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# DETECTION OF DIFFERENCES IN BROWN BEAR DENSITY AND POPULATION COMPOSITION CAUSED BY HUNTING

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**Abstract:** Liberalized hunting regulations in a portion of southcentral Alaska resulted in an increased sport harvest of brown bears (*Ursus arctos*). A reduction in population density caused by increased hunter harvest was demonstrated using modified capture-recapture techniques. Density differences were documented between 2 areas of generally equivalent habitats but different patterns of hunter access as well as in the same area at 2 different times. Density estimates (for bears >2.0-years-old) were 6.7 bears/1,000 km<sup>2</sup> (95% CI = 5.2-10.1) in the intensively hunted area compared to 10.5 (95% CI = 6.0-25.7) in the same area 8 years earlier, and 19.1 (95% CI = 16.7-23.2) in the less intensively hunted area. The total population density estimate was 10.51 bears/1,000 km<sup>2</sup> in the intensively hunted area. Males constituted a smaller proportion of the population in the heavily hunted area compared to the less intensively hunted area and to the same area studied prior to onset of increased hunting pressure. There were relatively more younger males and more older females in the heavily hunted population.

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Reductions in bear numbers usually result from killing by humans in excess of sustainable levels or from deteriorating habitats. Whatever the cause, managers of bear populations have found it difficult to document changes in bear abundance because they have lacked objective techniques which could be systematically applied. Such documentation is frequently necessary to recognize the problem and to initiate corrective measures. Because of the lack of adequate techniques, managers have often been forced to rely on indirect and sometimes subjective or imprecise methods to detect changes in bear abundance (Harris 1986). Such methods may prove inadequate to convince the public and other decision-makers that a problem exists.

In recent years, bear managers in Alaska have used modified capture-recapture techniques (Miller et al. 1987) to estimate bear density in different parts of the state (Miller et al. 1987, Schoen and Beier 1987 and 1988, Barnes et al. 1988, Reynolds and Hechtel 1988, Smith and Van Daele 1988, Ballard et al. 1990). These studies have provided baseline estimates of bear density that can be used to document future changes, which may occur as a result of overexploitation or habitat deterioration. Until the present study, however, these techniques had not been used to document changes or differences in bear density. This study provides another example of the use of these capture-recapture procedures to estimate density and uses the techniques to document changes in brown bear density and differences in population composition resulting from increased kill by hunters.

In a portion of southcentral Alaska (Game Management Unit [GMU] 13) brown bear hunting opportunity was liberalized during the period 1980-1983. This liberalization included initiation of a spring hunting season in 1980 followed by season liberalizations in subsequent years, and a change in bag limit from 1 per 4 years to 1 per year in 1982. Seasons changed from 1 September-10

October in 1979 to 1 September-31 May in 1983. Harvests of brown bear increased from an average of 65/year (range 41-73) during 1974-1979 to 116/year (range 67-146) during 1983-1988 (Alaska Department of Fish and Game [ADF&G] files). Recent harvests were about twice as high as could be sustained based on estimated population size in the unit (obtained by extrapolation from density estimates), on the reproductive characteristics of the population (Miller 1987), and on conservative estimates of natural mortality (Miller 1988). Indications of heavy harvest were also available in the sex ratio of bears killed by hunters; more than half of bears killed in fall seasons were females in recent years (Miller 1988). Average age of harvested bears showed little trend although mean age of males killed in fall seasons declined slightly in the 1980's (Miller 1988).

These data are indicative of a declining population but do not provide an unambiguous indication of a decline (Caughley 1974, Harris 1984, Miller 1990). It was hoped that comparisons of bear density in different parts of the unit at different periods would provide more convincing evidence of trend in this population. Two comparisons were possible.

In the 1st comparison, a spring 1987 density estimate in the Upper Susitna River area (UpSu87) was obtained using the capture-recapture techniques described by Miller et al. (1987). This estimate was obtained in a portion of the unit accessible by road where hunting pressure was thought to be heavy. This estimate was compared to an estimate obtained in the same area in 1979 (UpSu79) (Miller and Ballard 1982a), prior to the initiation of liberalized regulations. The UpSu79 estimate was obtained using somewhat different capture-recapture techniques and, correspondingly, had to be modified to make it directly comparable to the UpSu87 estimate and test the hypothesis that density had declined in this area between 1979 and 1987.

Hunting pressure was not uniformly distributed throughout GMU 13. In portions where hunter access was relatively easy and inexpensive, hunting pressure was greater than where it was difficult and expensive. The 2nd comparison made in this study was to examine for suspected changes in density between 2 nearby areas that had differences in hunting pressure caused by access differences. The UpSu87 density estimate was obtained in an area with road access where hunting pressure was thought to have been relatively high since prior to liberalization of brown bear hunting regulations. This estimate was compared to a previously reported estimate obtained in 1985 using identical techniques in the nearby Mid-Susitna River area (MidSu85) (Miller et al. 1987). The MidSu85 estimate was in an area that was similar in terms of habitat for brown bears but was more remote and difficult to get to except by hunters using airplanes; in this area harvest levels prior to 1980 were considered to be low and recent harvest levels were moderate to high.

In addition to changes in density resulting from differential intensity of hunting over time and between areas, heavy hunting was expected to result in changes in population composition over time and between areas. Under typical circumstances where males are more vulnerable than females, relatively heavily hunted bear populations should contain fewer males and more young animals than lightly hunted populations (Gilbert et al. 1978; Beecham 1980*a, b*; Bunnell and Tait 1980; Fraser et al. 1982; Tait 1983; Harris 1984). In this study changes in population composition were used to assess whether hunting was correctly identified as the causative factor for the observed changes in density.

This project could not have been completed without the efforts of L. Pamplin, D. Timm, G. Bos, and K. Schneider (ADF&G) who found funds to complete it when promised funds from another agency failed to materialize. D. McAllister provided essential logistic and field assistance. Important field assistance in 1986 and 1987 portions of this study was also provided by: E. Becker, P. Brna, G. Bos, D. Johnson, D. Sellers, N. Tankersley, B. Taylor, R. Tobey, J. Westlund, and J. Whitman (all ADF&G). R. Halford and G. Marston provided logistic support. Fixed-wing aircraft were piloted by H. McMahan, C. McMahan, J. Lee, and D. Deering and the helicopter was piloted by V. Lofstedt and C. Lofstedt. Simulation software was developed by N. Graves (ADF&G) based on an earlier version provided by D.E.N. Tait. The program for calculating binomial confidence intervals was developed by D. Reed and J. Venable (ADF&G). Helpful comments on earlier drafts of this manuscript were provided by J. Schoen, K. Schnei-

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## METHODS

Three density estimates were obtained and compared. One estimate was obtained in an easily accessible and heavily hunted area near the headwaters of the Susitna River in 1979 (UpSu79) (Miller and Ballard 1982*a*), a 2nd estimate (UpSu87) was obtained within a portion of this same area 8 years later following a period when hunting pressure increased, and a 3rd estimate (MidSu85) was obtained in an area of similar habitat where hunting pressure was less because of more difficult access (Fig. 1). Availability of different kinds of bear habitat was essentially the same in the UpSu79 and UpSu87 areas, which differed only in size. There were some ecological differences between these upper Susitna River areas and the MidSu85 area. In the middle Susitna River area there was more forested habitat, a resident population of black bears (*Ursus americanus*), and a stream nearby (Fig. 1), which about a third of the radio-marked bears visited during July and early August to fish for salmon (primarily *Oncorhynchus tshawytscha*) (Miller 1987). In my view, the upper Susitna and middle Susitna River areas were roughly equivalent in terms of brown bear carrying capacity with the upper Susitna area perhaps being somewhat better habitat. In terms of capability to support brown bears, any habitat advantage in the upper Susitna area was likely counterbalanced by increased levels of human activity and disturbance associated with the Denali Highway and by the anadromous fish stream near the middle Susitna area.

The procedures followed in 1985 and 1987 were described by Miller et al. (1987). In brief, these included selection of a search area containing radio-marked bears, treatment of radio-marked bears as "marked" animals and non-radio-marked bears as "unmarked" animals, daily searches of the study area from fixed-wing aircraft (Piper PA 18) to determine ratio of marked to unmarked animals, determination (by telemetry) of the number of marked bears present on each day of search (this corrects for lack of geographic closure of the population), and capture (by darting from a helicopter) and marking of unmarked animals seen during the searches.

### UpSu87 Estimate

The MidSu85 brown bear density estimate was described by Miller et al. (1987). The UpSu87 estimate was

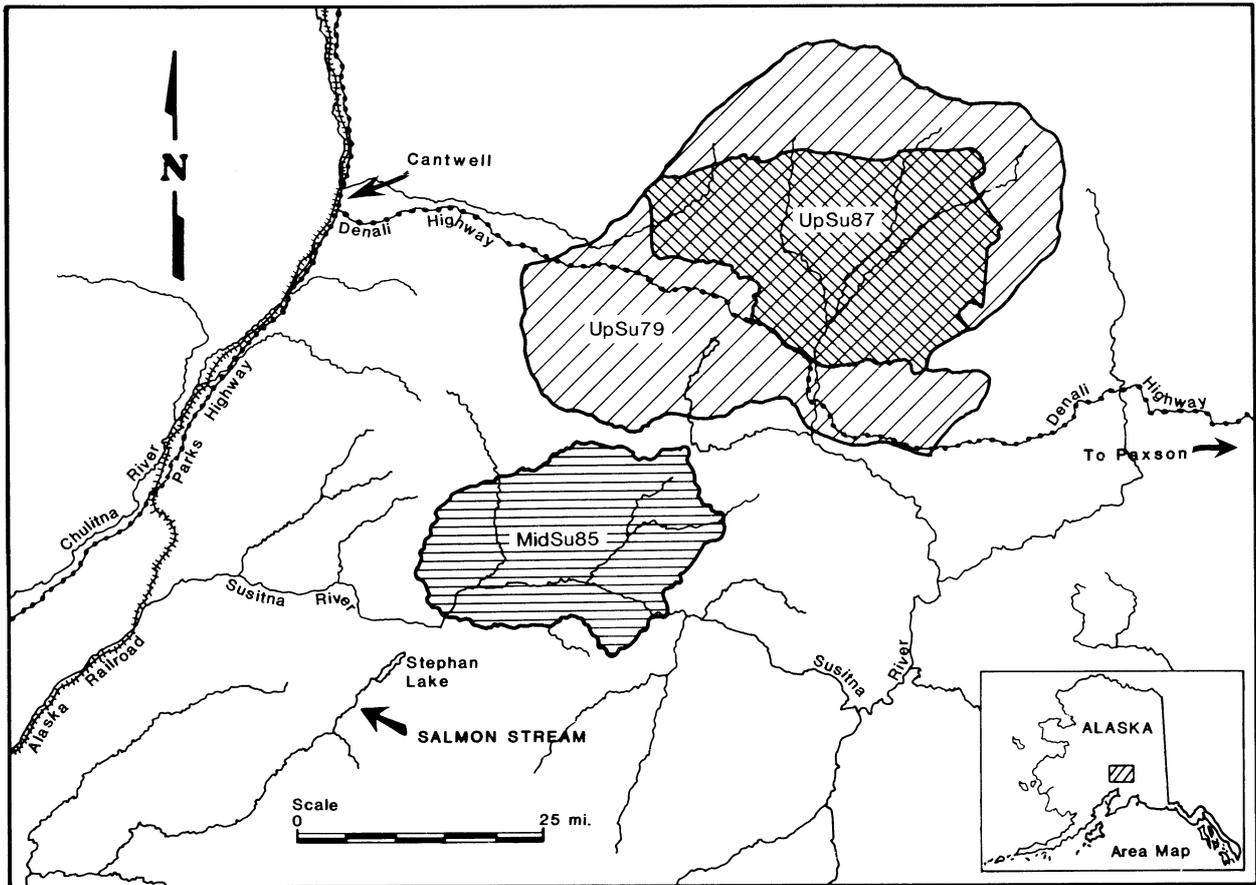


Fig. 1. The study areas in southcentral Alaska where bear density estimates were obtained and compared.

obtained using the same techniques in a 1,309 km<sup>2</sup> search area. Both areas, as well as the UpSu79 area, were typical in terms of the proportions of the different kinds of habitat used by bears throughout the year as was present in the northern portion of GMU 13. Approximately 51.7 km<sup>2</sup> of the UpSu87 search area was above 1,525m (5,000 feet) elevation. Following Miller et al. (1987), this high elevation area was not considered suitable bear habitat and was excluded from the density estimate calculations. The UpSu87 density estimate, then, was based on an area of 1,257 km<sup>2</sup>.

This area was further subdivided into 2 parts and density estimates were made for each. Part 1 (520.6 km<sup>2</sup>) contained mostly mountainous terrain and Part 2 (736.3 km<sup>2</sup>) contained mostly low elevation flatland. Six days of search effort were completed for Part 1 and 8 days for Part 2. Part 1 was also searched on a 7th day (the last) but no bears were seen or determined by telemetry to be present.

The UpSu87 study area was subdivided into 7 quad-

rats (3 in Part 1 and 4 in Part 2). These quadrats were used to allocate and document search effort. Average daily search effort varied from 0.8-1.2 min/km<sup>2</sup> (2.1-3.1 min/mi<sup>2</sup>). For all searches and quadrats, search intensity averaged 1 min/km<sup>2</sup>, the same as in the 1985 study (Miller et al. 1987). Complete searches of the study area were conducted on 7 days between 30 May and 7 June 1987. One additional search of just Part 2 was conducted on a day (6 June) when weather did not permit flying in Part 1. Three fixed-wing aircraft were used to conduct searches and do the telemetry flights during the first 3 days of the study and 4 were used during the last 4 days.

In order to minimize potential differences in capture probabilities based on reproductive status (Miller et al. 1987), 10 adult bears were radio-marked in spring 1986. These bears included 7 females (4 with litters of newborn cubs, 1 with a litter of yearlings, and 2 singles). These bears were relocated periodically during 1986 and their movements helped establish the boundaries of the 1987 search area.

During the density estimation phase in 1987, 14 bears >2.0-years-old were captured and marked. Some of these were captured outside of the search area and did not figure into calculations unless they subsequently moved in.

Calculation of density estimates followed Miller et al. (1987) except that binomial confidence intervals were calculated using a computer program instead of from Clopper-Pearson graphs.

One of the key assumptions of capture-recapture estimates is independence of observations (Seber 1982). When bears are sighted in family groups (a female with her offspring) or in breeding pairs this assumption is violated. Potential lack of independence in sighting a member of a breeding pair was avoided by careful instructions to searchers to not count members of breeding pairs that were not independently sighted (Barnes et al. 1988, Smith and Van Daele 1988). Non-independence of sightings of all members of family groups can be corrected by basing calculations only on independent bears (Barnes et al. 1988, Smith and Van Daele 1988). In this area almost all females separate from offspring when they are 2.3 years old (Miller 1987). Correspondingly, estimation of population size for bears >2.0-years-old is essentially the same as estimating population size for "independent" bears.

In addition to the estimate for bears >2.0-years-old, estimates were calculated for bears of all ages as was done by Miller et al. (1987). For this estimate all members of family groups were treated as independent sightings and offspring were considered to have the same status (marked or unmarked) as their mothers. This estimation procedure violates the independence-of-observation assumption and, as a result, the true confidence interval for this estimate is likely to be larger than indicated (Miller 1989). Sightability ratios were calculated as number of times marked bears were seen over the number of times they were known to be present (based on telemetry).

Sex and age composition of the population was based on marked bears known to have been present at least once in the search area during the search period. This procedure will tend to overestimate males because males in this area have larger home ranges than females (Ballard et al. 1982, Miller 1987) and, as a result, more males than females will overlap the search area.

The study area for the UpSu87 estimate was bordered on the north by the foothills of the Alaska Range, on the east by the crest of the Clearwater Mountains, on the west by Wells Creek, and on the south by the Denali Highway. Between these mountains is a broad flat plateau (approximately 830 m elevation) known as Monahan Flats crossed by the west, east and middle forks of the Susitna River.

Vegetation is predominantly shrubs dominated by dwarf birch (*Betula nana*) and willow (*Salix* spp.). Local areas of spruce (*Picea glauca* and *P. mariana*) are found at lower elevations along the rivers. Vegetation at higher elevations is open tussock grasslands.

#### Modifications to the UpSu79 Estimate

The UpSu87 density estimate was made in a portion of a 3,436 km<sup>2</sup> area where bear density was estimated using capture-recapture techniques in 1979 (Miller and Ballard 1982a). In 1979, bears were captured and transplanted from the UpSu79 area and the population estimate was based on the ratio of previously marked and unmarked bears captured; density estimates were based on the estimated population divided by the size of the search area without correcting for lack of population closure or periphery effect (Miller and Ballard 1982a). With some modifications to correct for differences in techniques used, this earlier estimate can be made more directly comparable to the UpSu87 estimate.

To convert population estimates to the same units, the earlier population estimate was recalculated to provide an estimate of 48.5 bears >2.0-years-old. This was done by including 2-year-old bears in the values of  $n_1$ ,  $m_2$ , and  $n_2$  used in calculating the Lincoln-Petersen index and including the (-1) correction of Chapman (Seber 1982). The recalculated 95% confidence interval based on the binomial distribution was 27.5-118.5 bears.

The area included in the 1979 estimate was recalculated to exclude habitats above 1,525 m (5,000 feet) as was done in the 1985 and 1987 estimates. The area below this contour in the 1979 area was calculated as 3,300 km<sup>2</sup>.

Finally, the 1979 density estimate was almost certainly an overestimate because of the assumption that the population was closed. Making this naive assumption for the MidSu85 estimate resulted in a population estimate that was 28.5% too high compared to the estimate obtained using telemetry to correct for movement of marked bears outside of the search area (Miller et al. 1987). The UpSu79 population estimate was reduced by this same percentage in an effort to correct for lack of population closure in the earlier estimate. This yielded a "closure-corrected" UpSu79 population estimate for bears >2.0-years-old of 34.7 bears. Applying the same correction to the limits of the 95% confidence interval yielded an approximate interval around this estimate of 19.7-84.7 bears.

Significance of differences between the UpSu87 and MidSu85 density estimates was evaluated using 1-tailed *t* test for differences between means. For each area, the

mean was calculated from the 7 Lincoln-Petersen estimates (bears >2.0-years-old) obtained for each search replicate.

Harvest statistics were combined from a 2,143 km<sup>2</sup> area along the Denali Highway from Cantwell to Paxson. These were contrasted with harvests reported by hunters from a 5,553 km<sup>2</sup> area centered on the MidSu85 study area. Both areas were subjectively defined based on similarity of bear hunting pressures and access to bear hunters.

## RESULTS AND DISCUSSION

### UpSu87 Density Estimate

*Bears >2.0-years-old.* — Using the bear-days estimator described by Miller et al. (1987) the population estimate for the whole UpSu87 area using 7 days of search effort was 8.37 bears >2.0-years-old (Table 1). The 95% binomial confidence interval was -23.5% to +54.1% of the estimate and the 80% confidence interval was -21.7% to +51.4% (Table 1). In percentage terms, this confidence interval was much broader than the 95%

interval (-9.8% to +18.5%) in the MidSu85 population estimate (Miller et al. 1987) (Table 1). This difference probably reflects the much larger population that was being estimated in the earlier study (25.1 bears >2.0-years-old). As was also observed in the earlier study, point estimates of bear numbers changed little with additional days of effort, but confidence intervals narrowed markedly (Table 1). This population estimate yielded a density estimate of 6.67 bears/1,000 km<sup>2</sup> (95% CI = 5.21-10.08 bears/1,000 km<sup>2</sup>). This is equivalent to 150.15 km<sup>2</sup>/bear (99.2-191.9), 58 mi<sup>2</sup>/bear (38.3-74.1), and 17.3 bears/1,000 mi<sup>2</sup> (13.4-26.1).

The mean of Lincoln-Petersen estimates calculated for each of the 7 days was 8.6 bears >2.0-years-old (Table 1), very close to the bear-days estimate of 8.4 bears >2.0-years-old. The 95% confidence interval for the mean Lincoln-Petersen estimate was  $\pm 2.43$  bears. An estimate for the same data based on the Schnabel estimator was 9.05 bears with a 95% CI based on the normal approximation to the Poisson of 6.28-11.11. Schnabel values were calculated as described by Miller et al. (1987).

*All Bears.* — If it is assumed that offspring in family

**Table 1.** Daily brown bear population estimates for bears >2.0-years-old obtained in the 1985 and 1987 studies. N\* is estimated number of bears based on a bear-days estimator (Miller et al. 1987). "Daily L-P" is the Lincoln-Petersen estimate for each day.

Day	No. marks present	No. marks seen	Total no. seen	Daily L-P	Sightability	N*	Est. density (No./1,000 km <sup>2</sup> )	Confidence interval around N*			
								95% CI		80% CI	
							Upper	Lower	Upper	Lower	
1987 study in area of 1,257 km <sup>2</sup>											
1	2	1	5	8.0	0.50	8.00	6.36	2.79	392.16	3.43	95.69
2	4	1	4	11.5	0.25	11.17	8.88	5.00	106.76	6.12	49.34
3	8	3	4	10.3	0.38	11.33	9.02	6.82	33.67	7.80	23.28
4	6	3	3	6.0	0.50	9.67	7.69	6.64	20.28	7.33	15.73
5	6	1	3	13.0	0.17	10.60	8.43	7.31	21.27	8.10	16.83
6	6	5	6	7.2	0.83	9.37	7.45	7.05	15.27	7.63	12.90
7	4	3	3	4.0	0.75	8.37	6.66	6.55	12.67	7.01	10.98
1985 study in area of 1,317 km <sup>2</sup> (Miller et al. 1987)											
1	10	2	5	21.0	0.20	21.00	15.95	11.72	189.75	13.27	89.13
2	13	1	1	13.0	0.08	20.50	15.57	13.04	97.38	14.39	57.24
3	14	4	7	23.0	0.29	21.83	16.58	15.27	49.08	16.75	37.27
4	17	5	9	29.0	0.29	24.08	18.28	17.85	41.91	19.41	34.72
5	19	5	9	32.3	0.26	26.11	19.83	20.09	40.52	21.68	34.89
6	22	6	6	22.0	0.27	25.17	19.11	20.42	35.37	21.70	31.48
7	19	4	5	23.0	0.21	25.09	19.05	20.76	33.91	21.94	30.58

groups have the same status (marked or unmarked, seen or not seen, present or not present) as their mothers, then a total population estimate can be calculated. These calculations using the bear-days estimator resulted in a total population estimate of 13.21 (95% CI = 10.6-18.5; 80% CI = 11.3-16.5) and a corresponding density estimate of 10.51 bears/1,000 km<sup>2</sup> (95% CI = 8.41-14.68). The difference between this estimate and the estimate for bears older than 2.0 years suggests that 37% of the population was composed of newborn cubs and yearlings. A similar result (32%) was calculated by Miller et al. (1987). Because cub production and survival can vary considerably between years (Miller 1988) and the young cohorts often constitute a large proportion of the population, it is preferable to exclude them when contrasting density estimates made in different areas or at different times. Thus, in the following sections density comparisons are made on the basis of bears >2.0-years-old.

**Sightability.** — Based on telemetry data and sightings, 15 different bears (>2.0-years-old) were known to have been present in the search area at some time during the density estimation period, 12 of these were seen at least once. During the search period, marked bears were known to be present on 36 occasions; these were seen on 17 of these occasions. From these data sightability for bears >2.0-years-old was calculated as 47.2%; in the 1985 study, sightability was 24% (Miller et al. 1987). Data were too few to permit calculation of differences in sightability based on sex or reproductive status.

**Part 1 and Part 2 Estimates.** — Independent estimates of bear density were obtained in 2 portions of the study area. The estimated mean number of bears (>2.0-years-old) present daily in Part 1 was 2.3 (95% CI = 1.7-7.5; 80% CI = 1.8-4.9). In Part 2, this number was estimated as 6.1 (95% CI = 4.7-9.9; 80% CI = 5.0-8.4). The sum of these 2 population estimates is 8.4 bears, identical to the estimate, derived above, for the whole study area. I was surprised that capture-recapture techniques resulted in apparently reasonable estimates for such small populations. Estimated density in the low-lying Part 2 (8.32 bears/1,000 km<sup>2</sup>, 80% CI = 6.8-11.4) was higher than in the mountainous Part 1 (4.4 bears/1,000 km<sup>2</sup>, 80% CI = 3.5-9.5). This was expected because in the spring many bears move out of the mountainous terrain used for denning into lower areas where plant phenology is more advanced and where moose (*Alces alces*) calves are available as prey (Miller and Ballard 1982a, Miller 1987).

### Comparison with MidSu85 Estimate

**Density.** — The carrying capacity of the brown bear habitat in the UpSu87 area was subjectively ranked as

equivalent to that in an adjacent area (MidSu85) where brown bear density was estimated, in 1985, to be 19.05 bears >2.0-years-old/1,000 km<sup>2</sup> (Miller et al. 1987). This density was almost 3 times higher than estimated above for the UpSu87 area. Identical estimation procedures were used in both studies. There was no overlap in the 95% confidence intervals between studies on days 6 and 7 of the estimation procedure (Fig. 2). The mean of the 7 daily Lincoln-Petersen density estimates (bears >2.0-years-old) in the MidSu85 area was larger (17.7 bears/1,000 km<sup>2</sup>) than for the UpSu87 study (6.8) ( $P = 0.04$ ). These results indicate the capability of the capture-recapture procedures used in these studies to document significant differences in bear densities.

**Hunter Access.** — The MidSu85 density estimate was made in a relatively remote area where access by hunters was more difficult and hunting pressure, as a result, was thought to have been lower than in the UpSu87 area, which is bisected by the Denali Highway. Hunting pressure on bears, especially during fall seasons when many bears are shot incidental to moose or caribou (*Rangifer tarandus*) hunts, will be more intense in areas with road access because they are relatively easy and inexpensive to hunt. Mandatory reports from successful bear hunters indicate that in the Denali highway area (including the UpSu87 study area), 37% of hunters taking bears used highway vehicles compared to 5% in the interior portion of the unit surrounding the MidSu85 area (ADF&G file data). Aircraft were used by 23% of the hunters in the Denali Highway area compared to 76% in the interior area (ADF&G files).

**Kill Density.** — Brown bear harvests per unit area in

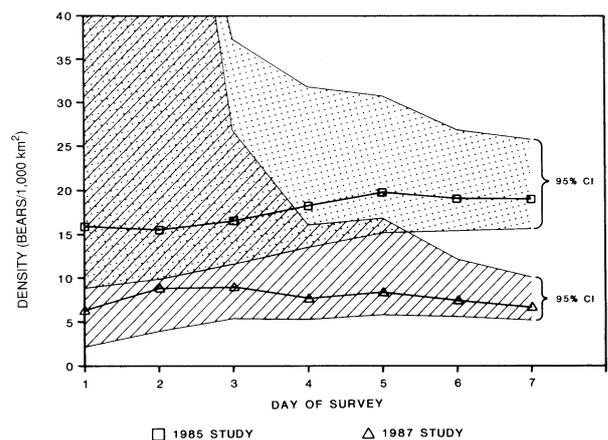


Fig. 2. Comparison of daily brown bear density estimates (bears >2.0-years-old) based on the animal-days estimator (Miller et al. 1987) in the 1985 and 1987 study areas. Ninety-five percent confidence intervals for the estimate on each day are illustrated.

the easily accessible Denali Highway area also have been higher than in the central, more remote, portion of the unit. During 1981-1988, an average of 10.1 bears/1,000 km<sup>2</sup>/year were killed in the Denali Highway area (2,143 km<sup>2</sup>) compared to 4.5 in the central portion (5,553 km<sup>2</sup>). This pattern has existed since the early 1970's with kill density in the Denali Highway area exceeding that in the less accessible area in 18 out of 19 years (Fig. 3). In my view, the decline in bears harvested/unit area in recent years in the Denali highway area (Fig. 3) probably reflects a situation where former harvests in excess of sustainable levels can no longer be compensated by increased immigration from surrounding, less heavily hunted, areas. Recent increases in kill in these surrounding areas may mean they no longer can produce a crop of emigrants that can be harvested in areas more accessible to hunters. Average numbers of bears killed annually by hunters in this central portion of GMU 13 during 1970-1978 was 11.3 bears (range 6-23). During 1979-1987 hunters killed an annual average of 24.1 bears/year in this same area (range 13-36) (ADF&G files).

### Comparison with UpSu79 Estimate

*Density.* — With some adjustments to correct for differences in techniques used, the UpSu87 density estimate can be compared to an earlier estimate in the same area (UpSu79) to determine if density had changed during the period 1979-1987. After corrections for lack of closure, for area of non-bear habitat (>1,525 m), and for unit conversion (bears >2.0-years-old instead of >3.0-years-

old), the recalculated UpSu79 density estimate was 10.5 bears >2.0-years-old/1,000 km<sup>2</sup> (95% CI = 6.0-25.7) or 27.2 bears >2.0-years-old/1,000 mi<sup>2</sup> (95% CI = 15.5-66.5). In contrast, the UpSu87 density estimate was 6.7 bears/1,000 km<sup>2</sup> (95% CI = 5.2-10.1). The 1987 estimate is 64% of the corrected 1979 estimate obtained in the same area (Fig. 2). The large confidence interval for the UpSu79 estimate (Fig. 4) results from this estimate being based on a single mark-recapture calculation rather than on a series of replicated procedures as was done for the MidSu85 and UpSu87 estimates.

*Hunter access.* — The UpSu79 density estimate is lower than the MidSu85 estimate (Fig. 4). This is consistent with the above interpretation that the readily accessible area along the Denali Highway that includes the UpSu79 area, has long been more heavily harvested than the interior MidSu85 area (Fig. 3). Because of this history of heavy harvests, it is likely that, prior to liberalization of regulations, the UpSu79 bear population had already been reduced to the point where there was little potential to increase the number of bears taken even with increased hunter effort.

*Hunter Effort.* — In the Denali Highway area, successful bear hunters during 1983-1987 have also reported spending more time hunting before killing a bear (4.4 days) than they did during 1970-1977 (2.9 days). Although these differences were not significant (*t* test, *P* > 0.1) if only because of high variability, they are in the direction that would be expected under the hypothesis that bears were declining in this area.

*Harvest Density.* — It is worth noting that kill density divided by population density provides a rough estimate of harvest rate. The 1981-1988 average kill density of 10.1 bears/1,000 km<sup>2</sup> in the expanded Denali Highway area divided by the MidSu85 density estimate of 19.05 bears >2.0-years-old/1,000 km<sup>2</sup> provides an annual harvest rate estimate of 53%. Based on long-term studies of bear reproductive rates in this area (Miller 1987) and conservative estimates of natural mortality rates, sustainable harvest rate in this area for the population older than 2.0 years was estimated to be less than 8% (5.8% for females >2.0-years-old) (Miller 1988). Even with considerable room for error in the harvest data, kill rate in the Denali Highway area has clearly exceeded sustainable levels. The decline in kill density in recent years (Fig. 3) doubtless reflects reduced availability of bears caused by these harvests in excess of sustainable levels.

Errors and inconsistencies in the harvest data are caused by hunters misreporting kill locations. During 1982-1986, for example, bag limits were 1/year in

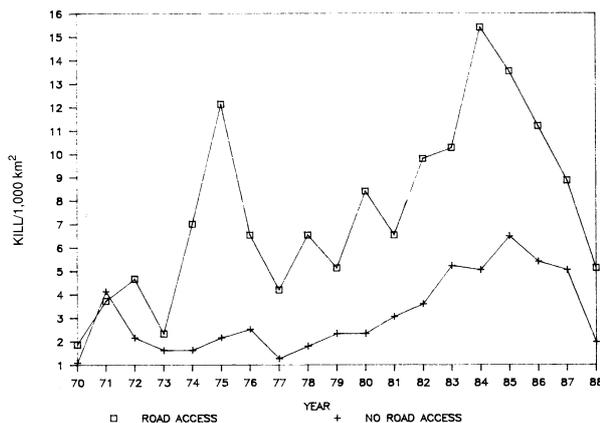


Fig. 3. Annual brown bear kill density (number killed/1,000 km<sup>2</sup>) in road accessible (Denali Highway area) and inaccessible (central) portions of Alaska's Game Management Unit 13 during 1970-1988. Bag limit was 1/year from fall 1982 through spring 1987, 1/4 years before and after this period; spring season was added in 1980 and remains in effect.

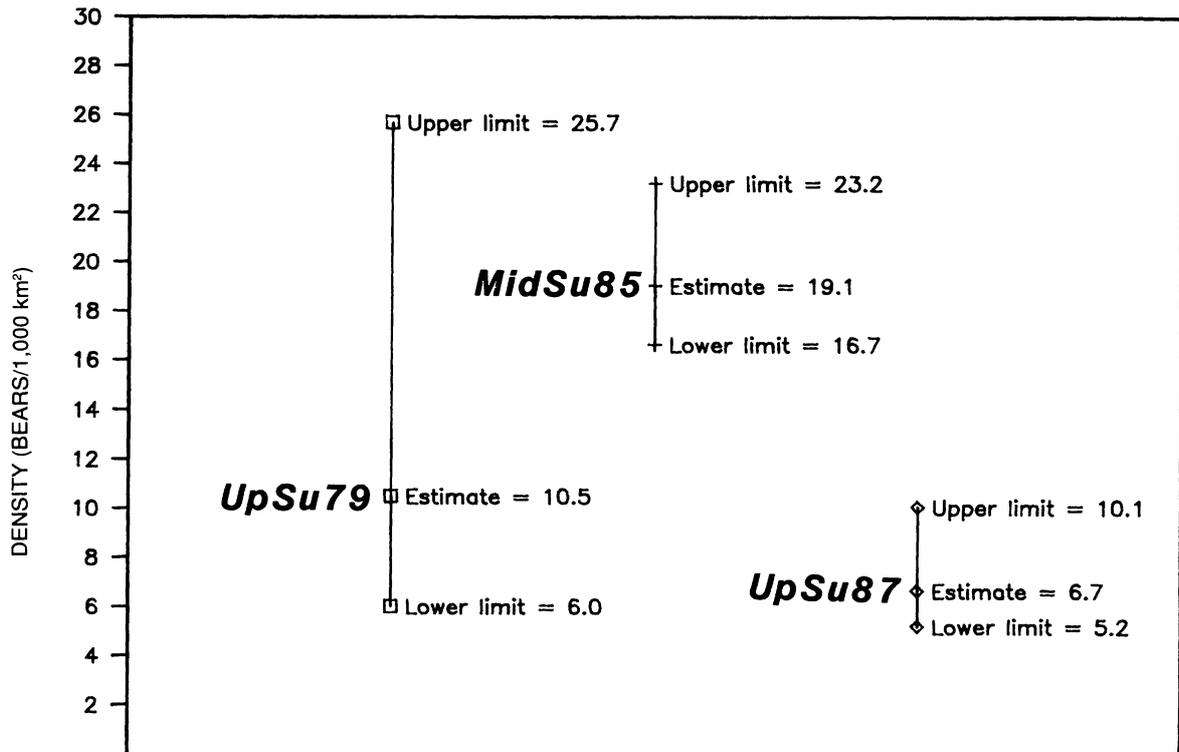


Fig. 4. Comparison of final brown bear density estimates for bears >2.0-years-old obtained in the same area in 1979 and 1987 and in a nearby area in 1985, 95% confidence intervals are illustrated. Differences in density are attributed to hunting pressure.

GMU 13 compared to 1/4 years in adjacent GMUs and this caused some hunters to misreport kills as having come from GMU 13. Also, some yearling bears, which are illegal to shoot, are included in the harvest statistics. Both of these sources of error inflated harvest statistics to some degree (Miller 1988) and may contribute to the extremely large discrepancy between calculated sustainable and reported actual kill densities.

#### Technique Limitations and Complicating Factors

*Assumption Violations.*— Violation of the underlying assumptions of capture-recapture techniques can lead to erroneous estimates of population size and confidence intervals. Such errors are most likely to occur and are potentially of larger magnitudes when estimating small numbers (White et al. 1982). In this study, the mean number of bears estimated for the UpSu87 estimate on an average day during the search period was small, only 8.4 bears >2.0-years-old (Table 1). This mean number was also small for MidSu85 estimate, only 25.1 bears >2.0-years-old (Table 1).

It is also possible that probability of capture or recapture was not equal for all classes (e.g., reproductive status) or individuals. Available data are inadequate to

reject the null hypothesis that bears have equal sightability based on reproductive status ( $P > 0.10$ ) (Miller 1988). However, this does not mean the null hypothesis is true; females accompanied by newborn cubs, at least, may have lower sightabilities than other classes (Miller and Ballard 1982a, Miller et al. 1987). If systematic bias based on sightability occurs, it would almost certainly lead to an underestimate of density as the individuals or classes with low sightability would have too few marks and too few sightings. From a bear manager's perspective, a systematic bias toward underestimation is probably preferable than the reverse situation. However, such a bias could exaggerate the density differences between UpSu87 (which had a single year of premarking) and MidSu85 (which had 5 years of premarking). The probability of having caught and marked the animals with lower capture probabilities, if such exist, would increase with the additional years of premarking and the likelihood of systematic bias would decline.

*Mining Disturbance.*— Some of the difference between densities measured in this study may result from an open pit gold mining operation initiated in 1982 in the UpSu87 area. At present, most mining activity is concentrated in a small area (52 km<sup>2</sup>) that is unlikely, so far, to

represent a significant loss of habitat to bears. Killing by miners of "nuisance" bears may be a more significant impact in the long term as this could become a constant drain into a population "sink" (Knight et al. 1988). Although this potential effect cannot be discounted, in the short period that the mine has been in operation there has been no evidence that such killing has occurred.

*Research Disturbance.* — Research previously conducted in the UpSu87 study area may also have contributed to the reduced density observed in comparison to the 1985 area. In 1979 we captured and transplanted 47 bears out of a 3,436 km<sup>2</sup> area which included the UpSu87 study area (Miller and Ballard 1982*a,b*). This was done as part of an effort to evaluate the impacts of reduced brown bear densities in spring on survival of moose calves (Ballard et al. 1981, Ballard and Larsen 1987, Ballard and Miller 1987, Ballard et al. 1987). This work also resulted in the bear density estimate discussed earlier (Miller and Ballard 1982*a*). This transplant may have had a residual impact on bear density in the area but there is no adequate way to evaluate whether it has. We observed that at least 60% of the transplanted bears returned and not all bears were transplanted (Miller and Ballard 1982*b*). Also, the area from which bears were transplanted was relatively small compared to movements made by bears in this area (Ballard et al. 1982, Miller 1987). Some immigration from surrounding areas, especially of subadults, would likely occur into vacant habitats left by bears that did not return following transplant. It is possible, however, that our 1979 study contributed to some degree to the reduced density in the UpSu87 study. Data on population composition, discussed below, are consistent with the explanation that the transplant had relatively little effect on the density estimates compared to the effect from hunting.

### Population Composition

*Sex Ratio.* — Population composition data are also consistent with the explanation that heavy hunting was the primary cause for the differences in densities documented in this study. Males constituted the highest proportion of the population in the UpSu79 study and the lowest proportion in the UpSu87 study (Table 2). This is consistent with the hypothesis of increasingly heavy harvest because hunters tend to selectively harvest males (Bunnell and Tait 1980). These data probably exaggerate the proportion of males present during the UpSu79 study area as in the 1979 study bears were captured over a 2-week period during which males from a larger area were exposed to capture than were females (because males have larger home ranges). The percent males in the UpSu79 data may also have been exaggerated in com-

parison with the MidSu85 and UpSu87 studies that occurred in a shorter time period and did not involve removal of bears.

*Age Ratio.* — Age data provide additional indications of the impact of heavy harvests on bear densities. Under conditions of heavy hunting, it is probable that the proportion of the population comprised of older individuals would be lower than under light hunting conditions (because older, larger animals are selected by hunters seeking trophies). On the other hand, it is possible that some bears may get more clever at avoiding hunters as they grow older. This is unlikely, however, to be very significant in these relatively open habitats which offer few safe hiding places from hunters during the long hunting season. Older females are less vulnerable to hunters than subadult females or males because of regulations which prohibit shooting females accompanied by cub or yearling offspring. These regulations effectively protect adult females during much of their lives. Under these circumstances mean age of females may increase under heavy hunting pressure, at least during the initial stages of a population decline (Harris 1984).

These patterns were evident in the age composition data. Mean ages of males were lower in the UpSu87 study than in the UpSu79 or MidSu85 studies (Table 2). Ages of females were about the same in the MidSu85 and UpSu87 studies but females were older in these studies than in the UpSu79 study (Table 2). Available data provide no evidence of increased juvenile survivorship associated with the hunter-induced decline in bear density (Miller 1988).

### Technique Considerations

*Procedures.* — In all of the studies discussed here all bears seen were captured and marked except on the last day of study when there was no need to increase the number of marks present in the population. Similar procedures were followed by Ballard et al. (1988, 1990) and Reynolds and Hechtel (1988). In estimating high density populations in southeastern Alaska (Schoen and Beier 1988) and on Kodiak Island (Barnes et al. 1988) bears were not captured during the density estimation phase of the study. Miller et al. (1987) noted that such "capture"-without marking procedures would have made little difference in their density estimate but recommended capturing unmarked bears in order to better estimate population structure. In high density areas, however, it is frequently impractical to capture all bears observed. Also, it is possible that operation of a helicopter during the density estimation phase may disturb bears and cause some to abandon the search area or be more

**Table 2.** Population composition in 1979, 1985 and 1987 studies. Composition is based on bears present in study area at least once during search period.

	1979			1985			1987		
	Males	Females	Both	Males	Females	Both	Males	Females	Both
Number >2.0-years-old	19	15	34	14	17	31	8	10	19
Number >5.0	9	8	17	10	13	23	3	8	12
Mean age (>2.0)	6.4	7.0	6.6	9.9	10.2	10.0	4.1	10.0	6.6
Median age (>2.0)	4	5	5	9	7	9	2	7	6
Bears >2.0									
% females			44			55			56
Males/100 females			127			82			80
Bears >5.0									
% females			47			57			73
Males/100 females			113			77			38

secretive. The decline in estimated number of bears present on each day over the search period in the UpSu87 study (Table 1) may reflect such a disturbance. I did not feel that this was a factor in the MidSu85 study (Miller et al. 1987). This may be because in the MidSu85 study bears had been exposed for 5 years to heavy helicopter traffic associated with a variety of engineering and environmental studies for a proposed hydroelectric project. In areas with high bear densities as well as in areas where capture operations might cause bears to leave the search area, it may not be desirable to capture bears during the density estimation phase of capture-recapture studies.

*Costs.* — Density estimates of the type obtained in these studies are expensive. The MidSu85 density estimate, conducted on a population that had been previously subjected to 4 years of marking effort, cost about \$60,000 in operating expenses (Miller et al. 1987). The density estimation portion of the UpSu87 study had similar costs, and about \$30,000 was spent in 1986 in the premarking effort. This brought the total cost of the UpSu87 density estimate to about \$92,000 not including salaries of personnel involved. Because it is extremely expensive to work in Alaska, these high costs should not discourage investigators from applying this technique where bear populations are reasonably dense and bears can be sighted from the air. Application of this technique for a 3-day estimation period cost <\$10,000 on populations of previously marked bears when unmarked bears were not captured during the density estimation phase (J.W. Schoen pers. commun., V.G. Barnes pers. commun., R.B. Smith pers. commun.).

*Available Software.* — To assist in the planning of capture-recapture density estimation procedures like those described here, simulation software, available upon request, has been developed in BASICA for IBM-compat-

ible computers with at least 640K RAM. This software compares 2 capture-recapture estimators (bear days [Miller et al. 1987] and the mean of daily Lincoln-Petersen estimates) and permits varying the following parameters: number of days effort, capture probability (1 value for all individuals), probability that an individual will be in the search area on any day (goodness of closure assumption), population size (maximum = 200), number of marks in population, and whether unmarked bears spotted will be marked. Up to 100 replications using these input variables can be specified. This program does not calculate confidence intervals for the estimates. A spreadsheet based in LOTUS 1-2-3 (Lotus Development Corporation, release 2.0) is also available to make density calculations for a capture-recapture application and calculate confidence intervals based on normal and binomial distributions. Another program has been written to generate parameters needed to calculate binomial confidence intervals in the spreadsheet.

## CONCLUSIONS

In a portion of southcentral Alaska, kill of brown bears by hunters increased in response to liberalized bear hunting regulations that were adopted with the intent of causing a moderate reduction in bear densities and increasing survival of moose calves. Even though the number of bears harvested increased under the liberalized regulations, there was both public and professional disagreement about the direction of trend in the bear population. Data on sex and age composition of harvests were inadequate to resolve these disagreements as available data could be interpreted in different ways. Following comparisons of density estimates obtained using capture-recapture techniques in different areas at different times, a consensus was reached that the population was declin-

ing and more conservative regulations were adopted.

This earlier disagreement demonstrates the inadequacy of the tools traditionally available to managers desiring to document trends in bear populations. Because these tools tend to be subjective to varying degrees and because differing interpretations of the data are possible, inaccurate or non-parsimonious interpretations may be accepted with resulting risk of management error. The techniques used in this study are objective, have an estimate of variance, and can be replicated. They give managers the ability to document changes in bear density that may occur as a result of human activities. Ideally, data on bear densities should be obtained in many areas so managers have a baseline upon which to judge how far densities have changed. Like many techniques for estimating numbers of wild animals, these procedures probably will be unconvincing in detecting small changes in bear density (<10-20%).

The decline in density resulting from hunting documented in this study also demonstrates that hunters can cause significant reductions in bear populations. Few biologists have doubted that this is the case. However, some have misinterpreted results reported by Young and Ruff (1982) and Kemp (1976) to the effect that increased hunting, because it tends to select for males which are predators on cubs, causes increased survival of cubs which compensates for the increased hunting mortality. At least under conditions where bear harvests are increasing, managers should not count on such magical mechanisms to make everything come out right in the end. There is no room for complacency in bear harvest management (Harris 1984).

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