SELLERS, H.V. REYNOLDS, J.W. SCHOEN, K. TITUS, V.G. BARNES, 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 capture-mark-resight techniques. Wildlife Monograph 133.

POLLOCK, K.H., S.R. WITERSTEIN, C.M. BUNCK AND P.D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management. 53:7-15.

SCHOEN, J., AND L. BEIER. 1990. Brown bear habitat preferences and brown bear logging and mining relationships in Southeast Alaska. Study 4.17. Alaska Department of Fish and Game. Juneau. 90pp.

SCHWARTZ, C.C., AND A.W. FRANZMANN. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monograph 113.

SELLERS, R.A. 1994. Dynamics of a hunted brown bear population at Black Lake, Alaska. Annual Progress Report - 1993. Alaska Department of Fish and Game. King Salmon, Alaska.

_____, AND L.D. AUMILLER. 1994. Brown bear population characteristics at McNeil River, Alaska. International Conference on Bear Research and Management. 09:283-293.

_____, AND S.D. MILLER. 1991. Dynamics of a hunted brown bear population at Black Lake, Alaska. Annual Progress Report - 1990. Alaska Department of Fish and Game. King Salmon, Alaska.

_____, 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. VANDAELE. 1991. Terror Lake hydroelectric project, Kodiak Island, Alaska. Final Report on brown bear studies (1982-86). Alaska Department of Fish and Game. Juneau. 188pp.

STEPHENSON, T.R., K.J. HUNDERTMARK, C.C. SCHWARTZ AND V. VANBALLENBERGHE. 1997. Prediction of body fat and body mass in moose using ultrasonography. *In* K.J. Hundertmark, C.C. Schwartz and T.R. Stephenson. Estimation of body composition in moose. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration Final Report. Grants W-23-5, W-24-1, W-24-2, W-24-3 and W-24-4, Study 1.42.

SWENSON, J.E., F. SANDEGREN, A. SÖDERBERG, A. BJÄRVALL, R. FRANZÉN AND P. WABAKKEN. 1997. Infanticide caused by hunting of male bears. Nature 386:450-451.

TAYLOR, W.P. JR., H.V. REYNOLDS AND W.B. BALLARD. 1989. Immobilization of grizzly bears with tiletamine hydrochloride and zolazepam hydrochloride. Journal of Wildlife Management. 53:978-981.

TAYLOR, M., ed. 1994. Density-dependent population regulation in black, brown and polar bears. International Conference on Bear Research and Management. Monograph Series Number 3. 43pp.

WEILGUS, R.B., AND BUNNELL, F.L. 1994. Dynamics of a small, hunted brown bear *Ursus arctos* population in southwestern Alberta, Canada. Biological Conservation. 67:161-166.

WHITE, G.C. 1993. Evaluation of radio tagging marking and sighting estimators of population size using Monte Carlo simulations. Pages 91-103 *in* J. D. Lebreton and P. M. North, eds. Marked individuals in the study of bird populations. Birkhauser Verlag. Basel, Switzerland.

WHITE, G.C., AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press. San Diego, Calif. 383pp.

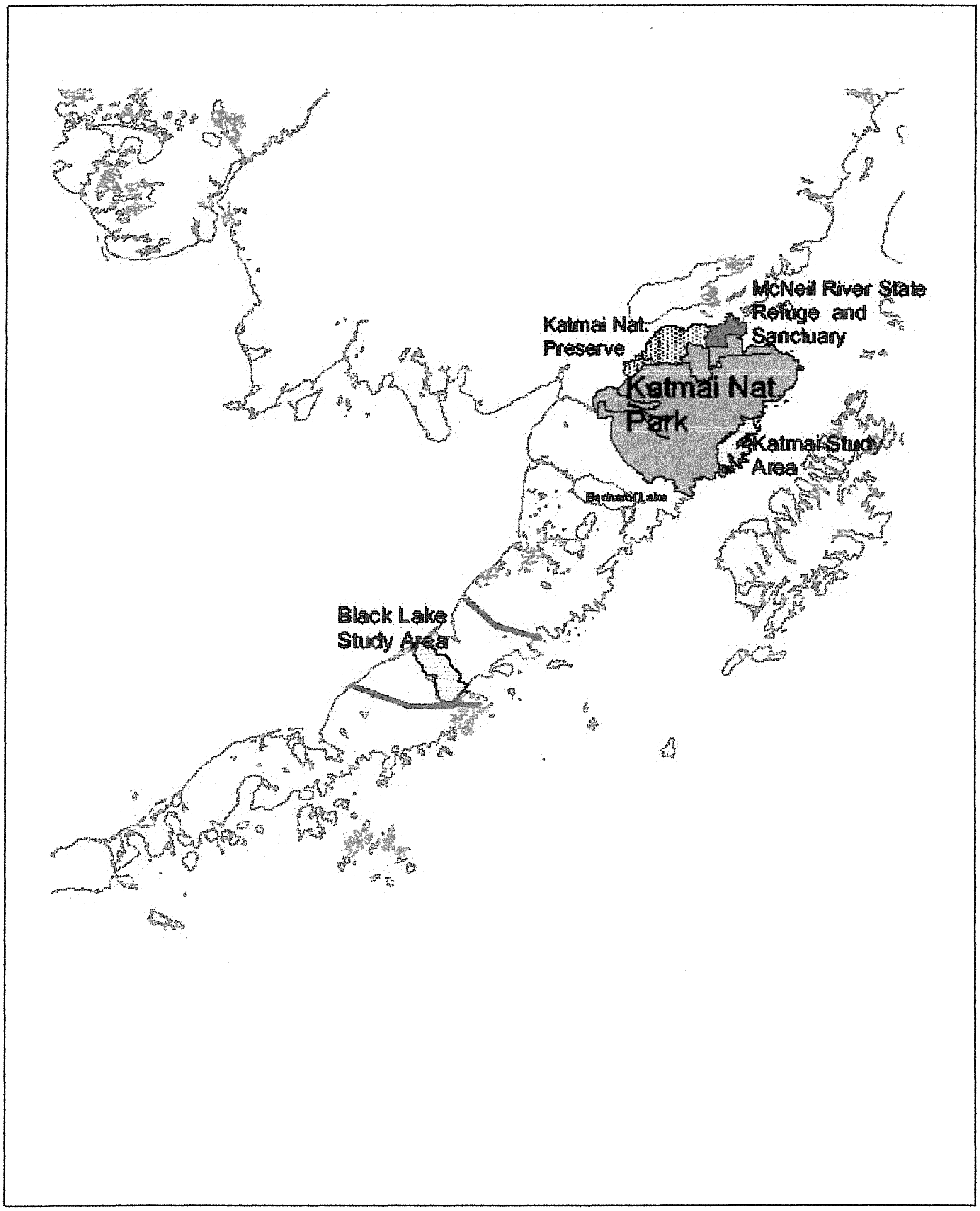

Figure 1. Brown bear study areas on the Alaska Peninsula

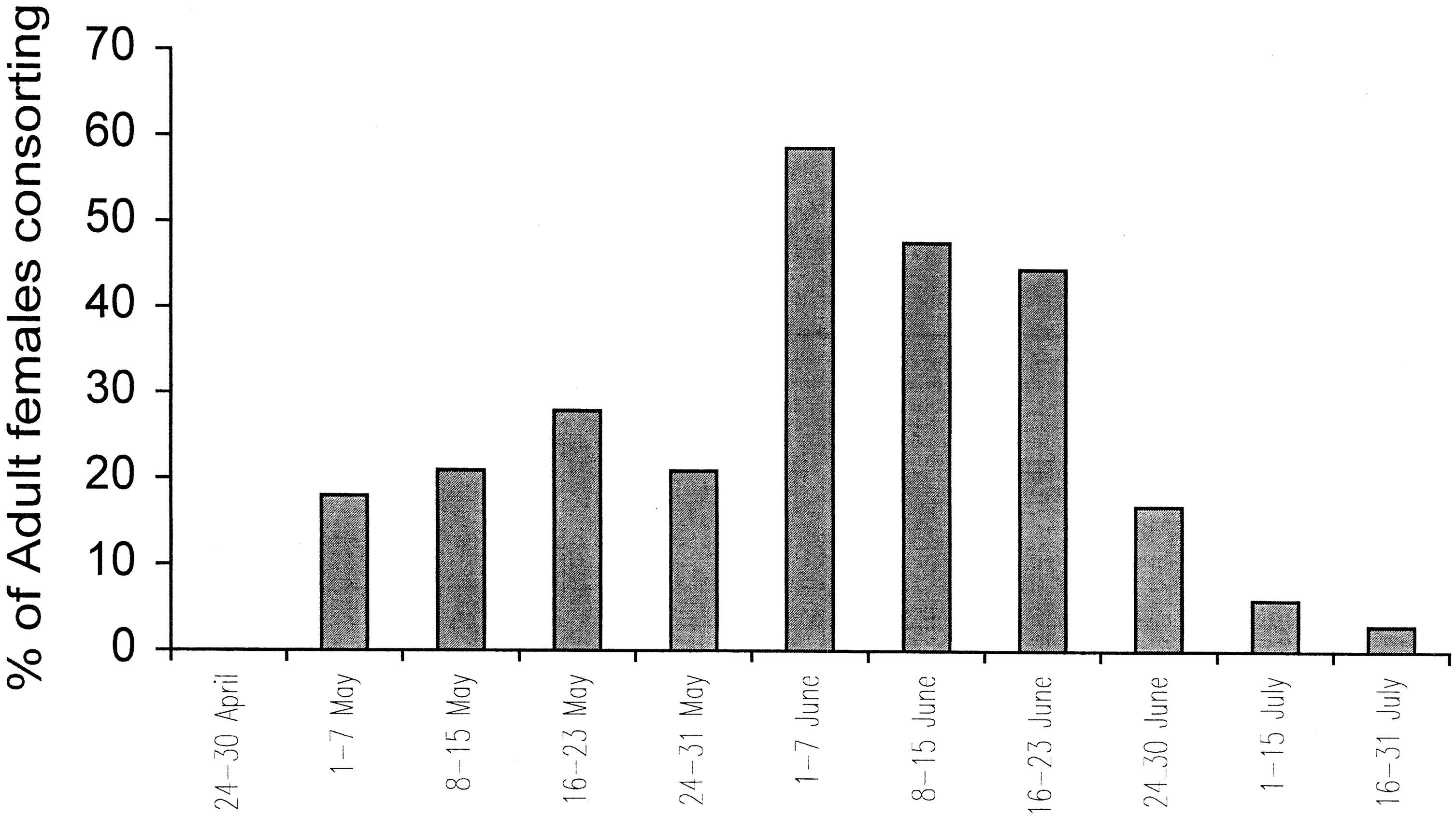

Figure 2. Progression of breeding activity at Katmai, 1989-1996.

Table 1. Brown bears captured in Katmai, 1989-1996.

Tattoo	Sex	Age	Weight[a]	Capture Date	Ear tags			Radio Collar Type	Hb[c]	PCV[d]	Comments
					Left	Right	Color[b]				
101	M	5	~400	5/31/89	42	41	R	Canvas	14.2	41.0	Alone
102	M	8	~800	5/31/89	2509	2651	R	None	16.5	45.0	With uncaptured female
103	M	4	~275	5/31/89	51	55	R	Canvas	13.9	41.0	Alone
104	F	14	425	5/31/89	53	54	W	Regular	15.0	43.0	With #105
105	M	20	~900	5/31/89	2641	95	R	None	17.0	45.0	With #104
106	F	6	~400	6/4/89	99	95	Y	Regular	16.2	48.0	With #107
107	M	13	~800	6/4/89	39	40	R	None	16.5	48.5	With #106
108	F	5	~250	6/4/89	3088	3086	Y	Regular	16.7	48.5	With uncaptured ad. male
109	M	7	~430	6/4/89	2634	2628	R	Canvas	16.0	46.5	Alone
110	M	7	~375	6/4/89	47	48	R	Canvas	14.6	42.0	Alone
111	F	10	~300	6/5/89	3066	3208	Y	Regular	15.9	46.5	W/2@2
112	F	12	~350	6/5/89	3098	86	Y	Regular	14.3	41.0	W/2@1
113	F	19	~375	6/5/89	NONE	300	Y	Regular			W/2@2, Becharof #05-02
114	F	9	~375	6/5/89	262	253	Y	Regular	13.8	37.5	W/2@0
115	F	4	~325	6/5/89	3001	3097	Y	Regular	15.0	42.0	With uncaptured adult male
116	M	4	~350	6/5/89	83	72	R	Canvas	16.2	48.0	Alone
117	F	6	~325	6/5/89	3298	3031	Y	Regular	13.8	41.0	Alone
118	F	12	~300	6/5/89	265	266	Y	Regular	17.6	48.5	With #119
119	M	10	~800	6/5/89	46	93	R	None	17.7	50.0	With #118
120	F	8	~400	6/5/89	256	260	Y	Regular	14.5	41.5	W/1@2
121	M	3	~350	6/5/89	2638	2685	R	Canvas	13.6	39.0	Alone
122	M	3	~200	6/5/89	61	2640	R	Canvas	15.5	43.0	Alone
123	F	11	~350	6/5/89	3039	3050	Y	Regular	15.0	40.0	W/1@0
124	F	8	~400	6/5/89	3051	3029	Y	Capt. mort.			With uncaptured adult male
125	M	8	~500	6/6/89	2644	2669	R	None	16.5	49.0	Alone
126	F	5	~300	6/6/89	257	259	Y	Regular	15.6	44.5	With uncaptured adult male
127	F	4	~225	6/6/89	3003	3030	Y	Canvas	18.7	49.5	Alone
128	F	16	~350	6/6/89	3285	3028	Y	Regular	14.5	39.5	W/1@1
129	F	15	430	6/6/89	267	272	Y	Regular	12.5	35.5	W/2@2
130	F	11	~300	6/6/89	3210	3041	Y	Regular	16.5	47.5	W/1@1
131	F	16	~350	6/6/89	3057	3096	Y	Canvas	10.2	29.0	Alone
132	F	10	~375	6/6/89	3038	3021	Y	Regular	15.9	44.0	With uncaptured adult male
133	F	8	~430	6/6/89	271	251	Y	Regular	16.7	45.5	Alone
134	F	4	~200	6/6/89	3280	3069	Y	Canvas	13.9	39.0	Alone

Table 1. Continued.

ID	Sex	Age	Weight[a]	Capture Date	Ear tags			Radio Collar Type	Hb[c]	PCV[d]	Comments
					Left	Right	Color[b]				
135	F	8	~325	6/6/89	100	3014	Y	Regular	16.3	47.0	W/2@1
136	F	8	~400	6/13/89	3073	3035	Y	Regular	14.6	45.0	W/2@1
127	F	5	~375	5/21/90				Regular	17.0	50.0	Alone
135	F	9	~325	5/19/90				Regular	13.8	36.4	Alone
137	M	16	~950	5/19/90	345	346	R	Glue-on			Alone
138	M	12		5/19/90	303	205	R	Glue-on	15.5	45.7	Alone
139	M	6	~250	5/19/90	211	306	R	Glue-on	15.0	44.2	Alone
140	M	8		5/19/90	207	222	R	Canvas	15.3	42.0	Alone
141	M	15	~850	5/19/90	327		R	Glue-on	16.0	47.5	Alone
142	M	14		5/19/90	181	197	Y	Glue-on	15.0	41.5	Alone
143	F	16	~300	5/19/90	185	177	Y	Regular	14.8	44.1	W/2@2
144	M	3		5/19/90	307	309	R	Canvas	15.0	43.6	Alone
145	F	11	~325	5/19/90	183	396	Y	Regular	16.7	48.3	With #146
146	M	16	~950	5/19/90	201	202	R	Glue-on	11.0	29.1	With #145
147	M	10	~750	5/20/90	394	388	R	Canvas	13.3		Alone
148	F	6	~275	5/20/90	156	151	Y	Canvas	13.0	36.0	Alone
149	M	12	~750	5/20/90	341	333	R	Glue-on	10.5	26.0	Alone
150	M	10	~950	5/20/90	304	311		Glue-on	18.0	45.0	Alone
151	F	4	~250	5/20/90	393	383	Y	Canvas	14.5	45.8	Alone
152	M	19	~1000	5/20/90	221	301	R	Glue-on			Alone
153	M	10	~550	5/20/90	219	220	R	Glue-on	14.0	41.7	Alone
154	F	11	~325	5/20/90	400	176	Y	Regular			W/1@2 or 3
155	M	3	~225	5/20/90	334	332	R	Canvas	13.3	37.4	Alone
156	M	23	~850	5/20/90	225	215	R	Glue-on	14.5	35.3	With uncaptured female
157	M	7	~450	5/20/90	314	313	R	Canvas	14.0	47.8	With uncaptured female
158	M	5	~250	5/20/90	316	319	R	Canvas	13.5		Alone
159	F	8	~275	5/20/90	397	180	Y	Regular	14.8	45.1	W/1@1
160	F	15		5/20/90	31	29	Y	Regular	14.3	28.4	W/1@2
161	F	8	~300	5/21/90	46	36	Y	Regular	15.5	50.0	W/2@2 or 3
162	M	5	~400	5/21/90	370	365	R	Canvas	17.0	51.7	With #163
163	F	5		5/21/90	420	409	Y	Canvas	15.0	41.4	With #162
164	F	4	290	5/21/90	392	394	W	Canvas	16.5	50.9	With uncaptured subadult

Table 1. Continued.

					Ear tags						
ID	Sex	Age	Weight[a]	Capture Date	Left	Right	Color[b]	Radio Collar Type	Hb[c]	PCV[d]	Comments
165	M	8		5/21/90	213	214	R	Glue-on	14.5	43.1	Alone
167	M	2	~175	5/21/90	340	343	R	Glue-on	14.0	46.6	Alone, killed by another bear
168	F	5		5/21/90	26	27	Y	Canvas	12.5	34.5	With uncaptured subadult
169	F	14	~375	5/21/90	176	416	Y	Regular	17.3	51.7	W/1@2
170	M	7		5/21/90	355	351	R	Glue-on	15.5	44.8	Alone
171	F	22	~500	5/21/90	042	33	Y	Regular	16.4	49.1	Alone
172	F	12		5/21/90	049	45	Y	Regular	15.0	44.8	W/2@1
173	F	10	~400	5/21/90	158	174	Y	Regular	14.5	44.0	W/2@2
174	F	14		5/21/90	408	407	Y	Regular	16.0	49.1	With #175, Becharof #84-09
175	M	9	~750	5/21/90	391	376	R	Glue-on			With #174
176	M	10	~575	5/22/90	352	359	R	Canvas	18.5	47.0	Alone
177	F	5	325	5/22/90	187	190	Y	Glue/Can	15.8	44.8	Alone
178	F	17	~450	6/12/90	270	268	Y	Regular			W/2@1
140	M	9	~700	10/23/91				Remove collar			With another large male
144	M	4	~550	10/23/91				Remove collar			W/3@0, Capture mortality
148	F	7	~375	10/23/91				Remove collar			Alone
158	M	6		10/23/91				Remove collar			Alone
104	F	17		6/6/92	053	054	Y	Regular		41.0	Alone
106	F	9		6/5/92	099	095	Y	Regular			With uncaptured bear
108	F	8	~350	6/6/92	3088	3086	Y	Regular		49.0	W/3@0
111	F	13		6/5/92	3066	3208	Y	Regular			With uncaptured adult male
113	F	22		6/5/92	036	217	Y/W	Regular			W/2@2
117	F	9	~350	6/4/92	3298	3031	Y	Regular		49.0	W/3@0
120	F	11		6/6/92	256	260	Y	Regular		49.0	W/1@0
126	F	8		7/16/92				Regular			W/3@0
128	F	19		7/16/92				Regular			W/3@0
130	F	13		6/5/92	3210	3041	Y	Regular		48.0	With uncaptured adult male
136	F	11		7/16/92				Regular			W/2@0
145	F	13	~375	6/6/92	183	396	Y	Regular		45.0	W/2@1
163	F	7	~375	6/6/92	420	409	Y	Regular		45.0	With uncaptured adult male
172	F	14		6/6/92	049	045	Y	Regular		40.0	Alone
174	F	16		6/7/92	408	407	Y	Regular		49.0	Alone
179	F	10	~400	6/4/92	205	206	W	Regular		43.0	W/2@2

Table 1. Continued.

ID	Sex	Age	Weight[a]	Capture Date	Ear tags Left	Ear tags Right	Ear tags Color[b]	Radio Collar Type	Hb[c]	PCV[d]	Comments
180	M	4	~450	6/4/92							Alone
181	F	8	~400	6/4/92	319	315	W	Regular		46.0	W/1@1
182	F	21	~450	6/4/92	309	305	W	Regular		41.0	W/1@2
183	F	13	~375	6/4/92	423	178	Y	Regular		49.0	With #184
184	M	9	~800	6/4/92				None			With #183
185	F	13		6/5/92	403	413	Y	Regular		48.0	W/2@2
186	F	11	~400	6/6/92	157	256	Y/W	Regular			W/2@1
187	F	10	~450	6/6/92	252	255	Y	Regular		45.0	W/2@2
188	F	19	~450	6/6/92	204	201	W	Regular		44.0	W/3@2
189	M			6/6/92	195	387	Y	Regular		43.0	Alone
190	F	14	~450	6/6/92	192	415	Y	Regular		41.0	W/2@1
191	F	15	~450	6/6/92	164	163	Y	Regular		39.0	W/3@0
192	F	17	~300	6/7/92	389	199	Y	Regular		43.0	W/1@1
193A	F	17	~450	6/7/92	40	050	Y	Regular		46.0	W/1@1
193B	F	8		7/17/92	3053	121	Y	Regular		48.0	W/1@2
135	F	12	295	5/17/93	121	121	R/Y	Regular	13.0	43.0	W/4@2
154	F	14	~380	7/15/93	400	176	Y	Regular			W/1@1
301	F	6	370	5/17/93	125	None	Y	Regular	12.7	46.5	With young male
302	M	2	210	5/17/93	108	108	Y/R	Expandable	14.3	42.0	With mother #193
303	M	2	~140	5/17/93	118	118	Y/R	None	14.0	49.5	With mother #186, Killed by male
304	M	2	~70	5/17/93	104	104	Y/R	Expandable	14.0	46.0	With mother #135 & siblings
305	F	2	~70	5/17/93	127	127	R/Y	Expandable	13.5	45.0	With mother #135 & siblings
306	M	2	~90	5/17/93	117	117	Y/R	Expandable	12.5	41.0	With mother #135 & siblings
307	F	2		5/17/93	126	126	R/Y	Expandable	10.9	39.5	With mother #185
308	M	2		5/17/93	105	105	Y/R	Expandable	13.2	43.5	With mother #145
309	F	2	~70	5/17/93	101	101	R/Y	Expandable	12.0	35.5	With mother #145
310	F	19	315	5/17/93	123	123	Y/R	Regular	14.5	45.5	W/3@1
311	F	3	~135	5/17/93	103	103	R/Y	Expandable	13.5	56.0	With mother #187
312	M	3	~140	5/17/93	124	124	Y/R	Expandable	13.8	44.0	With mother #187
313	F	5	350	5/18/93	114	114	R/Y	Regular	14.7	37.4	With uncaptured adult male
314	F	4	265	5/18/93	111	111	R/Y	Expandable	16.6	49.5	With mother #179

Table 1. Continued.

				Capture	Ear tags			Radio Collar			
ID	Sex	Age	Weight[a]	Date	Left	Right	Color[b]	Type	Hb[c]	PCV[d]	Comments
315	M	4		5/18/93	102	102	Y/R	Expandable	15.2	43.4	With mother #188
316	F	4	~110	5/18/93	106	106	R/Y	Expandable	16.5	47.0	With mother #188
317	F	12	525	5/18/93	122	122	Y/R	Regular	14.0	52.5	With uncaptured adult male
318	M	5	415	5/18/93	116	116	Y/R	none	14.7	44.5	With uncaptured adult male
319	F	10	330	5/18/93	109	109	R/Y	Regular	16.2	49.5	W/2@1
320	F	18	385	5/19/93				Regular	13.1	42.5	W/2@1
321	F	4	345	5/19/93	110	110	R/Y	Regular	13.2	41.5	With uncaptured adult male
322	F	21	260	5/19/93				Regular	12.7	37.5	W/2@2
323	M	2	~60	5/19/93	112	112	Y/R	Expandable	10.9	38.0	With mother #322
324	M	2	~80	5/19/93	129	129	R/Y	Expandable	10.7	37.5	With mother #322
325	F	23	340	5/19/93	128	128	Y/R	Regular	12.8	42.0	W/2@2
326	M	2	~120	5/19/93	132	132	Y/R	Expandable			With mother #325
327	F	2	~75	5/19/93	107	107	R/Y	Expandable	10.8	36.0	With mother #325
328	F	2	~140	5/19/93	120	120	R/Y	Expandable	12.8	41.0	With mother #190
329	M	2	195	5/19/93	131	131	Y/R	Expandable	15.0	42.0	With mother #190

[a] Weights are in pounds, and those preceded by a ~ sign were estimated.

[b] One letter (R - red; W - white; Y - yellow) indicates the same color in both ears. Two letters indicates the color of the L/R ear tag.

[c] Percent hemoglobin.

[d] Percent packed cell volume.

Table 2. Status of marked brown bears during density estimation on Katmai coast, 1990. Data on group size refer to females with dependent young; other types of groups are indicated as (P), pairs, or (S), siblings.

		Young		Rep.1 (6/3)			Rep.2 (6/5)			Rep.3 (6/6)			Rep.4 (6/7)								
ID	Sex	Int. no.	Est. age	In?	Group size	Seen?	In?	Group size	Seen?	In?	Group size	Seen?	In?	Group size	Seen?	No. out	No. in	No. seen	% in	% seen	Final family status
104	F			IN			IN			IN			IN			0	4		100	0	
106	F	1	0	IN	1?		IN	1?		IN	1?		IN	1?		0	4		100	0	W/AD MALE ON 6/8
108	F			IN	(P)	YES	IN			IN			IN			0	4	1	100	25	
111	F	2	3	IN	1?		IN	1?		IN	1?		IN	1?		0	4		100	0	W/AD MALE ON 6/8
113	F	3	0	IN	4		IN	4		IN	4		IN	4		0	4		100	0	W/3 COY ON 6/8
114	F	2	1	IN	3	YES	IN	3		IN	3		IN	3		0	4	1	100	25	W/2 @ 1 ON 6/8
117	F	1	0	IN	2		IN	2		IN	2	YES	IN	2	YES	0	4	2	100	50	W/1 COY ON 6/7
118	F			IN			IN			IN			IN			0	4		100	0	
120	F	1	3	IN	2		IN	2	YES	IN	2	YES	IN	(P)	YES	0	4	3	100	75	W/AD MALE ON 6/7
121	M			OUT			OUT			OUT			OUT			4	0		0		
123	F	3	0	OUT			OUT			OUT			OUT			4	0		0		
126	F			IN			IN	(P)	YES	IN			IN			0	4	1	100	25	
127	F			IN			IN			IN			IN			0	4		100	0	
128	F			IN	(P)	YES	IN			IN			IN			0	4	1	100	25	
129	F	2	3	IN	1?		IN	1?		IN	1?		IN	1?		0	4		100	0	ALONE ON 7/11
130	F	1	2	IN	2		IN	2		IN	2		IN	2		0	4		100	0	W/1 @ 1 ON 6/8
132	F	1	0	IN	2		IN	2		IN	2		IN	2		0	4		100	0	W/1 COY ON 6/12
133	F			IN	1	YES	IN	(P)	YES	IN			IN			0	4	2	100	50	ALONE BY 6/3
134	F			IN			IN			IN			IN			0	4		100	0	
135	F	2	2	IN	1?		IN	(P)	YES	IN	(P)	YES	IN			0	4	2	100	50	W/AD MALE ON 6/5
136	F			OUT			OUT			OUT			OUT			4	0		0		
139	M			IN			IN		YES	IN		YES	IN		YES	0	4	3	100	75	
140	M			IN			IN			IN			IN		YES	0	4	1	100	25	
143	F	2	2	IN	1?		IN	(P)	YES	IN			IN			0	4	1	100	25	W/AD MALE ON 6/5
144	M			IN			IN			IN			IN			0	4		100	0	
145	F			IN			IN			IN			IN			0	4		100	0	
146	M			IN			IN	(P)	YES	IN	(P)	YES	IN	(P)	YES	0	4	3	100	75	
147	M			OUT			OUT			OUT			OUT			4	0		0		
148	F			IN			IN			IN			IN			0	4		100	0	
151	F			IN			IN			IN			IN			0	4		100	0	
153	M			IN			IN			DROPPED			DROPPED			0	2		100	0	
154	F	1	2	IN	2		IN	2		IN	2	YES	IN	2		0	4	1	100	25	TOGETHER 6/6
155	M			IN			IN			IN			IN			0	4		100	0	
157	M			IN			IN	(P)	YES	IN			IN			0	4	1	100	25	
158	M			IN			IN			IN	(P)	YES	IN			0	4	1	100	25	
159	F	1	1	IN	2	YES	IN	2	YES	IN	2		IN	2		0	4	2	100	50	
161	F	2	2	IN	1?		IN	1?		IN	1?		IN	1?		0	4		100	0	SHED BY 6/27
162	M			IN			IN		YES	IN			IN			0	4	1	100	25	
163	F			IN			IN			IN			IN			0	4		100	0	
164	F	1	3	IN	1?		IN	1?		IN	1	YES	IN			0	4	1	100	25	ALONE ON 6/6
165	M			IN			IN			IN			IN	(P)	YES	0	4	1	100	25	
168	F			IN	(S)	YES	IN	(P)	YES	IN	(P)	YES	IN	(P)	YES	0	4	4	100	100	
169	F	1	2	IN	2	YES	IN	2?		IN	2?		IN	2?		0	4	1	100	25	UNKNOWN
171	F			IN			IN			IN			IN	(P)	YES	0	4	1	100	25	

Table 2. Continued.

		Young			Rep.1 (6/3)		Rep.2 (6/5)			Rep.3 (6/6)			Rep.4 (6/7)							
ID	**Sex**	**Int. no.**	**Est. age**	**In?**	**Group size**	**Seen?**	**In?**	**Group size**	**Seen?**	**In?**	**Group size**	**Seen?**	**In?**	**Group size**	**Seen?**	**No. out**	**No. in**	**No. seen**	**% in**	**% seen**	**Final family status**
172	F	2	1	IN	3		IN	3		IN	3	YES	IN	3	YES	0	4	2	100	50	W/2 @1 ON 6/27
173	F	2	2	IN	3		IN	3		IN	3	YES	IN	3		0	4	1	100	25	W/2 @ 2 ON 6/27
174	F			IN			IN			IN	(P)	YES	IN			0	4	1	100	25	
177	M			IN			IN			IN		YES	IN			0	4	1	100	25	
															TOTAL	16	174	40	92	21	

Table 3. Summary of observations of brown bears during brown bear density estimate on Katmai coast, June 1990. "Independent bears" excludes offspring, of whatever age, still with their mothers.

	REPLICATION						
	1	2	3	4	MEAN	MIN.	MAX.
Marked bears present, all ages (most likely number)	62	62	61	60	61.3	60	62
Independent marked bears present	44	44	43	43	43.5	43	44
Marked bears seen							
All ages	11	13	20	12	14.0	11	20
Independent	7	11	13	9	10.0	7	13
Unmarked bears seen, all ages	80	100	121	99	100.0	80	121
No. cubs-of-year	0	4	4	7	3.8	0	7
No. yearlings	12	19	10	1	10.5	1	19
No. older than yearlings	68	77	107	91	85.8	107	68
No. independent	64	72	88	79	75.8	64	88
Total marked and unmarked bears seen							
No. all ages	91	113	141	111	114.0	91	141
No. independent	71	83	101	88	85.8	71	101
Sightability, independent marked bears							
No. inside area	44	44	43	43	43.5	43	44
No. seen	7	11	13	9	10.0	7	13
% seen	15.9	25.0	30.2	20.9	23.0	16.3	29.5

Table 4. Population and density estimates for brown bears in Katmai National Park and Preserve coastal study area using bear-days estimator.

Estimates for bears of all ages

Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	% seen	Cumulative estimate no. bears	Density No. bears/ 1000km2	Number of bears		Bears/1000 km2	
								Lower	Upper	Lower	Upper
6/3/90	62	11	91	482	18	482	535	301	1002	334	1111
6/5/90	62	13	113	512	21	512	568	365	806	405	895
6/6/90	61	20	141	418	33	476	529	368	655	409	726
6/7/90	60	12	111	525	20	493	547	394	651	437	722
			cumulative % =		23						
			mean daily L-P=	484			537				
			SE=	20.5							

Estimate of population size based on independent bears only (excluded offspring with their mothers)

Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	% seen	Cumulative estimate no. bears	Density No. bears/ 1000km2	95% CI			
								Number of bears		Bears/1000 km2	
								Lower	Upper	Lower	Upper
6/3/90	44	7	71	404	16	404	448	228	1084	254	1203
6/5/90	44	11	83	314	25	363	402	247	621	274	690
6/6/90	43	13	101	320	30	352	390	260	519	288	576
6/7/90	43	9	88	391	21	367	407	280	514	311	571
			cumulative % =		23						
			mean daily L-P=	357			396.2				
			SE=	20.3							

Estimate for bears × 2 years old

Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	% seen	Cumulative estimate no. bears	Density No. bears/ 1000km2	95% CI			
								Number of bears		Bears/1000 km2	
								Lower	Upper	Lower	Upper
6/3/90	52	8	76	452	15	452	502	264	1116	293	1238
6/5/90	52	12	89	366	23	415	460	287	688	319	763
6/6/90	51	17	126	366	33	399	443	302	567	335	629
6/7/90	50	9	98	504	18	427	474	332	583	368	647
			cumulative % =		22.4						
			mean daily L-P=	422			468.3				
			SE=	29.5							

Table 5. Estimate of brown bear density using the bear-days estimator and maximum and minimum numbers of offspring still with their mothers.

Estimate for all bears with maximum number of offspring still with their mothers

Brown bears, based on normal distribution

DATE	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Sightability	Est. density No./1000km2	95% CI no. bears		95% CI for density	
							Lower	Upper	Lower	Upper
6/3/90	73	11	91	566	0.15	628	354	1179	393	1309
6/5/90	71	13	113	585	0.18	659	424	936	470	1039
6/6/90	69	20	141	472	0.29	608	424	754	471	836
6/7/90	68	12	111	593	0.18	627	452	747	502	828
			cumulative % sightability=		0.20					
			mean daily L-P=	554		615				
			SE=	24						

Estimate for all bears with minimum number of offspring still with their mothers

Brown bears, based on normal distribution

DATE	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Sightability	Est. density No./1000km2	95% CI no. bears		95% CI for density	
							Lower	Upper	Lower	Upper
6/3/90	60	11	91	467	0.18	518	291	969	323	1076
6/5/90	60	13	113	496	0.22	550	353	780	392	866
6/6/90	59	20	141	405	0.34	512	356	633	396	703
6/7/90	58	12	111	507	0.21	529	381	630	423	699
			cumulative % sightability=		0.21					
			mean daily L-P=	469		520				
			SE=	20						

Table 5. Continued.

Estimate for bears >2.0 with maximum number of offspring still with their mothers

Brown bears, based on normal distribution

DATE	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Sightability	Est. density No./1000km2	95% CI no. bears Lower	95% CI no. bears Upper	95% CI for density Lower	95% CI for density Upper
6/3/90	62	8	76	538	0.13	597	315	1330	349	570
6/5/90	60	12	89	421	0.20	539	337	807	374	346
6/6/90	58	17	126	415	0.29	514	351	659	389	282
6/7/90	57	9	98	573	0.16	548	383	674	425	289
	cumulative % sightability=				0.16					
		mean daily L-P=		487		549				
			SE=	35						

Estimate for bears >2.0 with minimum number of offspring still with their mothers

Brown bears, based on normal distribution

DATE	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Sightability	Est. density No./1000km2	95% CI no. bears Lower	95% CI no. bears Upper	95% CI for density Lower	95% CI for density Upper
6/3/90	50	8	76	435	0.16	435	254	1073	282	1191
6/5/90	50	12	89	352	0.24	399	276	661	307	734
6/6/90	49	17	126	352	0.35	384	290	545	322	605
6/7/90	48	9	98	484	0.19	410	319	560	353	622
	cumulative % sightability=				0.19					
		mean daily L-P=		406		407				
			SE=	28						

Table 6. Brown bear density estimate in the Katmai National Park and Preserve study area using the mean of Lincoln Petersen estimates and confidence interval based on sampling mean (Eberhardt 1990). Additional estimates made using maximum and minimum numbers of offspring still with their mothers.

Bears of all ages, most likely number of marks present

Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Mean of L-Ps	Sample Variance	Density #/1000km2	95% CI			
								No. of bears		No./1000km2	
								lower	upper	lower	upper
6/3/90	62	11	91	482	482		535				
6/5/90	62	13	113	512	497	450	551	306	688	340	763
6/6/90	61	20	141	418	471	2293	522	352	590	390	654
6/7/90	60	12	111	525	484	2252	537	409	560	454	621

Independent bears only, most likely number of marks present

Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Mean of L-Ps	Sample Variance	Density #/1000km2	95% CI			
								No. of bears		No./1000km2	
								lower	upper	lower	upper
6/3/90	44	7	71	404	404		448				
6/5/90	44	11	83	314	359	4050	398	-213	931	-236	1033
6/6/90	43	13	101	320	346	2543	384	221	471	245	523
6/7/90	43	9	88	391	357	2196	396	282	432	313	479

Bears > 2 only, most likely number of marks present

Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Mean of L-Ps	Sample Variance	Density #/1000km2	95% CI			
								No. of bears		No./1000km2	
								lower	upper	lower	upper
6/3/90	52	8	76	452	452		502				
6/5/90	52	12	89	366	409	3743	454	-140	959	-156	1064
6/6/90	51	17	126	366	395	2496	438	271	519	300	576
6/7/90	50	9	98	504	422	4643	468	314	530	348	589

Table 6. Continued.

Bears of all ages, maximum number of marks present

Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Mean of L-Ps	Sample Variance	Density #/1000km2	No. of bears lower	No. of bears Upper	No./1000km2 lower	No./1000km2 upper
6/3/90	73	11	91	566	566		628				
6/5/90	71	13	113	585	576	180	639	455	696	505	773
6/6/90	69	20	141	472	541	3659	601	391	692	434	767
6/7/90	68	12	111	593	554	3119	615	465	643	517	714

Bears > 2.0 only, maximum number of marks present

								95% CI			
								No. of bears		No./1000km2	
Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Mean of L-Ps	Sample Variance	Density #/1000km2	lower	upper	lower	upper
6/3/90	62	8	76	538	538		597				
6/5/90	60	12	89	421	480	6809	532	-262	1221	-290	1355
6/6/90	58	17	126	415	458	4786	508	286	630	318	699
6/7/90	57	9	98	573	487	6497	540	359	615	398	683

Bears of all ages, minimum number of marks present

								95% CI			
								No. of bears		No./1000km2	
Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Mean of L-Ps	Sample Variance	Density #/1000km2	lower	upper	lower	upper
6/3/90	60	11	91	467	467		518				
6/5/90	60	13	113	496	481	422	534	297	666	329	739
6/6/90	59	20	141	405	456	2160	506	340	571	378	634
6/7/90	58	12	111	507	469	2106	520	396	542	439	601

Bears >2.0 only, minimum number of marks present

								95% CI			
								No. of bears		No./1000km2	
Date	Marks present	Marks seen	Total seen	Daily L-P est. bears present	Mean of L-Ps	Sample Variance	Density #/1000km2	lower	upper	lower	upper
6/3/90	50	8	76	435	435		483				
6/5/90	50	12	89	352	394	3466	437	-135	923	-150	1024
6/6/90	49	17	126	352	380	2319	421	260	499	289	554
6/7/90	48	9	98	484	406	4269	450	302	510	335	566

Table 7. Brown bear population and density estimates in Katmai National Park and Preserve, using the joint-hypergeometric, maximum likelihood estimator (Miller et al. 1997). Data on most likely number of marks present when date of weaning was uncertain.

		Population	95% CI		Density	95% CI	
	T_i	estimate	Lower	Upper	(#/1000km2)	Lower	Upper
Bears of all ages	62	496	405	627	551	450	694
Independent bears	44	372	292	493	412	325	545
Bears >2.0	52	431	341	568	479	384	619

Table 8. Katmai estimates with variable number of offspring still with marked mothers when date of weaning was uncertain.

	Number of bears			Density (no./1000 km^2)			% difference from best estimate
		95% CI			95% CI		
	Estimate	Lower	Upper	Estimate	Lower	Upper	
Bear-days estimator							
All bears							
Minimum	477	381	630	529	423	699	-3.2
Best	493	394	651	547	437	722	
Maximum	565	452	747	627	502	829	14.6
Bears > 1							
Minimum	411	319	560	456	354	621	-3.7
Best	427	332	583	474	368	647	
Maximum	494	383	674	548	425	748	15.7
Mean Lincoln-Petersen estimator							
All bears							
Minimum	468	395	541	519	438	600	-3.3
Best	484	409	560	537	453	621	
Maximum	554	465	643	615	516	713	14.5
Bears > 1							
Minimum	406	302	510	451	335	566	-3.8
Best	422	314	530	468	348	589	
Maximum	584	456	712	648	506	790	38.4

Table 9. Brown bear population composition from three samples on the Katmai Coast, 1989-1991.

	Capture Samples[a]		CMR Observations[b]		Telemetry Observations[c]	
	n	%	n	%	n	%
Female with cubs	4	1.6	9	2.0	41	2.9
Females with ≥1-year-olds	32	12.4	59	12.9	146	10.3
Cubs	7	2.7	17	3.7	92	6.5
≥1-year-olds	54	20.9	96	21.1	246	17.3
Bears not in family groups	161	62.4	275	60.3	901	63.4
Total	258		456		1426	

[a] Bears captured or observed during capture operations, 31 May - 6 June 1989 and 19 May - 22 May 1990.

[b] Bears observed during CMR density estimation flights, 1990.

[c] Bears observed during summer (23 Jun - 21 Aug) telemetry flights, 1989-1991.

Table 10. Brown bear composition surveys of Katmai National Preserve, 22-30 May 1993.

Area	Date	Number minutes	Number w/ cubs Litter size		Number w/ yearlings Litter size		Number w/2-yr.-olds Litter size		Number breeding pairs	Number single bears			Total bears	Bears/ hour	
			2	3	2	3	1	2		small	medium	large			
Nanuktuk Cr.															
363 km^2	5/22/93	221	0	0	0	0	0	1	3	4	2	0	15	4.07	
	5/27/93	251	0	1	0	0	1	0	4	2	5	2	23	5.5	
	5/29/93	268	0	1	1	0	0	1	5	1	6	0	27	6.04	
Moraine Cr.															
388 km^2	5/24/93	107	0	0	0	0	0	0	1	0	1	0	3	1.68	Aborted
	5/27/93	286	0	0	1	1	0	0	0	2	1	1	11	2.31	
	5/30/93	307	2	0	0	1	0	0	0	0	2	2	14	2.74	
Branch															
145 km^2	5/22/93	101	0	0	0	0	0	0	0	0	0	1	1	0.59	
	5/29/93	78	0	0	0	0	0	0	1	0	1	0	3	2.31	
N. of Kukaklek															
197 km^2	5/24/93	102	0	0	0	1	0	0	0	0	0	0	4	2.35	
	5/30/93	93	0	0	0	0	0	0	1	0	0	0	2	1.29	
Total		**1,814**	**2**	**2**	**2**	**3**	**1**	**2**	**15**	**9**	**18**	**6**	**103**	**3.41**	(Avg.)

Table 11. Annual production by available[a] radiocollared adult female brown bears in Katmai National Park and Preserve, 1990-1996.

Year	Number of available females the previous year	Percent producing litters	Mean litter size	Number of cubs per available females
1990	11	45	1.80	0.82
1991	19	32	2.00	0.63
1992	14	57	2.50	1.36
1993	9	33	1.67	0.56
1994	20	65	2.08	1.35
1995	15	47	2.14	1.00
1996	7	57	1.75	1

[a] Available females were not accompanied by dependent offspring during at least a portion of the preceding breeding season.

Table 12. Annual Kaplan-Meier survival rates in Katmai, 1989-1996.

	n	Survival	95% CI
Adult female	210[a]	0.909	0.87 - 0.95
Adult male	25	0.955	0.72 - 1.00
Subadult female	19	1.000	1.00 - 1.00
Subadult male	19	0.938	0.75 - 1.00
Cub	99	0.342	0.26 - 0.42
Yearling	49	0.790	0.68 - 0.90

[a] Cumulative bear-years.

Table 13. Annual Kaplan-Meier survival rates of radiocollared females and their cubs and yearlings at Katmai, 1989-1996.

	Adult females		Cubs		Yearlings	
Year	*n*	Survival rate	*n*	Survival rate	*n*	Survival rate
1989	19	1.00	2	1.00	4	0.75
1990	35	0.94	9	0.23	7	0.57
1991	27	0.92	14	0.62	0	
1992	30	0.86	21	0.14	14	0.86
1993	32	0.94	5	0.80	10	0.79
1994	30	0.86	24	0.25	4	1.00
1995	25	0.92	15	0.36	9	0.67
1996	12	0.88	9	0.11	1	1.00
Total	**210**	**0.909**	**99**	**0.342**	**49**	**0.79**

Appendix. Observations of natural mortality in Katmai National Park and Preserve not previously published.

Sex/age class	Date	Location	Cause of Death	Observer/ Reporter
Cub (sex unk) of "Goatee"	1989	Brooks River	Conspecific predation by adult male	NPS
Cub (sex unk) of "Fluff"	1992	Brooks River	Conspecific predation by adult male	NPS
Cub (sex unk)	3 July 1996	Brooks Camp	Conspecific predation/killer unknown	H. Boyd, NPS
Cub (male)	16 Sept 1996	Brooks Camp	Conspecific predation/killer unknown	H. Boyd, NPS
Cub (female) of "Petite"	3 July 1997	Brooks River	Conspecific predation by adult male	NPS (video)
2 Cubs	Summer 1996	Swikshak	Conspecific predation by adult female w/cubs	D. Zatz
Cub (sex unk)	20 May 1989	Hallo Bay	Accidental fall	J. McFariane
Cub (presumably of 113)	10 May 1993	Amalik Bay	Conspecific predation by adult male	R. Sellers
Yearling (sex unk) of "Petite"	1988	Brooks River	Conspecific predation by adult male	NPS
Subadult female (4-yr-old)	~ 9 July 1989	Katmai Bay	Conspecific predation/killer unknown	R. Sellers
Subadult male (329)(2-yr-old)	~ June 1993	Becharof	Conspecific predation/killer unknown	R. Sellers
Subadult male	1969	Brooks River	Conspecific predation by adult male	NPS
Adult male (5-yr-old)	14 July 1997	Brooks River	Conspecific predation by adult male	NPS (video)
Adult male	~20 May 1989	E. of Big River	Accidental fall	B. Cook, NPS
Adult male (152)	~ 1 June 1990	Kaflia Bay	Conspecific predation/killer unknown	R. Sellers
Adult female (113)	~4 June 1993	Amalik Bay	Unknown	R. Sellers
Adult female (117) W/ 2 cubs	~ 25 July 1992	Kukak Bay	Conspecific predation/killer unknown	R. Sellers
Adult female (120)	~ 20 April 1996	Hallo Bay	Conspecific predation by adult male	R. Sellers
Adult female (123) W/3 cubs	~ 15 July 1990	Hallo Bay	Conspecific predation/killer unknown	R. Sellers
Adult female (126) W/2 cubs	~ March 1995	Kukak Bay	Injuries, presumably fight with another bear	R. Sellers
Adult female (130)	~15 July 1995	Missak Bay	Unknown	G. Wilker
Adult female (136)	April 1993	E. of Big River	Avalanche	R. Sellers
Adult female (143) W/2 cubs	Sept. 1991	Kukak Bay	Unknown	R. Sellers
Adult female (159) W/1@2	~1 July 1991	Cape Gull	Conspecific predation/killer unknown	R. Sellers
Adult female (160) W/1@2	28 May 1990	Missak Bay	Conspecific predation/killer unknown	R. Sellers
Adult female (173)	Fall 1991	Becharof	Unknown (radio not functioning)	R. Sellers
Adult female (174)	Aug. 1996	Becharof	Unknown	R. Sellers
Adult female (179)	~15 May 1994	Kukak Bay	Unknown	R. Sellers
Adult female (182) W/1@2	~ 10 July 1992	Kukak Bay	Unknown	R. Sellers
Adult female (183) W/2 cubs	~ 10 June 1994	Hallo Bay	Unknown	R. Sellers
Adult female (187) W/2 cubs	1 May 1994	Hidden Harbor	Conspecific predation by adult male	R. Sellers
Adult female (192) W/1@1	~ 1 Sept. 1992	Swikshak	Unknown	R. Sellers
Adult female (317)	~ Nov. 1993	Cape Chiniak	Conspecific predation/killer unknown	R. Sellers