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SIZE, TREND, DISTRIBUTION AND CONSERVATION OF THE BROWN BEAR *Ursus arctos* POPULATION IN SWEDEN

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Abstract

The density of adult (≥3 years) female brown bears Ursus arctos *was estimated in two areas of Sweden from ratios of radio-marked and unmarked females consorting with radio-marked adult males during the breeding season. The resulting densities were 1·2 ± 0·81 (95% confidence interval) adult females/1000 km² in a northern study area and 1·06 ± 3·44 adult females/1000 km² in a southern area. These estimates were extrapolated to obtain a population estimate for Sweden using relative densities throughout the range of the species in Sweden, based on hunter-kill statistics, and observed rates of reproduction and juvenile and subadult survival. The total population in spring 1991 was estimated to be about 620 bears, with almost all females confined to four geographically separated areas, termed female core areas. A supplementary estimate, based on estimated kill rates of adult females in the study areas, was about 660 bears. Estimates based on hunter kill rates of marked bears gave minimum and maximum estimates of about 300 and 900 bears, respectively. Although these are not confidence intervals of the total population estimate, we believe that the true population size is included within these limits. Densities within the female core areas varied from 50 to 100% of those in similar habitats in European Russia. The bear population in Sweden appeared to have increased at a stable rate of about 1·5% annually during the past 50 years. Mean annual rate of legal harvest during 1943–1991 was estimated to be 5·5% (±2·1% SD), suggesting a maximum sustainable rate of 7·0% for this population. The harvest increased at a rate of 9·6% annually during 1981–1991, and apparently was at the maximum sustainable level during 1987–91.*

Keywords: brown bear, Sweden, population estimates, mortality rates, hunting.

INTRODUCTION

The brown bear *Ursus arctos* was originally found throughout Sweden, but by the end of the 1800s it had been exterminated in southern Sweden. As it was believed that bears were also declining farther north, the payment of bounties on bears was discontinued in 1893. The population apparently continued to decline, so the bear received protection from hunting on Crown lands in 1913 and all dead bears became Crown property in 1927 (Lönnberg, 1929). The bear population then increased and in 1942 the total population was estimated to be about 300 (Selander & Fries, 1943). Based on this estimate, a bear hunting season was reopened on Crown lands in 1943 (Sandegren, 1992). During 1975–76, the distribution of bears was mapped in Sweden and the population was estimated at 400–600 (Bjärvall, 1980). Based on Bjärvall's (1980) study, hunting quotas were introduced in 1981. In 1981, the quota was 36 bears; by 1991 it had increased to 51. The kill also increased during this period, from 16 in 1981 to a high of 49 in 1989. In spite of the increasing quota and kill, the status of the brown bear has not been reevaluated in Sweden since Bjarvall's (1980) study in 1975–76. The goal of our study was to estimate the number of bears, determine the population trend and distribution of females, and make recommendations for conserving the species in Sweden.

METHODS

Density of adult females on study areas

We estimated the density of adult female bears in two areas where bears have been studied with radio-telemetry since 1984 and 1985. One area is in the southern portion of the bear's range in Sweden, and one in the northern portion (Fig. 1). We based our estimates on adult females because they are the least mobile, have the smallest home ranges, and are the most important part of the population to consider in the management and conservation of bear populations (Eberhardt *et al.*, 1986; Bjärvall *et al.*, 1990; Wabakken *et al.*, 1992).

Population estimates were based on observation of marked adult males and females during the breeding period (May–July). The mating behaviour of brown bears is variable; males and females may form pair bonds lasting up to several weeks or may simply

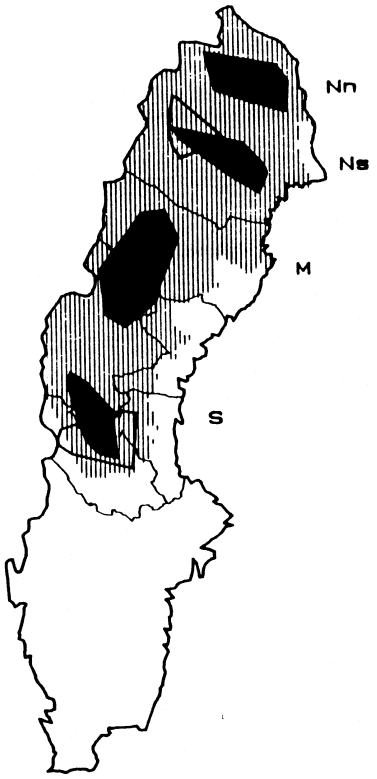

Fig. 1. Map of Sweden showing study areas (thick lines), core areas (shaded areas), the area where bear hunting was allowed during all or part of the period 1981–1991 (vertical lines), and county boundaries (thin lines) where bears are hunted. The letters refer to the four female core areas described in the text.

come together for a few hours (Craighead *et al.*, 1969; Herrero & Hamer, 1977). Males may mate with several females and females may mate with several males (Stirling & Derocher, 1990). To obtain observations of adult females, radio-marked adult male bears were monitored once to twice per week. Observations were usually from an airplane, but some were from the ground. A male was considered to be an adult when ≥4 years old. The number of monitored adult males varied from 2 to 11 per area and year (Table 1). Bears seen with a radio-marked adult male were determined to be radio-marked or unmarked. Bears with adult males were assumed to be females. Of 43 cases where a radio-marked adult male was observed with another radio-marked bear, only one observation was of two males, and they were fighting. Thus, the marked adult males led us to the females that constituted the marked–unmarked sample. If a female was observed with a male more than once in a day, only one observation was included. Monitoring rarely occurred on consecutive days. We assumed that a male spent the same amount of time with marked and unmarked females, i.e. there was no bias if a male was seen with the same female more than once. Our estimates were based on the Petersen method, using the equation:

$$\hat{N} = \frac{M\,(C + 1)}{R + 1} \qquad (1)$$

which is appropriate when a given animal can be counted more than once (Bailey, 1952), and where:

N = the estimated number of adult females without young, i.e. those that would be with adult males at time of observation;
M = the number of adult females without young that carried functioning radio transmitters;
C = total number of observations of females with marked adult males (captures); and
R = number of observations of marked females seen with marked adult males (recaptures).

Binomial confidence intervals were calculated for each area during each year in which a suitable sample size was available for an estimate (Krebs, 1989). Because bear populations change slowly in size (Harris & Metzgar, 1987*b*), a mean estimate was calculated for each area. Confidence intervals were calculated for the mean estimate using eqn (2) in Eberhardt (1990) for the estimate of variance. In both areas, we met the assumption of population closure by confining the study area to the convex polygon formed by the composite home ranges of all radio-marked adult female bears—7,576 km² in the north and 13,009 km² in the south. Thus, the marked population did not move in

Table 1. Estimates of numbers of adult female bears without cubs-of-the-year or yearlings at their side, by study area and year in Sweden

Area	Year	M (marked)	C (observed)	R (marked bears observed)	$\hat{N}$ (estimate)	95% CI[a] Lower	95% CI[a] Upper	Males[b]
North	1988	4	9	8	4·4	4·0	8·2	4
	1989	3	5	4	3·6	3·0	10·7	2
	1990	4	9	7	5·0	4·0	20·0	2
	1991	6	6	6	6·0	6·0	11·4	2
	Mean				4·5	1·6	8·0	
South	1988	3	13	3	10·5	5·6	60	7
	1989	4	19	10	7·3	5·1	13·8	11
	Mean				8·9	0	37·5	

[a] Note that the confidence intervals (CI) for individual years and for the mean values were calculated in different ways (See Methods).
[b] Number of adult males followed each year.

and out of the study area, which has been a problem in other estimates of bear population densities (Miller *et al.*, 1987; Eberhardt, 1990).

The population estimate included only adult female bears without young. In both areas three-year-old marked females were observed with adult males during the breeding season (May–July), and in the southern area two females first gave birth as four-year-olds. Therefore, females were considered to be adults at the age of three years. Adult females were observed with cubs of the year (COYs) or yearlings during the breeding season during 48% of 25 bear-years in the northern study area and 36% of 22 bear-years in the southern study area. This difference was due to the fact that about half of the females in the north weaned their young as two-year-olds, whereas all but one female observed in the south weaned their young during the yearling year. The year of first capture was excluded for all females in this calculation of percentage of time with young, because females with COYs were avoided during capture attempts. These figures include females that lost their COYs and were available for mating the same year. Thus, a given adult female was potentially in oestrus during 52% of the spring periods in the north and 64% in the south. Using these values, the population estimates were corrected to account for all adult females.

Estimate of number of adult females in Sweden

The estimated number of adult female bears in Sweden was based on the estimated density of adult females in the two study areas and the relative densities of females in four core areas from hunter harvest records. Female core areas were defined using the locations of female bears killed during 1981–1991. Convex polygons were drawn around four clusters of locations in the country, with the most extreme outlier excluded for each cluster, hereafter referred to as 'core areas' and designated, from north to south, as Nn (North-northern), Ns (North-southern), M (Middle), and S (South) (Fig. 1). All the bears associated with each core area are referred to here as a subpopulation of the same name. Both study areas included a similar proportion of a core area—35% in the north and 37% in the south. Therefore, the study area estimates included higher density areas within the core areas and lower density areas surrounding it.

The estimated number of adult females associated with each core area was determined from the following equation:

$$\hat{N} = \frac{(D_{ls}/D_{ks}) \times D_{kc}}{0{\cdot}36} \times S \qquad (2)$$

where

$\hat{N}$ = estimated number of adult females in the core area;

D_{ls} = estimated density of adult females in the study area (N/1000 km^2);

D_{ks} = density of hunter-killed females in the study area (N/1000 km^2);

D_{kc} = density of hunter-killed females in the core area (N/1000 km^2); and

S = size of the core area in 1000 km^2.

The denominator 0·36 in eqn (2) is the mean of the proportion of the study areas (35 and 37%) that were included within the core areas. All females were considered to be within the female core areas for the purpose of these calculations. Our field observations supported the assumption that female densities were much higher within the core areas than outside (see Results).

The density of hunter-killed females (D_{ks} and D_{kc}) was the mean annual number of females killed per 1000 km^2 of land open for bear hunting. This was first calculated for each municipality. A value for each study area and female core area was obtained by summing the values for each municipality weighted for the proportion of the municipalities within each area. Hunter effort is not recorded in Sweden, but an index to hunting pressure was calculated by dividing the densities of live females by the densities of hunter-killed females on the study areas (D_{ls}/D_{ks}). We assumed that hunting pressure in the core areas with study areas was the same as within the corresponding study area. In the core areas without study areas, we assumed that hunting pressure in Nn was the same as that for the nearest study area (Ns) and intermediate between the two study areas for M (see Fig. 1). This method is based on the assumption that, in areas with similar hunting pressure, the density of hunter-killed females is linearly related to the density of live adult females.

Bear hunting is allowed for all hunters who have hunting rights and own a rifle that is powerful enough to be permitted for bear hunting. There is no licence requirement and no limit on the number of bears shot by an individual hunter. Hunting over bait and with dogs is allowed, but most bears are shot incidentally by hunters hunting primarily moose *Alces alces* (Dahlström, 1991). The bear hunting season (1–30 September in the north and 1 September–15 October in central Sweden) corresponds roughly with the moose hunting season, and moose hunters are numerous and widely distributed over the country. Total bear harvest during 1981–1991 was limited by a quota. The Swedish Environmental Protection Agency, after consultation with the county administration and hunting administration officials in each county, decides the quota each year. Each municipality where hunting is allowed, or sometimes two or more combined, has a quota. After the quota is met in a municipality, or the hunting season ends, all hunting of bears stops for the year. Females with young and COYs are protected from hunting. Harvest reached 90% of the quota in only three of the 32 municipalities during the entire period 1981–1991. In addition, the quota was reached in less than 20% of the years that hunting was allowed in any municipality. Thus, harvest numbers were not seriously constrained by limits imposed by the quotas. The annual legal harvest of bears was obtained from the Swedish Forest Service for 1943–1958 and from the Swedish Hunters' Association for 1959–1991. A population estimate was calculated for each year during 1943–1991 from the regression equation given in the Discussion of this paper.

Annual legal harvest rate was the harvest divided by the population estimate.

Total population estimate in Sweden

To obtain a total estimate of all bears in Sweden, we expanded from the estimated number of adult females. We used a 50:50 sex ratio (see Results) to obtain the number of males ≥3 years old. The number of COYs was calculated from observed reproductive rates of radio-marked females. The number of yearlings was estimated by multiplying the number of COYs by observed cub survival rates. Similarly, the number of two-year-olds was estimated using observed yearling survival rates. These estimates are of the population in spring 1991.

Supplementary population estimates

The number of adult females was also estimated another way to compare with the results from the primary method described above. The estimated density of adult females in each study area was divided by the density of adult females killed there annually by hunters. This provided two estimates of harvest rates of adult females. The annual harvest of adult females was divided by the mean of these rates to obtain an estimate of adult females in the entire country.

The total number of bears in Sweden (excluding COYs) was also estimated from the harvest rates of marked bears both from bears in areas open to hunting during the hunting season, and all marked bears. The total harvest was divided by these two harvest rates to obtain total estimates.

Table 2. Estimates of densities of adult female bears (number/1000 km²) without young-of-the-year or yearlings at their side and all adult female bears, by study area and year in Sweden

Category	Area	Year	Estimate	95% CI[a] Lower	Upper
Without young	North	1988	0·58	0·53	1·08
		1989	0·47	0·39	1·41
		1990	0·66	0·53	2·63
		1991	0·79	0·79	1·50
		Mean	0·63	0·21	1·05
	South	1988	0·81	0·43	4·61
		1989	0·56	0·39	1·06
		Mean	0·68	0	2·88
All females	North	1988	1·12	1·02	2·08
		1989	0·90	0·77	2·71
		1990	1·27	1·02	5·06
		1991	1·52	1·52	2·88
		Mean	1·21	0·40	2·02
	South	1988	1·27	0·67	7·20
		1989	0·88	0·61	1·66
		Mean	1·06	0	4·50

[a] Note that the confidence intervals (CI) for individual years and for the mean values were calculated in different ways (see Methods).

When statistical tests involved a 2 × 2 contingency table, the χ^2 value was corrected for continuity with Yate's correction (Sokal & Rohlf, 1981) and indicated as χ^2_c. If the data were insufficient for a $\chi 2$ test, a Fisher's exact test was used (Sokal & Rohlf, 1981).

RESULTS

Density of adult females in the study areas

Estimates of the number of adult females without young were made for four years in the northern study area (1988–1991) and two years in the southern study area (1988–1989) (Table 1, Fig. 1). The mean estimates were 4·8 (95% confidence intervals of 1·6–8·0) adult females without young in the north and 8·9 (0–37·5) in the south. The estimates of density for all adult females were similar in the two areas, 1·21/1000 km² (0·40–2·02) in the north and 1·06 (0–4·50) in the south. The confidence intervals were relatively narrower in the north than in the south (Table 2). In the south, males were intensively marked during the early part of the study, but later effort was concentrated on females so an adequate sample of marked males and females was available only during two years.

Estimate of adult females in Sweden

The harvest of female bears was concentrated in four areas in Sweden, termed female core areas (Fig. 1). Females are found outside these core areas, but are not common there. Of the 166 females shot during 1981–1991, only 4% were killed outside these core areas, compared with 32% of the 196 harvested males. The harvest consisted of 54% females (n = 293) within the core areas, compared with 10% (n = 69) outside. The distribution of the sexes was significantly different with respect to core areas (χ^2_c = 42·0, d.f. = 1, $p < 0·0001$).

The number of adult females in each female core area was calculated from the estimated density within the study areas and the relative densities, based on densities of hunter-killed females. The results yielded 19–74 adult females for the four subpopulations, for a total of 161 for the entire country (Table 3). Although this method is based on the female core areas, the method of calculation includes the females that were associated with a core area but outside its boundaries (i.e. within the subpopulation).

Total population estimate for Sweden

The total population estimate was based on the estimates of adult females, a 50:50 sex ratio, observed reproductive rates, and observed survival rates of COYs and yearlings. Some studies have shown that hunted bear populations can have a biased sex ratio, due to a greater vulnerability to hunting among males (Gilbert *et al.*, 1978; Fraser *et al.*, 1982). During 1981–1991, the sex ratio of the harvested bears in Sweden was 54% males (n = 375), which was not statistically different from a 50:50 sex ratio (one-group χ^2 = 2·55, d.f. = 1, p = 0·11). In addition, there was no significant relationship between sex ratio and age among hunter-

Table 3. Estimated number of adult female bears (≥3 years old) for each subpopulation in Sweden based on densities of hunter-killed female bears in the two study areas and four female core areas, sizes of the areas and estimated or calculated densities of live adult females

Type of area	Location[a]	Density		Size of area (km²)	Number of adult females
		Killed	Live		
Study areas	Ns	0·188	1·21[b]	7 600	9
	S	0·237	1·06[b]	13 000	14
Core areas	Nn	0·085	0·55[c]	12 600	19[d]
	Ns	0·189	1·22[e]	10 100	34[d]
	M	0·213	1·14[f]	23 500	74[d]
	S	0·279	1·25[e]	9 700	34[d]
Total					161

[a] See Fig. 1 for locations.
[b] Estimated, from the Petersen estimator, Table 2.
[c] Calculated, assuming the harvest rate in Nn was the same as in Ns.
[d] Calculated using eqn (2) in Methods.
[e] Calculated, using the relationship between kill density and live density found in the study area.
[f] Calculated, assuming a harvest rate intermediate between Ns and S.

killed bears (logistic regression, $G = 0{\cdot}89$, $p > 0{\cdot}25$). Therefore, we could not reject the null hypothesis that the sex ratio is 50 : 50 and the number of adult males was considered equal to the number of adult females.

The observed reproductive rates of radio-marked females ≥3 years old was 0·763 in Ns (29 COYs in 38 years) and 0·750 in S (33 COYs in 44 years). These rates were not statistically different (Mann-Whitney U test, $U = 844{\cdot}5$, d.f. = 81, $p = 0{\cdot}34$). Therefore, the combined reproductive rate (0·76 COYs per year) was used to calculate the number of COYs produced per year per subpopulation based on the estimated number of adult females.

The number of yearlings was calculated from the number of COYs using observed survival rates of COYs from emergence in spring to emergence as yearlings the following spring; this was 88% ($n = 26$) in the north and 67% ($n = 35$) in the south. We used the combined survival rate (77%) because they were not statistically different ($\chi^2_c = 2{\cdot}31$, d.f. = 1, $p = 0{\cdot}13$). The number of two-year-olds was calculated the same way, using yearling survival, which was 90% ($n = 10$) in the north and 84% ($n = 19$) in the south. We used the combined value of 86% because they were not statistically different (Fisher's exact test, d.f. = 28, $p > 0{\cdot}50$).

The resulting population estimates ranged from 73 to 284 for the four subpopulations and totalled 619 for the entire country (Table 4).

We estimated densities within the four female core areas, based on the population estimates for each subpopulation (Table 4) and the assumption that the sex of the harvest in and outside the core areas was representative of the distribution of the bears. As stated earlier, 96% of the female harvest and 68% of the male harvest were killed within the female core areas. We

Table 4. Estimates of the total number of bears in each subpopulation (one for each core area) and for the entire country based on an estimate of 161 adult females (≥3 years old)

Age category	Subpopulation (by core area)				Entire country
	Nn	Ns	M	S	
Adult females[a]	19	34	74	34	161
Adult males[b]	19	34	74	34	161
Cubs[c]	14	26	56	26	122
Yearlings[d]	11	20	43	20	94
Two-year-olds[e]	10	17	37	17	81
Total	73	131	284	131	619

[a] From Table 3.
[b] Using a 50 : 50 sex ratio, see text.
[c] Using the observed reproductive rates of 0·76 cubs/adult female/year.
[d] Using the observed survival rate of cubs, 77%.
[e] Using the observed survival rate of yearlings, 86%.

multiplied the sum of the number of adult females, COYs, yearlings, and half of the two-year-olds (the females) by 0·96 and the sum of the adult males (≥3 years old) and half of the two-year-olds (the males) by 0·68. These products were summed and divided by the size of the female core areas (Table 3). The result was 5·0 bears/1000 km² in the Nn female core area, 11·3 in Ns, 10·5 in M, and 11·7 in S. Based on these calculations, about 87% of the bears in Sweden occurred within the four female core areas.

Supplementary population estimates

A supplementary estimate of the number of adult females in Sweden was made using the estimated density of adult females in the study areas and the density of adult females, both marked and unmarked, killed in the study areas. In the northern study area, four adult females were killed during six years (1986–1991), or 0·088/1000 km²/year. This was 7·3% of the estimated density (1·21/1000 km²). In the southern study area, three adult females were killed during three years (1989–1991), or 0·077/1000 km²/year. This was also 7·3% of the estimated density (1·06/1000 km²). Hunting had been opened in most of the southern area by 1989. The annual kill of adult females in all of Sweden during 1986–1991 (12·2) was divided by the mean rate of 0·073, and yielded a national estimate of 167 adult females. Using the same relationship between number of adult females and total population size as in Table 4, a total estimate of 663 bears was calculated for Sweden.

A third method was based on the observed harvest rates of marked bears. Due to small sample sizes, all bears were combined from both areas. A problem with this technique is that our marked bears were more concentrated in areas closed to hunting than the population as a whole. Areas closed to hunting included national parks, municipalities with no bear hunting season, and company forests that did not allow bear hunting on their properties. Although on average 75% of the land was open to bear hunting in the municipali-

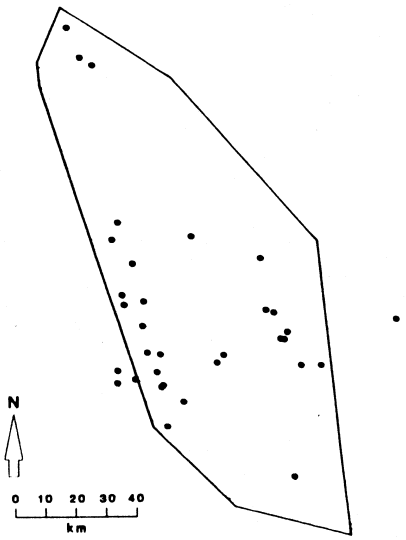

Fig. 2. Observations of unmarked bears with marked adult males (i.e. presumably adult females) during the breeding season in relation to the southern female core area, as defined from kill locations of female bears.

ties where bear hunting is allowed in a given year, 67% (n = 206 bear-years) of our bears were in areas closed to hunting during the hunting season, even though they were mostly in municipalities that allowed bear hunting. This distribution was significantly different from expected, based on the proportion of land open to hunting (one-group χ^2 = 193·7, d.f. = 1, $p < 0{\cdot}0001$). Therefore, we calculated this estimate two ways, one biased too low and one biased too high.

The low estimate was based on the marked bears known to be in areas open to hunting during the hunting season. It is low because it assumes that all bears in the country were in areas open to hunting. During 68 bear-years, 12 marked bears were killed, or 17·6% per year. The mean bear harvest during 1987–1991 was 43·8; few marked bears were available for hunting before 1987. The resulting estimate (43·8/0·176) was 249 bears. This estimate does not include COYs, which are protected from hunting by law. Adding the proportion of COYs from Table 4 (20%), we obtain a total low population estimate of 299 bears.

The high estimate was based on all marked bears. It is biased high because we know that a large portion of the bears were in areas closed to hunting during the hunting season. During 206 bear-years, 12 marked bears were killed, or 5·8% per year. The resulting high estimate (43·8/0·058) was 755, or 906 including COYs.

Validity of female core areas

As stated earlier, the female core areas were defined from the kill sites of female bears, and 96% of the female kills were located within the four core areas. However, variations in hunting pressure, hunting techniques, and locations of areas closed to hunting could have affected the size and locations of the core areas as we defined them. We evaluated the validity of the female core area concept in the southern female core area by plotting observations of unmarked bears with marked adult males during the 1988–1991 breeding seasons. Observations from Norway were excluded, as the core areas were defined from hunter-killed females in Sweden; there is no bear hunting season in Norway. This test was performed after the female core areas had been defined. Of 34 observations of unmarked bears, probably adult females with marked males, 88% were associated with the female core area (29 within it, one on the border, Fig. 2). This was not significantly different from the distribution of 166 killed females (96% in core areas, χ^2_c = 1·81, d.f. 1, p = 0·18). Too few observations of unmarked females with marked males were available from the northern study area for a similar test there.

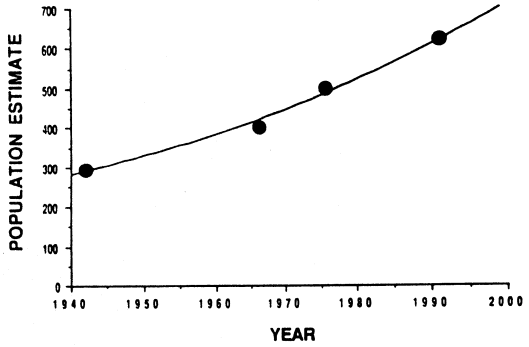

Fig. 3. Population trend of the brown bear in Sweden, 1942–1991, based on four population estimates of the total bear population.

Harvest rate

Bears have been hunted in Sweden in the autumn hunting season since 1943. During 1943–1991, the annual legal harvest rate was 5·5% (SD = 2·1%, n = 49 years). There is no estimate of illegal harvest.

DISCUSSION

Population trend and density

The total population estimate in Sweden was 619 (300–900) bears in spring 1991. Earlier estimates were 294 in 1942 (Selander & Fries, 1943), 350–450 in 1966 (Haglund, 1968), and 400–600 in 1975–76 (Bjärvall, 1980). A regression of the natural logarithms of these four estimates on year since 1900, using midpoints where appropriate, yielded a significant positive relationship with a regression line of y = 0·0154x + 5·021 (r = 0·995, d.f. = 2, p = 0·0055, Fig. 3). This suggests a long-term population increase from 1942 to 1991 of about 1·5%/year, or a doubling of the population every 46 years. Using only the estimates from 1975–76 and 1991 yielded a similar rate of increase (1·4%) to that for all four estimates. Different methods were used to esti-

mate the bear populations over these years, but the 1991 figure was completely independent of the earlier estimates. This suggested that our estimate is reasonable in relation to earlier estimates, and that the population is increasing at a relatively stable rate.

The calculated densities of bears within the female core areas were similar for three areas (10·5–11·7 bears/1000 km^2), but lower in the Nn area (5 bears/1000 km^2). These densities were 50–100% of those reported for brown bears in bear habitat (not total area as we calculated it) from the north and middle taiga in European Russia (5–21 bears/1000 km^2 of bear habitat, Chestin *et al.*, 1992). A test using observations of unmarked females with marked adult males during the breeding season in and near the southern study area supported the validity of the female core area concept. The four female core areas probably represent remnant populations that survived when the bear population declined to a low level around the turn of the century. This is supported by comparing the female core areas with the distribution of the brown bear in Sweden in the early 1900s (Ekman, 1910). All of the present core areas include areas where bears had survived to 1910.

Any effort to estimate the total bear population will be inaccurate. We consider the greatest weakness of our method to be our extrapolation from densities in only two study areas, and that the confidence intervals were rather large in the southern study area. Our estimate could be improved by recensusing the southern area, by censusing females in more areas, and by improving the demographic data base. However, the estimate of about 620 bears is the best available at this time. It is supported by the supplementary estimates; one gave an estimate of about 660 bears, and the other an estimate of more than about 300 but less than about 900 bears. Also, the estimates of population increase and comparisons of bear densities with those in similar areas suggested that our estimate was reasonable. We recommend using this in management plans until a better estimate becomes available.

Recommendations for conservation

Our most important conclusion for conservation is that bear hunting in Sweden should be managed on a subpopulation, not a county, basis. The national policy goal is to increase the numbers and distribution of the bear in Sweden. It is apparent that this can be achieved with the level of hunting that has occurred during the past 50 years. However, it is important to have restrictive quotas in areas peripheral to the core areas where expansion is desired. Female bears are slow to colonise new areas (Glenn & Miller, 1980; Rogers, 1987; Schwartz & Franzmann, 1992; our unpublished results), and a high hunter pressure in the peripheral areas can slow or stop expansion into them. Genetic isolation of the subpopulations does not appear to be a problem because of the large distances that males cover (Bjärvall *et al.*, 1990; Wabakken *et al.*, 1992).

During the period 1981–1991, when bears have been hunted on the quota system, the harvest in Sweden has increased steadily (Dahlström, 1991). This increase has averaged 9·6% annually (r = 0·89, d.f. = 9, p = 0·0003); the harvest doubled every 7·2 years. The harvest during 1987–1991 averaged 43·8 bears annually. Thus, the legal harvest was 7·1% of the total bear estimate for Sweden. Similar values were obtained by comparing harvests of females and estimated densities on the two study areas (both 7·3%) and the total harvest loss of marked bears (5·8%) However, hunter kill of marked bears in areas open to hunting was much higher (17·6%). The harvest rate during the earlier part of the quota-hunting period (1981–1986) seemed to be less, about 4·5% annually. This is based on an average annual harvest of 23·6 bears during this period and a mean population size of 530 bears, calculated from the long-term trend regression line. The long-term legal harvest (1943–1991) was 5·5% annually. The illegal kill of bears in Sweden is not known. Haglund (1968) felt that it could not be high because of the relatively high legal harvest and increasing population, but Bjärvall (1978) calculated that it could be as high as equalling the legal harvest. The illegal kill rate has been estimated to be 48% and 38% of the legal harvest in areas of Montana, USA, and Alberta, Canada, respectively (Dood *et al.*, 1986; Horejsi, 1989).

There have been several attempts to determine the maximum sustainable harvest rates for grizzly bear populations in North America. Knight and Eberhardt (1985) estimated that an 8% mortality rate (all mortality) of adult females caused a decline in grizzly bears in the Yellowstone Ecosystem; their model suggested that the population trend would stabilize if the mortality rate were 5%. Miller (1990) calculated maximum harvest rates, including illegal harvest, of 6% for male and 2·5% for female grizzly bears in the Yukon Territory. His model suggested that, with generous reproductive rates, the maximum sustainable harvest rate, including illegal harvest, for grizzly bears is 5·7%. Our data suggest that the Swedish brown bear population can sustain a higher hunting mortality. The population increased on average 1·5%/year during 1942–1991, while being harvested at a legal rate of 5·5%/year. This suggests that the sustainable legal harvest rate is about 7%/year. It is obvious that the present rate of increase in harvested bears, 9·6%/year, cannot continue when the population has a long-term rate of increase of 1·5%/year. Although our estimate of sustainable legal harvest is preliminary, it suggests that the harvest rate during 1987–1991 was at the maximum sustainable level and would not have allowed further population increase. We hope to determine the sustainable harvest rate for our population in the future based on demographic data.

We recommend that a separate female quota restriction be established for each subpopulation in addition to the present system of either-sex quotas for each municipality. This would entail that each municipality be assigned to the most appropriate subpopulation. If the female quota is reached within a subpopulation in a given year, then the hunting of bears would stop in

all of the municipalities within that subpopulation, whether or not the municipality quotas were reached. This female quota should include legal, known illegal, and self-defence kills, and perhaps other forms of man-caused mortality. If the female quota were exceeded in a subpopulation in a given year, the excess number of females should be subtracted from the quota for the next year. This system has been used successfully in Montana to guard against overharvest of females (Dood *et al.*, 1986). Because the mortality rate of adult females is of key importance to the dynamics of a bear population (Knight & Eberhardt, 1985), the consequence of error in population management of bears is high. Brown bears reproduce slowly, so reduced populations require years to recover, and overharvest, unless it is severe, is difficult to detect (Harris & Metzgar, 1987*a,b*; Miller, 1990). Therefore, conservative harvest strategies are appropriate for bear populations (Craighead *et al.*, 1974; Beecham, 1980, Bunnell & Tait, 1981; Waddell & Brown, 1984; Knight & Eberhardt, 1985; Miller, 1990). Such a system was initiated in Sweden in 1992.

A measure of relative bear density is needed that is not dependent on hunter-killed bears. It is important to compare the relative densities of the various core areas and their peripheral areas. One possibility is an expansion of the bear observation network during the first week of the moose season. This method has the advantage of having a measure of effort, and data on moose observations are already gathered routinely, so it is not necessary to establish a new programme. Other methods, such as tracking surveys, should also be considered. Observations of females with young should be given priority in programs that are based on general bear observations (Eberhardt *et al.*, 1986).

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