BLACK AND BROWN BEAR DENSITY ESTIMATES USING MODIFIED CAPTURE-RECAPTURE TECHNIQUES IN ALASKA

STERLING D. MILLER, Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, AK 99518-1599
EARL F. BECKER, Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, AK 99518-1599
WARREN B. BALLARD, Alaska Department of Fish and Game, P.O. Box 1148 Nome, AK 99762-1148

Abstract: Population density estimates were obtained for sympatric black bear (*Ursus americanus*) and brown bear (*U. arctos*) populations inhabiting a search area of 1,325 km^2 in south-central Alaska. Standard capture-recapture population estimation techniques were modified to correct for lack of geographic closure based on daily locations of radio-marked animals over a 7-day period. Calculated density estimates were based on available habitat in the search area (1,317 km^2 for brown bears and 531 km^2 for black bears). Calculated density was 2.79 brown bears/100 km^2 (2.52–3.30 bears/100 km^2) and 8.97 black bears/100 km^2 (7.74–10.21 bears/100 km^2). Calculated 95% confidence intervals were ±13.7% of the estimate for black bears and −9.8% to +18.5% of the estimate for brown bears.

Probabilities of capture based on calculated sightability indices were not equal in some instances, so confidence intervals should be interpreted cautiously. Increasing the number of marked bears during the study period resulted in altered brown bear estimates and smaller confidence intervals, but because closure was a relatively good assumption for black bears in our study area, had little effect on black bear estimates or confidence intervals. When telemetry data were used to correct input values for lack of geographic closure, the Schnabel estimator and the mean of 7 separate daily estimates yielded estimates close to our results.

We recommend our technique for additional testing as a method to objectively compare bear densities between different areas or between different times. These procedures may also be appropriate for use with other species.

Int. Conf. Bear Res. and Manage. 7:23–35

Biologists have few good techniques to derive accurate, objective, and replicable estimates of population size and density for many wildlife species, including bears. Such estimates are basic to understanding aspects of bear biology and management that are of primary concern to managers and researchers. Many of the techniques that have been employed to estimate bear population size have been subjective to varying degrees (Harris 1986). Typically, such estimates have no statistical variance and are not replicable.

When density estimates are derived from such population estimates, an additional element of subjectivity is commonly introduced. This derives from uncertainties about the size of the area inhabited by the estimated population. Density estimates are often more meaningful than population estimates because differences in density are likely to reflect corresponding differences in habitat suitability between areas or changes resulting from human-induced impacts. Also, density estimates derived from a small study area can be extrapolated to obtain a population estimate for a larger area of management significance (park, refuge, game management unit, and so forth). This large-area population estimate may be combined with information on numbers of animals harvested to estimate harvest rate.

Bears typically exist in low densities, are secretive and difficult to see during direct surveys, and move over great distances. These characteristics make bear populations difficult to enumerate. Capture-recapture techniques (also called Lincoln or Petersen indices) have been used to estimate population size for many species, including bears (Miller and Ballard 1982). Two critical assumptions of these techniques are that the population is geographically closed and that all individuals in the population have equal probabilities of capture (Seber 1982). Except for island or otherwise restricted populations, the geographic closure assumption is almost always violated to some degree. This leads to errors in the population estimate that many investigators are forced to ignore because no alternatives exist. Lack of closure also creates uncertainties about the size of the area inhabited by the estimated population; this in turn compounds the error in making density estimates.

In this study we used radiotelemetry to document movements of marked bears across search area borders in an effort to compensate for lack of geographic closure. Our methods also permitted us to evaluate the assumption that individuals were equally catchable.

Many Alaska Dep. of Fish and Game (ADF&G) employees assisted in this project, including J. Whitman, C. Gardner, B. Taylor, M. McNay, S. M. Miller, and K. Bovee. Others have assisted in previous years. Special thanks to D. McAllister, who was critical to the success of this project, and to K. Schneider. Teeth were sectioned and read by E. Goodwin and M. Chihuly. G. Cooey (Harza-Ebasco Joint Ventures) assisted in many aspects of logistic support. J. Lee, H. McMahan, and D. Deering piloted fixed-wing aircraft and C. Loftstedt piloted the helicopter. We acknowledge valuable comments made by G. White, D. Anderson, and S. M. Miller during design and analysis phases of this project and helpful reviews of earlier drafts by R. Harris, J. Whitman, K. Pitcher, and S. Peterson. D. E. N. Tait assisted in preliminary simulations that tested the performance of our population estimator. Funding was provided by the Alaska Power Authority as part of impact assessment studies for the proposed Susitna Hydroelectric project. Additional support came from ADF&G.

STUDY AREA AND METHODS

The study area is in the Talkeetna Mountain Range of south-central Alaska (Fig. 1), centered near the confluence of the Susitna River and Watana Creek. Vegetation at lower elevations along the Susitna River is dominated by spruce (*Picea glauca* and *P. mariana*), birch (*Betula papyrifera*), and alder (*Alnus* sp.). Away from the river and adjacent to these forested lowlands is a shrub zone dominated by dwarf birch (*B. glandulosa*) and willow (*Salix* spp.). Above approximately 800 m elevation vegetation grades into shrub tundra and then into mat and cushion tundra. The study area's northern border is about 35 km south of the area we studied earlier (Miller and Ballard 1982). Black bears were not present in this earlier study area. We identified a search area of 1,325 km^2 in the middle of a larger study area where marked black and brown bears had been captured and studied during the period 1980–85. We used telemetry data obtained in these studies to assure that all habitats used by bears were included in the search area. This

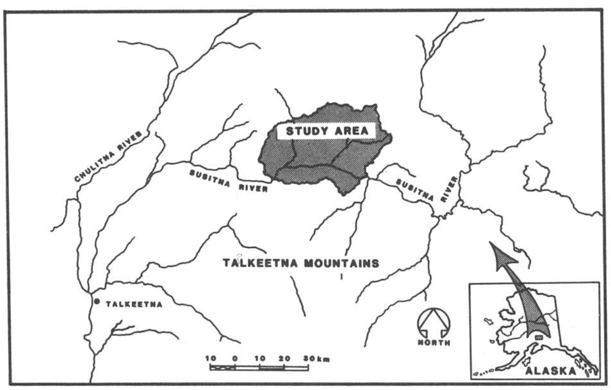

Fig. 1. Location of the search area in south-central Alaska.

search area centered on the relatively low-elevation course of the Susitna River, which is used selectively by brown bears during early spring (Miller, unpubl. data). (References in this report to "Miller, unpubl. data" refer to data in 4 reports that are not widely available: Miller, S.D. 1983, 1984, and 1985, Susitna Hydroelectric Project Phase II Annual Reports, Big Game Studies, Vol. VI. Black Bear and Brown Bear, Alaska Dep. of Fish and Game; and Miller and McAllister 1982, same citation except Phase I final report, 233pp.). We also included surrounding areas at higher elevations used primarily as denning habitat (Miller, unpubl. data) in the search area. Of the 1,325 km^2 in the search area, 33.3% was below 762 m elevation, 56.5% between 762 and 1,219 m, 9.0% between 1,220 and 1,524 m, and 0.6% above 1,524 m.

We defined brown bear habitat as below 1,524 m elevation (5,000 feet); this included 1,317 km^2, or 99.4%, of the whole search area. Previous studies from 1980 to 1984 revealed that only 1% of all observations (N = 2,418) of radio-marked bears were above this elevation (Miller, unpubl. data). The pattern of brown bear movements during spring in this area is for most bears to move from high-elevation den sites on the periphery of the search area to lower-elevation south-facing slopes along the Susitna River and its major tributaries (Miller, unpubl. data). The search area included the den sites of 7 of the 14 previously radio-marked adult brown bears that were radio-located in the search area at least once during the capture period.

Black bears did not use the entire search area. Black bear habitat, including dens, was largely confined to a strip of forested habitat bordering the Susitna River and its tributaries (Miller, unpubl. data). The area along the river defined as black bear habitat included 97.6% of 2,273 observations of radio-marked black bears obtained from 1980 to 1984. The amount of this black bear habitat within the search area was 532 km^2, most of which was below 762 m elevation (83%).

We divided the search area into 9 quadrats using natural landmarks as boundaries. These quadrats were used to allocate and document search effort. We attempted to search each quadrat each day but were unsuccessful on some days. Quadrats averaged 5.8 complete searches (5–7). Incompletely searched quadrats on 1 day were searched 1st during the following day's effort. We did not correct for incompletely searched quadrats. We spent 128.13 hours actively searching for bears (1.02 min/km^2 searched [2.65 min/mi^2]).

Search efforts began on 1 June 1985. At this time all previously radio-marked bears had left their dens, and trees and shrubs had not yet leafed-out. By 12 June paper birch and alder leaves had emerged at lower elevations. This reduced observability enough to make further search efforts significantly less efficient than on previous days, so we ended the study after 7 full days of search effort. We omitted from the analysis those days during which poor weather prevented a complete search (5–8 June).

We conducted searches in 2 fixed-wing airplanes (PA-18), each piloted by a hunting guide we considered highly skilled at spotting bears. A biologist was also present in each search plane. Pilots searched quadrats in rotation on different days. We identified previously captured bears without radio-collars by visual marks and considered these equivalent to sightings of unmarked bears in calculations. Only resightings of previously captured bears with radio-collars (and offspring with such bears) were considered resightings of marked bears. We individually identified these bears by radiotelemetry but we did not use radiotelemetry to find bears. We captured and marked all unmarked brown bears that we spotted; 3 unmarked adult black bears spotted in terrain where capture was too difficult escaped capture. On the last day of the search no effort was made to physically capture unmarked bears (only 1 unmarked bear, a black bear, was seen). Capture was accomplished using immobilizing darts fired from a helicopter (Bell 206B Jet Ranger).

A 3rd plane also spent the morning of each day searching for bears. In the afternoon of each day, a biologist in this plane determined whether each previously radio-marked bear was within or outside of the search area boundary. The number of radio-marked bears found within the search area on each day was the entry value for number of marks present (n_1) on that day in capture-recapture equations. This value could increase or decrease from day to day instead of being held constant (or only increasing as more marks are added) as in capture-recapture calculations that assume closure.

We considered young bears accompanied by their mothers to have the same status (previously marked or unmarked) as their mothers. The capture period occurred during the breeding season for both species of bears so adults were occasionally together. We treated such observations as independent sightings. We accidentally killed 2 black bears during the capture process and classified both as single sightings of unmarked bears.

Calculation of population estimates followed Seber (1982) where:

$$N^* = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1 \qquad (1)$$

However, instead of using the daily values of n_1, n_2, and m_2, as would be done if the population was closed, we obtained values used for these parameters by cumulating the daily values recorded during the capture period. This resulted in a different population estimator, N_d^*. We defined N_d^*, conceptually, as the total number of bear-days our search area was occupied during the search period. The average number of bears that inhabited the search area during a search period of (n) days was then (N_d^*/n). Substituting N_d^* for N^* in eq. 1 required redefining the parameters of eq.1 as:

n_1 = cumulative number of radio-marked bear-days in the study area during a study period of n days as determined by telemetry (1 radio-marked bear verified in the study area during 1 day = 1 marked bear-day present); and
n_2 = cumulative number of bear-days observed by spotter planes during a study period of n days (1 bear, either marked or unmarked, seen in any 1 day = 1 bear-day observed); and
m_2 = cumulative number of radio-marked bear-days observed by the spotter planes during a study period of n days.

Confidence intervals for N_d^* were similarly calculated by substituting the previously defined values of n_1, n_2, and m_2 into the appropriate equations provided by Seber (1982). These were approximations to the hypergeometric distribution based on the binomial or normal distributions. Seber (1982) recommended criteria for choosing which distribution to use based on the values of n_2 and p^*, where p^* was estimated as (m_2/n_2).

When the normal approximation was appropriate according to these criteria, the variance of N_d^* was calculated according to the formula given by Seber (1982):

$$v(N_d)^* = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2 (m_2 + 2)} \quad (2)$$

Confidence intervals for circumstances when the binomial approximation to the hypergeometric distribution was appropriate, according to criteria given by Seber (1982), were calculated using Clopper-Pearson graphs (example in Overton and Davis 1969:413). Using p^* as the entering variable on the x axis of the Clopper-Pearson graph, corresponding values for upper (p_u)and lower (p_l) limits that were associated with the isoclines for n_2 were read from the y axis of the Clopper-Pearson graph. Then the upper and lower limits of the confidence interval were, respectively:

$$N_d^*u = n_l/p^*_u \quad \text{and} \quad N_d^*_l = n_l/p^*_l$$

These limits, as well as the estimate for N_d^*, can be converted from bear-days to bears by dividing by (n), the number of days in the search period.

We compared the estimator N_d^* with a Schnabel estimator for the same data sets (Seber 1982) and also with the average of 7 separate daily estimates calculated using eq. 1. For the average Petersen estimate the 95% confidence interval, assuming independence between samples, was obtained using:

$$\frac{(1.96)\ \Sigma\ [v(n_i)]}{r^2}$$

where r equals the number of daily sample periods included and v[n_i] is the variance of the estimate obtained on the ith day (obtained from eq. 2). This estimated interval included variances from days where all bears seen were marked ($n_2 = m_2$); on these days $N^* = n_2$ and $v[N^*] = 0$.

For capture-recapture data sets with small sample sizes and low probabilities of recapture of marked bears, capture opportunities are sometimes pooled to provide a population estimate (e.g., Miller and Ballard 1982, Greenwood et al. 1985). Commonly, this has been done in attempts to deal with problems resulting from low catchability and small sample sizes. In our study such desperate measures were not necessary, but to compare our study with others, we calculated estimates obtained by combining data from all 7 days into a single Petersen estimate based on eq. 1. In these analyses no more than 1 capture or recapture per individual was counted during each period of pooled days, and a marked bear had to have been in the search area only once during the period to contribute to the value of n_1.

We made similar comparison calculations using the N_d^* estimator to see how much the capture and marking of new animals during the capture period influenced the population estimates and confidence intervals. In this analysis only bears radio-marked before search effort began on 1 June could contribute to the values of n_1 or m_2. We considered sightings of bears marked during the capture period equivalent to sightings of unmarked bears; they contributed to the value of n_2 but not to m_2.

Because biologists frequently are forced to assume geographic closure of their population even though they know it to be a naive assumption (e.g., Miller and Ballard 1982), we calculated a comparison estimate making this assumption. For these calculations we assumed that each bear (marked or unmarked) that was present at least once in the search area was always present. Radio-marked bears that were near, but never in, the search area according to the telemetry data were not included in the value of n_1 in this estimate. Radio-marked bears that were verified, by telemetry, to have been in the search area at least once were included in the value of n_1 even if they were never seen ("recaptured"). Correspondingly, this "naive" estimator included more information than would typically be available to an investigator using capture-recapture data and making assumptions about geographic closure that were unconfirmed by telemetry data.

All these population estimators assumed equal sightability of individuals. Violation of this assumption because of behavioral differences between individuals of different sex-age groups or temperments, however, remains a potential problem. We examined this type of bias by calculating a daily "sightability index." This index was (m_2/n_1), using daily, not cumulative, values for m_2 and n_1.

We estimated ages of bears based on sections of the 1st premolar (Mundy and Fuller 1964). Ages of cubs and yearlings were estimated by size and degree of canine eruption. We used chi-square analysis to test for differences in sex ratios and sightability. Student's *t*-test statistic was used to test for differences between mean ages. All reported confidence intervals are 95%.

RESULTS

Brown Bear Density Estimates

Of the previously marked brown bears ≥ 2 years old that were present at least once in the search area during the search period, 7 were males and 9 were females. All had functioning radiocollars applied in previous years. Five of these females were accompanied by 12 newborn cubs, 3 were accompanied by 7 yearlings, and 1 was unaccompanied by offspring. Previously marked brown bears of all ages totaled 35 bears.

Of the newly captured previously unmarked bears ≥ 2 years old present during the search period, 7 were males and 8 were females. None of the females had newborn cubs, 1 had a single yearling, and 7 had no offspring. New captures totaled 16 brown bears. Three of the newly captured females without offspring were of reproductive age (≥ 5.0 years old).

We calculated an index to degree of geographic closure of the population as the mean of percent of times each radio-marked bear was present in the search area. Of 16 previously radio-marked bears, 2 were present only once during the 7-day search effort, 1 twice, 1 three times, 3 four times, 2 five times, 2 six times, and 5 were present on all 7 days. The mean for previously marked bears was 68% (71% for 7 males and 65% for 9 females). Results for bears radio-marked during the capture period were 3 adult males present on 11 of 13 possible times subsequent to marking and 7 adult females present on 27 of 28 possible times.

Table 1 shows daily and cumulative values used to calculate N_d*. The estimated cumulative number of bear-days present in the study area (N_d*) was 256.9. This value divided by the 7 days in the search period yielded a population estimate of 36.7 bears present on an average day of the search period (95% CI = 33.1–43.5 bears).

The proportion of marked brown bear-days in N_d* (p*) was estimated as m_2/n_2, or 0.79. For this value of p* (or 1-p*), the normal approximation to the hypergeometric distribution can be used for $n_2 > 200$ (Seber 1982). Because $n_2 = 77$ in this case, the binomial approximation was used to calculate the previously stated confidence interval (−9.8% to +18.5% of the estimate). Figure 2 shows comparison results obtained from the N_d* estimator for time periods of from 1 (1 June only) to 7 (1–10 June) days. The estimated number of brown bears changed little during days 4–7, but confidence intervals, based on binomial and normal approximations, declined with successive days of effort (Fig. 2).

The estimated number of bears and the area defined as brown bear habitat (1,317 km^2) yielded a density estimate of 2.79 bears/100km^2 (7.22 bears/100 mi^2). Confidence intervals were 2.52–3.30 bears/100 km^2 (6.52–8.56 bears/100 mi^2). Subsequent comparison calculations in this paper (summarized in Tables 2

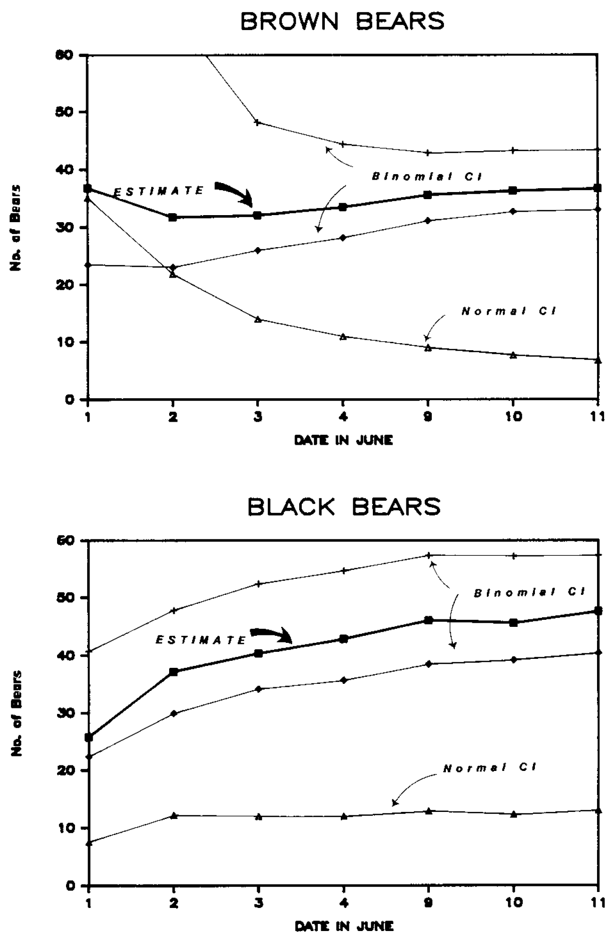

Fig. 2. Changes in population estimates and 95% confidence intervals over time. Confidence intervals are based on binomial (upper and lower limits illustrated) and normal (half of illustrated value above and below estimate) approximations to the hypergeometric distribution.

Table 1. Daily availability and observations of marked and unmarked brown bears during spring 1985 within the Susitna River search area of south-central Alaska.

	Date in June							
	1	2	3	4	9	10	11	Total
Number of marked bears known present (n_1)								
Males ≥2	5	7	7	8	6	8	5	46
Females ≥2	5	6	7	9	13	14	14	68
Cubs	10	8	8	8	8	8	8	58
Yrlngs.	0	1	4	3	8	8	8	32
Totals	20	22	26	28	35	38	35	204
Number of marked bears seen (m_2)								
Males ≥2	1	0	2	2	1	3	0	9
Females ≥2	1	1	2	3	4	3	4	18
Cubs	2	2	2	4	4	0	2	16
Yrlngs.	0	0	3	2	5	4	4	18
Totals	4	3	9	11	14	10	10	61
Total number of bears seen (n_2)								
Males ≥2	2	0	3	5	3	3	1	17
Females ≥2	3	1	4	4	6	3	4	25
Cubs	2	2	2	4	4	0	2	16
Yrlngs.	1	0	3	2	5	4	4	19
Totals	8	3	12	15	18	10	11	77

and 4) will compare only the population estimates; conversions to density estimates are straightforward.

The mean of 7 individual daily estimates using eq. 1 was 2.2% lower than the estimate based on N_d* and had a slightly smaller confidence interval (Table 2). The Schnabel estimator for these data was 7.1% larger than the estimate based on N_d* and had a slightly larger confidence interval (Table 2).

A population estimate calculated with the naive assumption that the population was geographically closed was 40% larger than the estimate corrected for lack of population closure (Table 2). This naive estimate was very close to the value that would have been obtained with a single Petersen estimate using eq. 1 if each bear had only 1 possibility of being captured or recaptured during the 7-day period (Table 2). A single Petersen estimate obtained by pooling days 1–7 of the capture period also resulted in a higher population estimate than the N_d* estimator (+43.9%) (Table 2). All 3 of these estimates are close to the total number of individual brown bears known to have been present in the search area at least once during the search period (Table 2).

We calculated a separate estimate just for the brown bears ≥ 2 years old (data are in Table 1). This yielded a population estimate of 25.1 bears ≥2 years old (Table 2). Comparison of this estimate with the previous estimate for all bears suggests that 32% of the estimated total number of bear-days was contributed by newborn cub or yearling bears.

We made another comparison to see how much the capture and marking of new brown bears during the search period affected the final estimate. The estimate, had no new marks been added during the capture period, was 11.5% less than the estimate obtained from increasing the number of marks during the capture period by capturing and marking 16 new brown bears (Table 2). The estimate for bears ≥2.0 years old had no new bears been captured was 18.6% lower than the estimate for bears ≥2.0 years old obtained by capturing and marking 15 new bears $\geq$2.0 years old (Table 2).

Brown Bear Sightability

During the capture period, there were no evident trends in brown bear sightability (Fig. 3). The pattern of sightability over time for previously marked adults was similar to that for all bears (Fig. 3).

Sightability did not differ between sexes for 16 females (19/68 = 28%) and for 10 males (9/46 = 20%) (P = 0.21). Four females with yearling offspring had higher sightability (8/17 = 47%) than 5 females with newborn cubs (8/29 = 28%) (P = 0.04). The females with newborn cubs had sightability similar to 7 females without offspring (3/22 = 14%) (P = 0.14). No significant difference in sightability was observed between the 16 brown bears that had been radio-marked before 1 June (22/76 = 29%) and the 10 bears that were marked during the capture period (6/38 = 16%) (P = 0.07). This was a nearly significant result; if 1 less newly marked bear had been seen, the difference would have been significant (P = 0.03).

Capture bias against females with newborn cubs was evident in 8 years of capture data in or near this study area (Spraker et al. 1981; Miller and Ballard 1982; Miller, unpubl. data). Of 48 female brown bears $\geq$5-years-old captured in May and June during this 8-year period, 8 were accompanied by newborn cubs, 16 by yearling offspring, 8 by 2-year-old offspring, and 16 were alone (Miller, unpubl. data). The null hypothesis that females with cubs, with yearlings, and alone (single bears were lumped with females accompanied by 2-year-olds) each represented one-third of the total was rejected (P = 0.02).

Black Bear Density Estimates

Of the previously marked black bears $\geq$2-years-old that were present at least once in the search area during the search period, 6 were males and 9 were females. Four females were accompanied by 9 newborn cubs, none had yearling offspring, 4 were alone, and 1 separated from 3 2-year-old offspring during the search period. There were 24 previously marked black bears of all ages.

Of the captures of previously unmarked bears $\geq$2-years-old during the capture period, 12 were males and 8 were females. None of the females had newborn cubs, 2 had 3 yearling offspring, 1 was accompanied by a captured 2-year-old, and 5 were alone. Four of the females without offspring were adults $\geq$5 years old. New captures numbered 24 black bears. Nine additional unmarked bears, 3 of which were apparent

Table 2. Comparisons of results using different estimators on brown bear data.

Estimator	Parmeters[a] n_1	n_2	m_2	Estimated total no. bear-days (%)	Estimated total no. bears (%)	Variation from N_d[a] (%)	95% CI based on normal approx. = plus/minus (%)	95% CI based on binomial approx. = plus (%)	minus (%)
N_d^a (all bears)	204	77	62	256.9	36.7	—	9.4	18.5[b]	9.8[b]
Avg. of daily values for N^a	—	—	—	—	35.9	−2.2	9.1	—	—
Schnabel index	—	—	—	—	39.3	+7.1	10.9	—	—
Total no. individuals known in area $\geq$ once during period	—	—	—	—	51.0	+39.0	—	—	—
Simple Petersen with only 1 capture/bear possible during days 1-7 pooled	33	41	25	—	53.9	+46.9	11.5	—	—
N_d^a (with naive assump. of pop. closure)	290	77	62	359.3	51.3	+40.0	9.5	20.5[b]	9.3[b]
N_d^a (if no new bears were captured)	160	77	54	227.3	32.5	−11.5	11.6	22.4[b]	12.0[b]
N_d^a (bears >2.0)	114	42	27	175.6	25.1	—	18.8	35.3[b]	16.8[b]
N_d^a (bears >2.0 if no new captures)	76	42	22	143.0	20.4	−18.6	23.0[b]	51.9	20.7

[a] Cumulative values used for the estimates based on N_d*.
[b] Recommended confidence interval (CI).

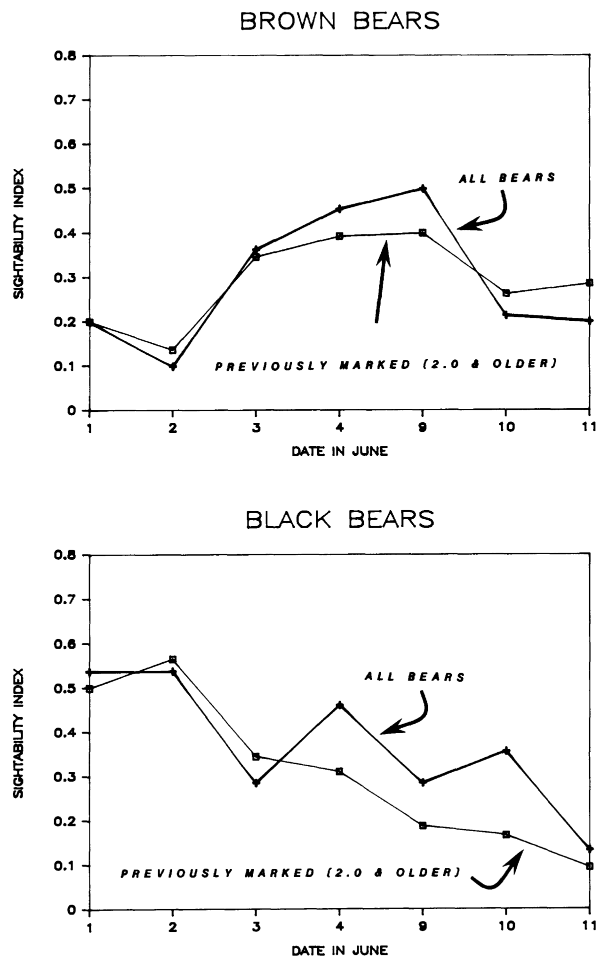

Fig. 3. Changes in daily sightability of marked bears during the capture period.

adults, were sighted but escaped capture. Some of these sightings were probably of the same individual.

Geographic closure was a relatively good assumption for black bears. All but 1 of the 15 adult black bears captured before the search effort began were present on all 7 days of the search effort. This yielded an average percent present of 95% (88% for males and 100% for females). Similar results were obtained for 5 adult males and 5 adult females radio-marked during the search effort. These females were present on all of 20 possible times subsequent to marking, and these males were present on 18 of 24 possible times.

Table 3 shows daily and cumulative results. The estimated cumulative number of black bear-days present in the study area (N_d*) was 334. This, divided by the 7 days in the search period, yielded a population estimate of 47.7 black bears present on an average day during the search period (95% CI = ±6.6 bears, or 13.7%).

The proportion of marked bear-days in the population (p*) was estimated as m_2/n_2, or 0.59. For this value of p* (or 1-p*) the normal approximation to the hypergeometric distribution can be used for n_2 > 50 (Seber 1982). Because n_2 = 97 in this case, the normal approximation was used to calculate the previously stated confidence interval. Figure 2 compares results obtained using the N_d* estimator for time periods of 1–7 days. The confidence interval remained constant after day 2 of the search effort, although the estimated number of black bears increased through day 5.

This population estimate and the the area defined as black bear habitat (531 km^2)yielded a density estimate of 8.97 bears/100km^2 (23.13 bears/100 mi^2). Confidence intervals were 7.74–10.21 bears/100 km^2 (19.95-26.31 bears/100 mi^2).

The average of 7 separate daily estimates of bear numbers in the search area yielded a population estimate of 47 bears (± 16%). This estimate was only 1.5% less than the estimate obtained from the N_d* estimator but had a larger confidence interval (Table 4). The Schnabel estimator from these data was the same as the N_d* estimator but also had a larger confidence interval (Table 4). For the black bear data, all 3 of these estimators provided results close to the total number of individual black bears known to have been in the search area at least once during the capture period (Table 4).

Under the naive assumption that the population was closed, the population estimate using the N_d* estimator was 12.5% higher than the estimate modified to correct for lack of population closure through use of telemetry data (Table 4). The estimated number of black bears using eq. 1 on data pooled for days 1–7 was 18.7% higher than the estimate based on N_d* and had a smaller confidence interval (Table 4).

Excluding cubs and yearlings (Table 3), the population estimate based on the N_d* estimator was 31 bears $\geq$2 years old (± 14.2%) (Table 4). Comparison of this estimate with the previous estimate indicated that about 35% of the total estimated bear-days was contributed by cub and yearling black bears.

The black bear population estimate, had no new black bears been captured and marked during the search period, was only 1.3% lower than the estimate based on marking 24 new bears (Table 4). The confidence interval, however, was ±17.1% instead of ±13.7%. The estimate obtained for bears $\geq$2 years old, had no new bears been marked, was 6.2% less than that obtained from marking 21 new bears ≥2 years old (Table 4).

Black Bear Sightability

Sightability between the sexes was not different for 10 male (14/48 = 29%) and 12 female (19/69 = 28%) radio-marked black bears (P = 0.77). Four females with newborn cubs had lower sightability (5/28 = 18%) than did 8 females without newborn cubs (14/41 = 34%) (P = 0.007). The 12 bears that had been radio-marked before 1 June did not differ in sightability (22/79 = 28%) from the 10 bears that were radio-marked during the capture period (11/38 = 29%) (P = 0.88).

The reproductive status of 31 adult (≥5.0 years old) black bear females captured in May or June in this study area during the period 1980–85 also suggested a capture bias against females with newborn cubs. Six of these females had newborn cubs, 11 had yearlings, 1 had 2-year-olds, and 13 had no offspring. In this study area female black bears typically separate from yearling offspring and have a new litter the following year (reproductive interval of 2 years) or skip a year before their next litter (interval of 3 years) (Miller, unpubl. data). The null hypothesis that there were as many captures of adult females with newborn cubs as of other adult females was rejected ($P < 0.001$). The null hypothesis that one-third of the captures were females with newborn cubs was not rejected (P = 0.10). A bias against females with newborn cubs may exist only in the spring. Of 8 captures of adult females in this area in August, 4 had newborn cubs and 4 were alone.

DISCUSSION

The density estimation procedure used in this study corrected for 1 of the 2 most commonly violated

Table 3. Daily availability and observation of marked and unmarked black bears in spring 1985 within the Susitna River search area of south-central Alaska.

	Date in June							
	1	2	3	4	9	10	11	Total
Number of marked bears known present (n_1)								
Males ≥2	4	5	9	8	9	7	9	51
Females ≥2	9	9	11	12	14	14	14	83
Cubs	9	9	9	9	9	9	9	63
Yrlings.	0	0	0	0	0	0	0	0
Totals	22	23	29	29	32	30	32	197
Number of marked bears seen (m_2)								
Males ≥2	2	3	4	4	3	2	1	19
Females ≥2	5	5	4	5	3	3	2	27
Cubs	4	5	2	0	0	0	0	11
Yrlings.	0	0	0	0	0	0	0	0
Totals	11	13	10	9	6	5	3	57
Total number of bears seen (n_2)								
Males ≥2	4	7	6	7	6	2	1	33
Females ≥2	5	9	6	7	4	4	3	38
Unknown ≥2	0	2	1	0	0	0	1	4
Cubs	4	6	3	0	0	0	0	13
Yrlngs.	0	3	0	2	2	0	2	9
Totals	13	27	16	16	12	6	7	97

Table 4. Comparisons of results using different estimators on black bear data.

Estimator	Parmeters[a] n_1	n_2	m_2	Estimated total no. bear-days (%)	Estimated total no. bears (%)	Variation from N_d^*[a] (%)	95% CI based on normal approx.= plus/minus (%)	95% CI based on binomial approx.= plus (%)	minus (%)
N_d^a (all bears)	197	97	57	333.6	47.7	—	13.7[b]	20.5	15.0
Avg. of daily values for N^a	—	—	—	—	47.0	−1.5	16.0[b]	—	—
Schnabel index	—	—	—	—	47.7	0.0	16.3[b]	—	—
Total no. individuals known in area ≥ once during period	—	—	—	—	48.0	+0.6	—	—	—
Simple Petersen with only 1 capture/bear possible during days 1-7 pooled	24	52	22	—	56.6	+18.7	8.7[b]	—	—
N_d^a (with naive assump. of pop. closure)	258	99	68	375.4	53.5	+72.8	11.2[b]	16.8	11.6
N_d^a (if no new bears were captured)	159	96	46	329.2	47.0	−1.3	17.1[b]	28.8	16.7
N_d^a (bears >2.0)	134	75	46	217.3	31.0	—	14.2[b]	34.1	17.8
N_d^a (bears >2.0 if no new captures)	96	75	35	203.8	29.1	−39.8	18.6[b]	34.6	21.5

[a] Cumulative values used for the estimates based on N_d^*.
[b] Recommended confidence intervals (CI).

assumptions in capture-recapture population estimates, that of geographic closure. Our procedure assumed closure on each day of the capture period but permitted marked and unmarked individuals to move in or out on different days. The movements of marked individuals were tracked by telemetry and the number of marked animals present on each day varied accordingly. The resulting population estimate was specific to the search area and could be straightforwardly converted to a density estimate. This density estimate did not require guesses about the size of a periphery strip that should to be added to the search area to correct for lack of closure (Dice 1938) or information about daily movement rates (Wilson and Anderson 1985a, 1985b).

Numerous models have been developed for making capture-recapture estimates for closed populations under a variety of conditions (White et al. 1982). Because geographic closure is such a critical assumption, even though seldom met and difficult to measure (White et al. 1982), researchers need estimators for which geographic closure is less critical. The techniques and N_d* estimator used in this study are efforts in this direction. The N_d* estimator has yet to be adequately tested in simulation studies, but preliminary simulations indicate that it yields estimates that rapidly converge toward "true" population values.

Lack of closure was demonstrated for the brown bear estimate as bears moved across the borders of the search area. For brown bears, adding successive days of search effort caused population estimates to converge toward the final value and confidence intervals to decrease.

For black bears in this study, closure was demonstrated to be a reasonable assumption, as little movement across search area borders occurred. This may, to some degree, be an artifact of our study area, which was naturally "closed" to black bear movements in 2 directions by habitat constraints. Partially as a result of this natural closure, black bear estimates and confidence intervals changed little during the last 5 days of search effort. Because closure was a relatively good assumption for black bears, there was high similarity among results from the black bear estimators that assumed closure, the total number of individuals present at least once, and our estimator that corrected for potential lack of closure using radiotelemetry data.

Increasing the number of marked animals during the search period decreased confidence intervals for the brown bear estimate but not, after day 2, for the black bear estimate. Mathematically, this was because the proportion of marked black bears (m_2/n_2) remained relatively constant over time for black bears, even though new bears were marked. This ratio increased over time for brown bears. The reason for this result in our black bear estimate was unclear; we expect that in future applications, black bear estimates should have a pattern more similar to that found for brown bears (Fig. 2).

The other commonly violated assumption of capture-recapture population estimates is equal catchability (sightability) of individuals in the population. Sightability indices calculated for bears in different sex-age categories in this study indicated that this is a poor assumption, at least for our brown bear data. Correspondingly, the calculated confidence intervals should be viewed skeptically.

White et al. (1982) outlined models for dealing with unequal catchability for closed populations; similar techniques are needed for estimators like N_d*, which compensate for lack of closure. Separate estimates could be calculated for each subpopulation (based on sex, age, or reproductive status) that had a sightability index different from another subpopulation (Overton and Davis 1969). Separate estimates for subpopulations of females based on reproductive status could not be calculated in this study because no unmarked brown bears accompanied by newborn cubs were found.

We found no significant differences in sightability between previously marked and newly marked individuals, although for brown bears there was a tendency toward lower sightability for newly marked animals. Had it been necessary we could have calculated a separate estimate for the subpopulation of newly marked animals. This, added to the average number of previously marked bears in the search area over the 7-day period, would have resulted in an estimate corrected for behavioral response.

In this study sightability was the same for male and female bears of both species, but each species had sightability differences correlated with reproductive status. Brown bear females with yearlings had the highest sightability, and single females had the lowest. Females with yearlings may be more observable than other bears because they constitute a larger visual image, because they are more active, or both. We were surprised by the low sightability index for single female brown bears; single black bear females had the highest sightability, and this result was expected for brown bears as well. Additional studies should be done before concluding that the low sightability for single brown bear females observed in this study is a general characteristic.

Eight years of brown bear capture data, including this study, suggest that females with newborn cubs have the lowest sightability. These data indicate a capture bias against females with newborn cubs and a bias in favor of single females (including bears that were about to separate from 2-year-old offspring). The real bias is probably more extreme than indicated by these data, as more than one-third of adult females should have newborn cubs in an average year. This is because many bears produce their 1st litters at ages 5–6 and there are more bears in this younger age-class than in older age-classes. This is also because some intervals between successive litters are < 3 years (when cub or yearling litters are completely lost and the female has another litter the following year) (Miller, unpubl. data).

Changes in sightability over time were apparent for black bears. This did not affect the estimate as long as the relative sightability of marked and unmarked individuals remained constant. Errors in sightability indices could have resulted from incompletely searched quadrats on some days; this should be avoided in future applications.

When using this technique for estimating bear densities, investigators should consider the following:

1. The search area should be carefully selected to assure complete coverage each day.
2. Once an adequate sample of bears has been radio-marked (approximately $p^* = 0.5$ for $n_2 > 50$), additional unmarked bears do not need to be captured if only a density estimate is required. In these cases only searching and radio-tracking efforts need to continue to estimate N_d*. This can substantially reduce costs but will reduce the size of the sample available for estimating population structure. This trade-off may not be worthwhile to managers of exploited bear populations. Furthermore, if bears of unknown sex and age constitute the unmarked portion of the recapture sample (n_2), separate estimates cannot be calculated for unrecognizable subpopulations within n_2.
3. Although estimates may be obtained in a single year of study, accuracy may improve if the estimation procedure is used with a bear population that has been subjected to previous telemetry stud-

ies. Some bears with low sightabilities based on their reproductive status will have been captured during the previous years when their status was different.

4. If this technique is used to evaluate trends in bear population densities through successive applications separated by a number of years, an attempt must be made to assure that the distribution of marks within various sex-age categories of bears are equivalent in each application.

5. Sightability of different population segments (i.e., sex-age-reproductive status categories) does not have to be the same as long as the average probability of seeing an individual in the population of marked animals is close to the average probability of seeing an individual in the unmarked population (Overton and Davis 1969). To achieve this investigators should attempt to allocate marks to the different segments of the population in close to the proportion that these segments occur in the population.

The estimates that would have been obtained in this study had the 24 black bears and 16 brown bears not been captured and marked during the study period would have been close for both black bears (−1.3%) and brown bears (−11.5%). Aircraft charter costs of this study were about equally split between the helicopter (used to capture bears) and fixed-wing aircraft. Our charter costs would have been more than halved if unmarked animals had not been captured during the search period. Our sample size for estimating the sex and age composition of the population (not discussed in this paper) would also have been approximately halved if we had not captured new bears.

Total operating costs of this study were about $60,000 from 1 to 10 June. Our fixed-wing and helicopter charter costs were $110/hour and $390/hour respectively. We conducted our study in a remote area requiring about 2.5 hours/day/aircraft commuting time; this added substantially to total cost. Actual fixed-wing search time was about half of total fixed-wing charter expense because of commuting time and time spent circling bears before darting and capture. We estimated costs of conducting a similar density estimate on an easily accessible black bear population requiring no new captures (because of the presence of a large number of previously marked animals) to be about $5,000. The high costs of working in Alaska should not discourage investigators from applying this technique in their areas.

The brown bear density estimate obtained in this study (2.79 bears/100 km^2) was higher than estimated in an adjacent area in 1979 (2.44 bears/100 km^2) (Miller and Ballard 1982). The sample size (especially m_2 and n_1) was smaller in the 1979 study and the design was different. In the earlier study we were forced to assume population closure and we also pooled capture periods; both would have resulted in higher estimates, compared to N_d*, had they been necessary in this study. Correspondingly, our earlier density estimate for this nearby area was probably too high. Greenwood et al. (1985) used a design similar to that in this study and noted that 10 capture-recapture population estimators underestimated the "true" population size of skunks (*Mephitis mephitis*) on their trapping grid. They studied a population that was incompletely closed geographically and defined "true" population size as the number of radio-marked individuals known to have been present at least once. Such a definition of "true" population size will always overestimate the population size that should be used to calculate density from animals on trapping grids where there is incomplete geographic closure. Greenwood et al. (1985) noted this distinction and did not attempt to estimate skunk density. We believe their data, however, could be used to estimate skunk density using the N_d* estimator.

Our study was conducted to estimate the number of bears inhabiting a larger area that would be influenced by a proposed hydroelectric development. The density estimates obtained from this study, when extrapolated to this larger area, provided an objective and replicable estimate of the size of bear populations. If the project is built, these density estimates will provide the baseline data needed to evaluate the impacts the project has on bear densities. Population estimates for large areas based on extrapolations from density estimates in a representative but smaller area can also be used to estimate harvest rates when harvests in this larger area are known.

We believe density is a more valuable parameter than population size for many biological applications. Such applications include population estimations for areas large enough to be of management significance when such areas are too large for complete estimates of population size because of logistic and financial constraints. This was certainly the case for our brown bear population. Capture-recapture estimates of population size for populations that lack geographic closure may be mathematically unsound if investigators nevertheless assume closure. More importantly, however, population estimates may not be as interesting or useful biologically as density estimates.

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