FACTORS ASSOCIATED WITH LOSS OF BROWN BEAR CUBS IN SWEDEN

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Abstract: We documented the loss of brown bear (*Ursus arctos*) cubs-of-the-year (cubs) in 2 Swedish populations for 11 years in the north and 12 years in the south, and made spatial and temporal comparisons to examine whether nutritional, social (sexually selected infanticide), or den disturbance factors best explained the observed variation. Annual cub loss was 0.04 (*n* = 78) in the north and 0.35 (*n* = 126) in the south. The loss of cubs at both levels of comparison was best explained by social factors. Disturbance was only evaluated in the south and explained significant variation. In the north, few adult males died and 3 adult males lost early in the study there were not replaced for many years, presumably due to little immigration of new males. Immigration was probably low due to high illegal mortality around the study area and lack of bear habitat on one side of the study area. In the south, 5 times as many males died annually, and in years with recorded adult male mortality, an average of 20% of the adult males died. The number of adult males remained stable, presumably due to immigration by new males. Illegal mortality appeared to be less in the south, and the study area was surrounded by bear habitat. Number of adult males dying in cub areas (the composite area of all radiomarked females with cubs) 2 years previously was correlated negatively with cub survival in the south. In the north, no factors correlated with temporal patterns of cub loss, but loss of adult males 1–2 years previously was the best variable we tested. We suggest that immigrating males kill cubs, as predicted by the sexually selected infanticide hypothesis. Some other studies have yielded similar results. We recommend that managers assume that loss of adult male bears is depensatory until this question is adequately resolved.

It was once thought that young bears with their mothers experienced little mortality, but this is now known to be in error (Bunnell and Tait 1985). Survival of cubs-of-the-year (termed "cubs" throughout this paper) has been found to vary temporally within an area (LeCount 1982, Rogers 1987, Miller 1994, Derocher and Stirling 1995, 1996, Swenson et al. 1997*a*) and spatially among areas (Clark and Smith 1994, Derocher and Taylor 1994, Garshelis 1994, McLellan 1994, Mattson and Reinhart 1995, Swenson et al. 1997*a*). In a review of the evidence for density-dependent population regulation in North American bears, Taylor (1994) suspected that density-related survival of cubs was the most likely mechanism of density effects, although no such density-dependent effects have yet been documented. Although important in understanding the dynamics of bear populations, the factors influencing cub survival are poorly documented and may vary among species, areas, and years. One reason is, of course, the difficulty of determining the cause of death of small cubs and of separating proximate and ultimate causes. In addition, variables may interact (Derocher and Stirling 1996).

Several factors have been proposed as important for cub survival. They can be grouped into nutritional, social, and disturbance factors. The most direct nutritional factor is food availability to cubs. This has been correlated with cub survival in some studies (Rogers 1987, Derocher and Stirling 1996), although not in others (LeCount 1982, Lindzey et al. 1986, Elowe and Dodge 1989, Clark and Smith 1994, Sellers and Aumiller 1994, Mattson and Reinhart 1995, Kasbohm et al. 1995). An indirect effect of nutrition is through the condition of the mother. Maternal effects have been suggested by Rogers (1987) and Derocher and Stirling (1996).

The most direct social factor affecting cub survival is intraspecific predation, either by males or females. Lindzey et al. (1986) proposed that adult females might decrease the recruitment of female progeny. However, many others have implicated males in killing cubs (reviews in Garshelis 1994, McLellan 1994). Hrdy (1979) classified the potential reasons for infanticide and concluded that infanticide can benefit the perpetrator if it is linked to competition for limited resources. When these resources are mates, the competition is intrasexual and the infanticide is termed sexually selected. The sexually selected infanticide (SSI) model predicts that infanticide will be directed at offspring unlikely to be direct descendants of the killer, and on average, elimination of the infant increases the infanticidal male's own opportunity to breed, typically by shortening the interval until next ovulation in the mother of the killed infant (Hrdy 1979). According to Miller (1990), some authors have suggested that, because adult males kill cubs, a reduction in the number of adult males should reduce cub mortality. Empirical evidence for this comes from analyses of the Craighead data from the Yellowstone grizzly bear (*Ursus arctos*; McCullough 1981, 1986; Stringham 1983), from comparisons of reproductive potential and proportion of adult males in 6 grizzly bear populations (Stringham 1980), and from a comparison of cub survival and proportion of adult

males in 2 American black bear (*Ursus americanus*) populations (Clark and Smith 1994). Stringham (1983) cautioned against using the results of his and the Yellowstone studies to justify harvesting adult males to increase the production of cubs, because in both data sets, the proportion of adult males and nutrition were correlated, confounding the results. The opposite effect also has been postulated, that increased hunting of adult males can increase cub mortality through SSI by immigrating males (Stringham 1980). The empirical evidence for this comes from 1 population of American black bears and a comparison of 2 populations of brown bears (LeCount 1987, Swenson et al. 1997*a*). Miller (1990) presented evidence showing that cub mortality remained stable during a period of heavy hunting mortality and declining proportion of adult males in a grizzly bear population that was declining due to overhunting. He also concluded that neither effect of killing adult males described above had been adequately demonstrated at that time. An indirect social factor, which includes the nutritional factor, is that females with cubs may avoid productive habitats in an attempt to avoid potentially infanticidal males. Habitat use by adult female brown bears in North America has been observed that is consistent with this explanation (Wielgus and Bunnell 1994*b*, 1995).

Disturbance can also be an important mortality factor in some populations. Elowe and Dodge (1989) found that this was the major cause of death for American black bear cubs before emergence from the den in Massachusetts. In central Sweden, human disturbance appeared to be a major cause of den abandonment by brown bears in winter, and pregnant females that changed dens prior to parturition lost young in and near the den significantly more often than those that did not move (Swenson et al. 1997*b*).

In an earlier paper (Swenson et al. 1997*a*), we presented circumstantial evidence from 2 Swedish brown bear populations suggesting that SSI by immigrant males, after adult males were killed by hunters, was an important factor influencing cub survival. We present data from 3 additional years for these 2 populations and expand the analysis to evaluate nutritional, social, and disturbance factors to explain the observed temporal and spatial variation in cub survival.

STUDY AREAS

The study areas were in northern Sweden (about 8,000 km^2) and central Sweden-southeastern Norway (about 13,000 km^2), and are described in Bjärvall and Sandegren (1987). These study areas are about 600 km apart and are near the northern and southern edges of the species' range in Sweden. There are mountains in the north and a rolling landscape in the south. The bears in the north spend

>1 month longer in the den (Sandegren and Swenson 1997), and some categories of bears (yearlings all year and females in the spring) were seen at ungulate carcasses more often there than in the south (Stabell 1999). Both moose (*Alces alces*) and domestic reindeer (*Rangifer tarandus*) were available in the north, but only moose in the south. The study populations belong to separate mirochondrial DNA lineages (Taberlet et al. 1995). However, nuclear DNA analyses have revealed that, although there are differences between the populations, there has been extensive gene flow throughout the Scandinavian brown bear population (Waits et al. 2000). Both populations showed rapid growth, *r* (exponential rate of increase) = 0.13 in the north and *r* = 0.15 in the south; environmental variance was statistically different from zero in the south (s^2_e = 0.003) but not in the north (Sæther et al. 1998).

Bear hunting was generally allowed during the autumn in both areas, but the northern area includes 3 national parks where bear hunting is forbidden. Hunting pressure has increased since 1995 in the southern study area. In the northern area, there is evidence of considerable illegal killing of bears (Swenson and Sandegren 1999). This is less important on the study area than in the surroundings, where it appears to have a major effect on the population. This has been documented through the loss of radiomarked bears, particularly immigrating males leaving the study area, and changes in the distribution of females as determined from the distribution of legally killed female bears (Sandegren and Swenson 1997, Swenson and Sandegren 1999).

METHODS

We documented the disappearance of cubs accompanying radiomarked females during 1988–98 and assumed that cubs that disappeared had died. We observed a family as soon as possible after they left the den, again around the end of the mating season in late June–early July, and again before they entered the den in the autumn. Cubs that died in the den were not considered in this study, but cubs that left the den and disappeared before they were observed were included. In our analyses, we considered a litter that was lost prior to being observed to have consist of 2 cubs, the most common litter size in both areas. We visited dens only in the south to determine if young had been present outside the den, based on tracks or markings from their climbing in nearby trees. The northern study area was inaccessible to vehicles. However, the longer period of snow cover in the north and the less dense forest made it easier to count cubs from the air shortly after they left the den.

We immobilized the bears early in the spring by darting them with a mixture of tiletamine/zolazepam and

medetomidine from a helicopter. We marked captured bears with radio transmitters and weighed them with spring scales. We recaptured growing bears each spring to fit them with a larger collar. We first captured many bears as yearlings, shortly after emerging from their dens with their radiomarked mothers. For bears that were not the yearlings of radiomarked females, we collected a premolar tooth, which we sent to Matson's, Inc. (Milltown, Montana, USA) for age estimation based on the cementum annuli in the tooth root (Craighead et al. 1970).   In the north, virtually all bears that we saw were captured and marked. Because the marking season coincided with the mating season and occurred when snow covered the ground, we feel confident that few unmarked adult bears were present on the study area. During 1988–91, 86% of 29 females observed consorting with radiomarked males during the mating season were radiomarked (Swenson et al. 1994); we captured and marked the unmarked females. In the south, the marking season was before the mating season because the snow melted prior to the mating season. Similar observations there in 1988, 1989, and 1993 revealed that 47% of 53 observations were marked females (Swenson et al. 1994, 1995). When we observed marked females with another bear during the breeding season, we recorded whether it was radiomarked. From these observations, we annually estimated the number of breeding adult males in our southern study area with an unbiased Petersen population estimator (Krebs 1989).

As marking occurred only in a short period, we calculated survival rates using the Kaplan-Meier procedure (Kaplan and Meier 1958). We located radiomarked bears generally weekly during the nondenning period. In the south, we located them at least once monthly while denned. We followed most bears over many years, often from the time they were born. Thus, it was possible to accurately determine reproductive parameters such as age of first reproduction and litter interval, among others. We compared these parameters to indirectly assess nutritional status of bears in the 2 areas, because higher reproduction has been found to vary positively with plane of nutrition in populations of brown bears, American black bears and polar bears (*Ursus maritimus*; reviews in Taylor 1994).

Following Garshelis (1994), we used yearling weights as a surrogate measure of food abundance. Yearlings were weighed to the nearest 0.5 kg shortly after den emergence ($n = 53$ in the north, and $n = 66$ in the south). A body mass index for a given year was calculated as the mean of the deviations in body masses for yearlings from the appropriate area, expressed in standard deviation units, from the overall mean for all yearlings for all years for each sex and area. Thus, body masses from both sexes in an area were standardized and could be combined. The pregnant female food index in a year was the yearling body mass index in that year (when the yearlings emerged, they had lived during the time the females that gave birth that year had been pregnant). The cub food index in that year was the yearling body mass index in the following year, because the cubs emerged the following year and were weighed then as yearlings.

In Sweden, all bears killed by hunters must be shown to the authorities, the exact location of the kill must be reported (and can be verified), and samples from the carcasses must be turned in, including a tooth. The locations where adult males ($\geq$5 years old) were known to have died were compared with the locations of radiomarked females with cubs. We produced a composite minimum convex polygon area that included all locations of radiomarked females with cubs for each year. We termed these "cub areas", which varied in size annually, depending on the number and distribution of radiomarked females with cubs. Cub areas averaged 2,488 km² (SE = 550, $n = 11$ years) in the north and 4,108 km² (SE = 924, $n = 12$) in the south. The southern cub areas are *not* comparable to the southern area reported in Swenson et al. (1997a). We used a different method in this analysis to ensure that the males died close to the cubs we were monitoring. We assumed a home range diameter for adult males of 16 km in the north and 18 km in the south, based on home range sizes of 830 km² ($n = 9$) and 1,000 km² ($n = 22$), respectively (B. Dahle, Scandinavian Brown Bear Project, Norwegian University of Science and Technology, Trondheim, Norway, unpublished data). For each cub area, we tallied the number of adult males known to have died within the cub area and within 1 male home-range diameter from it at time lags of 1, 2, and 3 years. We considered all known adult male deaths, not just those due to hunting, as reported earlier (Swenson et al. 1997a). Most males were killed by hunters during the autumn prior to denning, but a few died just after den emergence (marking-induced losses, suspected illegal killing from snowmobiles, killed in traffic). Biologically, the effect on the male social organization was probably the same if a male was killed prior to entering or just after leaving the den. Therefore, we counted deaths in the early spring as occurring in the previous autumn. Also, when we strongly suspect illegal killing of a radiomarked adult male in the north and the male was never recaptured, in spite of our intensive efforts, nor reported as killed legally, we considered it to be dead.

All females with cubs were considered to have been disturbed if they changed den sites or were otherwise known to have been disturbed by people at the den, even if they did not abandon the den. This was recorded only in the southern area.

We analyzed annual variations in cub survival in each study area using a stepwise multiple logistic regression.

The dependent variable was cubs survived or lost, and the independent variables were pregnant female food index, cub food index, number of adult males dying in or near the cub areas for time lags of 1, 2, and 3 years, whether the female had been disturbed during denning (south only), and year, which was a surrogate variable for density in these rapidly growing populations. We entered independent variables into the model and removed by backward elimination using the likelihood ratio statistic for removal (Norušis 1997). Statistical tests were carried out in Statistical Package for the Social Sciences (SPSS) or Statview (Norušis 1997).

RESULTS

Comparison Between Areas (Spatial Scale)

Annual cub loss was 0.35 in the south (n = 126) and 0.04 in the north (n = 78). This difference was highly significant (χ^2_c = 24.51, 1 df, P < 0.0001; Table 1). Among litters that lost cubs during 1987–98, total loss was more common in the south (68%, n = 34 litters losing at least 1 cub) than in the north (0%, n = 3, Fisher's exact test, P = 0.034). Thirty-four cubs (85% of those lost) disappeared during the 2-month breeding season (May–Jun), compared with 6 in the following 4-month period. This was a significantly greater loss during the breeding season than expected from its length (1-way χ^2 = 48.27, 1 df, P < 0.0001).

We documented the cause of death for very few cubs, as none were radiomarked. We found a few carcasses, however. In the south, 3 dead cubs from 3 litters were found not far from the den; 1 of these apparently died of malnutrition. Near another den, we saw the tracks of the female, cubs, and an adult male, judging from the track measurements. These cubs were never observed with the female. In another case, a female that had 4 cubs was observed on 17 May 1996 with only 2 cubs, 1 of which appeared to be injured. An unmarked male followed these bears. Backtracking revealed that 1 cub had been killed and consumed and another was in a tree. The female never returned to the abandoned cub. On 27 May she was with a marked adult male and no cubs. Another cub carcass was found in October 1998; it may have been injured in a traffic accident.

Sex ratios of yearlings marked in the early spring, usually while still with their mothers, were compared in the 2 study areas. The sex ratio of yearlings was the same as for cubs in the north, because annual cub loss there was only 0.04. Captured yearlings were 56% males (n = 59) in the north and 49% (n = 76) in the south. This difference was not significant (χ^2_c = 0.44, 1 df, P = 0.51), suggesting that there was not a sex-specific loss of cubs in the south.

A comparison of reproductive parameters between the 2 areas showed that age of first reproduction and litter interval (all litters) was significantly lower in the south (Table 2). There was no difference in litter size. However, the high cub loss in the south, which particularly affected first-time breeders, resulted in an increased age of first successful reproduction and interval between successful litters. These values did not differ between the areas (Table 2).

A comparison of spring body masses, taken shortly after the bears emerged from their dens, and usually while snow was still present, revealed that the bears in the north grew faster until age 3 years. From age 4 to 6 years, there

Table 1. Loss of cubs-of-the-year with radiomarked female brown bears in the northern and southern study areas in Sweden, 1987–98, with yearling body mass index and number of adult (≥5 years) males dying within the cub areas 1, 2, and 3 years previously.

	North					South				
	Cub	Mass	Males dying[a]			Cub	Mass	Males dying[a]		
Year	survival (n)	index	-1 yr	-2 yr	-3 yr	survival (n)	index	-1 yr	-2 yr	-3 yr
1987	-	-				0.000 (2)	-	0	0	0
1988	1.000 (5)	-	0	0	0	1.000 (3)	-	0	1	0
1989	1.000 (4)	-0.17	2	0	0	1.000 (5)	-0.39	0	0	3
1990	0.800 (5)	+0.17	0	1	0	1.000 (2)	+0.60	0	0	0
1991	1.000 (5)	+2.07	0	0	1	0.529 (17)	-1.68	1	2	0
1992	1.000 (8)	+0.69	0	0	0	0.625 (8)	-0.46	4	1	2
1993	1.000 (7)	+0.19	0	0	0	0.600 (15)	-0.48	2	4	1
1994	1.000 (7)	-0.28	0	0	0	0.546 (11)	-0.34	0	2	4
1995	1.000 (9)	+0.27	0	0	0	1.000 (15)	-0.21	1	0	2
1996	1.000 (6)	-0.98	0	0	0	0.333 (15)	-0.19	0	1	0
1997	0.833 (12)	-0.47	1	0	0	0.524 (21)	+2.01	3	1	1
1998	1.000 (10)	+0.35	0	1	0	0.571 (21)	+0.41	0	3	0

[a] Adult males. Numbers can change when tracked diagonally, because cub areas were different each year.

Table 2. Brown bear reproductive parameters for the northern and southern study areas in Sweden, 1987–98.

Parameter	North	South	Statistical test	
Age, first litter (yr)	5.4 ± 0.15 (11)[a]	4.5 ± 0.15 (17)	$t_{26} = 3.71$	$P < 0.001$
Age, first successful litter (yr)	5.4 ± 0.15 (12)	5.2 ± 0.24 (15)	$t_{25} = 0.72$	$P = 0.48$
Litter size	2.4 ± 0.14 (33)	2.3 ± 0.11 (55)	$t_{86} = 0.51$	$P = 0.61$
Litter interval (yr), all	2.6 ± 0.15 (21)	1.6 ± 0.08 (46)	$t_{65} = 5.90$	$P < 0.001$
Litter interval, successful	2.6 ± 0.14 (18)	2.4 ± 0.12 (23)	$t_{39} = 1.18$	$P = 0.25$

[a] Mean ± SE (N)

Table 3. Comparison of spring body mass of radiomarked brown bears in the northern and southern study areas in Sweden 1987–98.

		Spring body mass (kg) mean ± SE (*n*)			
Age (yr)	Sex	North	South	Statistical test	
1	M	29.9 ± 1.7 (28)	25.8 ± 1.1 (33)	$t_{59} = 2.10$	$P = 0.04$
	F	24.0 ± 0.9 (25)	21.8 ± 0.8 (33)	$t_{56} = 1.79$	$P = 0.08$
2	M	59.0 ± 3.4 (22)	42.8 ± 1.6 (23)	$t_{30.2} = 4.26$[a]	$P < 0.0001$
	F	49.5 ± 2.7 (20)	38.2 ± 1.6 (19)	$t_{30.5} = 2.00$[a]	$P = 0.054$
3	M	106.7 ± 11.2 (15)	68.0 ± 2.9 (21)	$t_{15.9} = 3.35$[a]	$P = 0.004$
	F	69.9 ± 3.0 (21)	58.8 ± 2.0 (19)	$t_{38} = 3.01$	$P = 0.005$
4	M	114.5 ± 8.4 (11)	104.4 ± 4.8 (17)	$t_{26} = 1.13$	$P = 0.27$
	F	83.1 ± 3.3 (15)	77.2 ± 2.7 (16)	$t_{29} = 1.40$	$P = 0.17$
5	M	137.2 ± 12.0 (6)	137.2 ± 10.4 (10)	$t_{14} = 0.002$	$P = 0.99$
	F	90.9 ± 7.0 (5)	78.9 ± 4.2 (8)	$t_{11} = 1.57$	$P = 0.14$
6	M	172.8 ± 12.4 (6)	149.0 ± 12.0 (8)	$t_{12} = 1.36$	$P = 0.20$
	F	83.8 ± 4.2 (7)	93.0 ± 7.3 (9)	$t_{14} = 1.01$	$P = 0.33$

[a] Corrected for unequal variances.

were no differences in spring body masses, although most mean body masses were greater in the north (Table 3). Weights of older bears were not compared by age due to low sample sizes.

Adult males died within the cub areas during 5, 8, and 6 of the 12 years in the south, at time lags of 1, 2, and 3 years, respectively (Table 1). The number that died varied from 1–4 and averaged 2.1 in the years an adult male died and 1.1/year totally. In the north adult males only died during 2 of 11 years, averaging 1.2/year in the years an adult male died and 0.2/year totally. These deaths occurred early and late in the study.

In the north, 2 of the 4 marked adult males died in 1988 and another died while being marked for the first time in early spring 1989. These 3 males were never together within a cub area. Despite our intensive efforts to mark all unmarked bears in the area, we found very few immigrating males, and the number of marked adult males remained stable at a low number during 1989–95. The number increased in 1996 and has remained 3–4 times higher than before (Table 4). This was due primarily to recruitment of locally produced young males into the adult age class. In the south, we were not able and did not attempt to mark all of the bears. Observations of breeding females with other bears suggested that we had marked about 56% of the adult breeding males there (Table 4, marked males divided by the number marked plus the

corrected number of unmarked males). The average number of adult males/year was 9.7 for the 10 years we estimated. There was no temporal trend in the estimated number of adult males present ($r = 0.004$, 8 df, $P = 0.99$). If we combined all the data for all 12 years, a composite estimate was 9.8 males present annually.

These results suggest that there was a greater availability of immigrating males in the south than in the north. This is supported by our data on survival of radiomarked males (Table 5). The probability of a male surviving from den emergence as a yearling through his first year as an adult was 0.223 in the north, including survival of bears that emigrated from the study area. The corresponding value in the south was 0.499, about twice as high, although the differences were not significant for any individual age. In addition, the southern area was surrounded by occupied bear habitat, a potential source of immigrants, whereas the northern area was bounded on the west by mountains above timberline, with few or no bears.

Comparison within Areas (Temporal Scale)

In the southern area, 3 of the factors entered into a multiple stepwise logistic regression (cub food index, number of males dying in and near cub areas 2 years earlier, and whether the female had been disturbed in her den) showed significant negative correlations with cub survival

Table 4. Adult ($\geq$5 years old) male brown bears radiomarked on the northern study area in Sweden and point estimates of the total number of adult males consorting with marked females on the southern study area, 1986–98.

Year	North[a] Marked adult males	South[b] Marked males[c]	Consorting with marked females Marked males	Unmarked bears	Total, corrected[d]	Breeding males[e]
1986	0	2.6	5	0	5	3.6
1987	1	3	3	5	7.4	8.4
1988	4	7	3	5	7.4	16.8
1989	2	10.2	10	3	12.6	13.8
1990	2	4.4	5	5	9.4	9.4
1991	2	3	0	6	5.3	-
1992	2	2	0	6	5.3	-
1993	1	6	15	3	17.6	8.1
1994	2	5	6	3	8.6	8.2
1995	3	6	5	1	5.9	8.0
1996	8	3	3	5	7.4	8.4
1997	6	5	6	8	13	12.0
1998	6	—	—	—	—	—

[a] Virtually all adult males were marked.

[b] Marking all adult males was not attempted.

[c] Males losing radiocollars were treated as the fraction of the breeding season they were marked. Only males with home ranges overlapping radiomarked adult females were included.

[d] The number of unmarked males was reduced by 12%, because marked adult females without cubs during the breeding season were seen together in 12% of 72 sightings of marked females.

[e] Calculated from Krebs (1989:23, eq. 2.2).

Table 5. Survival rates of radiomarked male brown bears ages 1–5 years in the northern and southern study areas in Sweden, 1985–98.

Age (yr)	North mean $\pm$ SE (n)	South mean $\pm$ SE (n)	Statistical test	
1	0.793 ± 0.075 (29)[a]	0.938 ± 0.043 (32)	$z = 1.68$	$P = 0.09$
2	0.857 ± 0.077 (25)	0.909 ± 0.062 (25)	$z = 0.64$	$P = 0.52$
3	0.700 ± 0.115 (18)	0.669 ± 0.096 (25)	$z = 0.25$	$P = 0.80$
4	0.750 ± 0.125 (13)	0.954 ± 0.044 (22)	$z = 1.61$	$P = 0.11$
5	0.625 ± 0.172 (9)	0.917 ± 0.080 (19)	$z = 1.64$	$P = 0.10$

Table 6. Results of a stepwise multiple logistic regression with brown bear cub survival in the southern study area in Sweden during 1986–98 as the dependent variable. Independent variables were cub food index, number of adult males dying 1, 2, and 3 years earlier within or adjacent to the cub area, whether the female had been disturbed in the den while pregnant or with cubs, year (surrogate variable for density), and food index in the year the female was pregnant.

Variable	Slope	Wald χ^2	df	P	R[a]
Constant	1.639	15.46	1	0.0001	
Cub food index	-0.887	10.50	1	0.0012	-0.242
Adult males dying 2 years earlier	-0.546	8.33	1	0.0039	-0.209
Den disturbance	-1.767	5.19	1	0.0227	-0.148
Entire model		17.69	3	0.0005	

[a] Partial regression coefficient.

(Table 6). When considering only whether an adult male had died in or near the cub area with various time lags, a significant difference was found only with a 2-year time lag, but this difference was highly significant (Table 7).

In the north, there were so few years with dead adult males that another variable, whether an adult male died 1 or 2 years earlier, was included in the stepwise multiple logistic regression. No significant model was obtained. The last independent variable to be removed from the model was whether an adult male died 1 or 2 years earlier; it was negatively related to the survival of cubs. The last 4 variables to be removed were the 4 variables including males dying within the cub areas. The loss of cubs when an adult male had died 1 or 2 years previously was

Table 7. Loss of brown bear cubs-of-the-year in relation to whether adult (≥5 years) males were known to have died within or adjacent to the cub area at various time periods prior to the year the cubs were lost, southern study area, Sweden, 1986-98.

Time lag	Loss after an adult male was known to have died (*n* cubs)	Loss after no adult male was known to have died	Statistical test	
1 year	0.36 (76)	0.42 (57)	$\chi^2_c = 0.35$	$P = 0.55$
2 years	0.45 (109)	0.08 (24)	$\chi^2_c = 9.66$	$P = 0.002$
3 years	0.32 (75)	0.47 (58)	$\chi^2_c = 2.35$	$P = 0.13$

0.08 ($n = 36$), compared with 0.00 ($n = 42$) if no adult male was known to have died at either time lag. This difference was only marginally significant, however (Fisher's exact test, $P = 0.09$).

DISCUSSION

We found support for the social factor to explain the spatial variation in cub loss. Cub loss was very low in the north (0.04). Few adult males died there and, perhaps more importantly, there appeared to be an extremely low immigration rate. This low immigration rate would explain why the number of males on the northern study area remained low for 7 years, although the area supported more adult males both before and after this period. The reason for a low number of immigrants appears to be the high rate of illegal killing of bears around much of the study area and the lack of bear habitat on one side of the study area. In the south, cubs had a significantly higher loss rate and 5.5 times more adult males died annually than in the north. Subadult male survival was much higher in the south and the study area was surrounded by bear habitat. There, immigration was apparently adequate to maintain a relatively constant number of adult males on the study area, despite the higher loss of adult males.

Loss of entire litters, a phenomenon predicted by the SSI hypothesis, was significantly more common in the south than in the north. However, we did not consider whether males were successful in apparent attempts at infanticide and subsequent mating with the mother. We based our analyses on loss of all cubs, not just loss of entire litters, because we were interested in trying to identify the cause of the loss of cubs, among many potential causes, and the effect of this loss. When males kill cubs, they are not necessarily successful in killing all the cubs in the litter. We observed incomplete loss of a litter due to male predation, as have others (Olson 1993, Hessing and Aumiller 1994), and mothers can successfully defend their young from males (Olson 1993, Hessing and Aumiller 1994). We have not recorded scarring of adult females in our study areas, but we would expect more scarring where there is a higher loss of cubs, if infanticide is an important factor. We will begin recording scarring when we capture females.

Social factors also helped explain much of the temporal variation in cub loss in the south. Cub survival was negatively correlated with the number of adult males dying 2 years earlier in a multivariate analysis, corrected for den disturbance and cub food index. Also, a highly significant difference in cub survival was found when comparing whether any adult male died in or near the cub area 2 years earlier. No factor explained a significant amount of the temporal variation in cub loss in the north, which is probably not surprising, given the low amount of variation in cub loss there. But of all factors examined, whether an adult male had died 1–2 years earlier best explained the observed variation and was marginally significant.

The disturbance factor was also important in explaining the temporal variation in cub loss in the south. We did not examine this factor in the north.

Little support for a nutritional effect was found. Both populations increased at the highest rates reported for brown bears, and the southern population was increasing faster than the northern population, despite the higher cub loss (Sæther et al. 1998). Southern bears had an earlier age of first reproduction and shorter litter intervals than those in the north, although the difference disappeared when only successful litters were considered.

Northern bears were generally heavier than southern bears, but this was only statistically significant for young bears. In the south, the cub food index correlated best with cub survival of all the factors examined, but the relationship was negative with higher survival when cubs were lighter at emergence the following spring. This was counter-intuitive, based on the literature and logic. Perhaps the lightest cubs died consistently, resulting in a lower mean weight following years of higher survival. This seems to be a poor explanation, and it is not consistent with the heavier yearling males and marginally heavier females in the north, where survival was consistently high. There was no significant relationship in the north.

We found a negative correlation earlier between cub survival and spring body mass of adult females in the south (Swenson et al. 1997*a*). Thus, we do not consider nutrition to be an important factor in explaining cub loss either at the temporal or spatial scale. Opseth (1998) found that the bears' use of major food items in the south varied little during 1994–96, a period with great variation in cub sur-

vival (Table 1). Although the faster growth in the north could be explained by a higher availability of protein through ungulate carcasses (Stabell 1999), bears in the south also had a high availability of protein in the form of ants (30–38 tons/bear; Swenson et al. 1999). An alternate explanation is that northern bears prioritized growth to be able to store more fat (Lindstedt and Boyce 1985), which they needed for the >1-month longer hibernation period (Sandegren and Swenson 1997). Growth may have been prioritized over early reproduction.

The social factor best explained spatial and temporal variations in cub survival in the 2 Swedish brown bear populations. We stress that this is a correlative study, and the results must be viewed accordingly. However, we arrived at the same conclusion earlier (Swenson et al. 1997*a*), although we now analyzed the data quite differently, adding adult males that were not killed by hunters, examining the location of death at a more local, and appropriate, level in relation to the observed cubs, and more fully examining alternative explanations. We could not determine whether the presumed primary mechanism was direct infanticide (LeCount 1987) or indirect, through female avoidance of productive habitats to avoid potentially infanticial males (Wielgus and Bunnell 1994b, 1995). We often located females with cubs in the alpine zone, where adult males are rarely located, during the breeding season in the north. There is virtually no alpine zone present in the south.

Our results suggest that the key factor was immigration of subadult(s) following the death of 1 or more established adult males. The density of subadult males apparently increases in an area following the death of many adult males, as shown by Young and Ruff (1982) for American black bears. We suggest that resident adult males were not an important factor in the loss of cubs, because (1) cub survival was high in the northern study area, with little adult male mortality and little immigration, (2) cub survival was high in the southern study area when no adult males had died 2 years earlier, and (3) cub survival was low when adult males died 2 years earlier. Thus, we suggest that it is the loss of adult males and the ensuing immigration of new males, not the presence or abundance of adult males *per se*, that is important. We documented that males were recruited into the adult male category during the last few years in the north, but this was not associated with elevated cub loss (Table 1). Most of these males grew up on the study area, which may have influenced infanticidal behavior. Also, preliminary data from genetic fingerprinting suggests these males were able to first breed successfully as 3-year-olds, compared to 5 years in the south (L. Waits, Scandinavian Brown Bear Research Project, University of Idaho, Moscow, Idaho, USA, unpublished data). Such young males may have difficulty

killing cubs defended by their mother.

LeCount (1987) found high cub mortality, caused primarily by other bears, in a heavily hunted black bear population with few adult males and many presumably immigrating young males. In a comparison of 2 populatons of grizzly bears, Wielgus and Bunnell (2000) reported lower reproduction in the population with higher adult male mortality and higher subadult male immigration. They concluded that the lower reproductive rate was not caused by higher cub mortality, but because adult females avoided food-rich habitats used by the potentially infanticidal immigrant males.

The conclusion that SSI occurs in bear populations is considered controversial by some wildlife management agencies and researchers (Wielgus and Bunnell 2000). Our discussions with bear biologists about these results have centered on 2 points: (1) whether it is reasonable that the documented loss of adult males could have such an effect of cub survival, and (2) whether bears should be expected to behave in a manner consistent with the SSI hypothesis, because it is commonly associated with social mammals.

In the southern study area, we estimated an adult male breeding population of 9.8 males, which was constant during the study period. In the years adult males died, the mean loss was 2.1. This is about 20% of the breeding adult males and should be sufficient to disturb the social organization of adult males. The cub areas averaged 4,000 km² in size, and adult male home ranges there are about 1,000 km² in size (median of both 95% fixed kernel and 95% minimum convex polygon methods), or 1,400–2,400 km², if the median and mean, respectively, of 100% minimum convex polygons are used (B. Dahle, Scandinavian Brown Bear Research Project, Norwegian University of Science and Technology, Trondheim, Norway, unpublished data). Using the conservative value implies that the loss of 2 males would affect 25–50% of the cub area, depending on degree of male home range overlap. It is difficult to know which proportion of this area would be affected by settling immigrant males, but we may expect that the number of immigrating males exceeds the number of dying adults (Young and Ruff 1982). Thus, a substantial proportion of females with cubs within a cub area would be affected. The estimated loss of adult males, reported above, is within the 95% confidence limits of the mortality estimated from radiomarked bears. Over the study period in the south, 1.08 adult males were known to have died annually, a rate of 0.110, based on 9.8 males present. Actually, a loss of 0.98, excluding marking-induced mortality, is better to compare with the survival estimate from radiomarked males, which does not include marking-induced mortality. This mortality rate is 0.100. The mortality rate of radiomarked bears, based on 95 bear-years (a bear-year is a bear marked during all or part of a

year), was 0.074 (SE = 0.032), and the 95% confidence interval was 0.011–0.137.

Our results also suggest that the adult male social organization can be disrupted for up to 2 years after the removal of about 20% of the adult males. We suggest that this time lag is not unreasonable for brown bears. Males are generally killed during the autumn, when fattening for winter denning is important. The breeding season starts in the spring not long after den emergence and continues to midsummer. Thus, there is a relatively short time for an immigrating male to become established if he is to participate in breeding the first year after an adult male dies and a vacancy is available.

We do not expect a linear relationship between the loss of adult males and cub mortality due to SSI. It is probable that the per capita effect of removing adult males declines rapidly as the number of males increases, which could account for the stable cub mortality with increasing mortality of adult males reported by Miller (1990). His study did not include a situation where no adult males had been killed. Also, if the mortality of adult and sub-adult males becomes very high, cub mortality due to SSI might decline if the few immigrating males enter the breeding pool while they are too young to effectively kill defended cubs. We suggested that this happened in the northern study area.

Is it reasonable to expect SSI in a bear population? Infanticide is usually a relatively uncommon event and is most easily observed in social species. Males have been observed killing infants in situations consistent with the predictions of the SSI hypothesis in many social mammals, such as the mountain gorilla (*Gorilla gorilla*, Robbins 1995), Hanuman langur (*Presbytis entellus*, Mohnot 1971), arctic ground squirrel (*Spermophilus parryii*, McLean 1983), Alpine marmot (*Marmota marmota*, Coulon et al. 1995), African lion (*Panthera leo*, Pusey and Packer 1994), red deer (*Cervus elaphus*, Bartos and Madlafousek 1994), hippopotamus (*Hippopotamus amphibius*, Lewison 1998), bottlenose dolphin (*Tursiops truncatus*, Patterson et al. 1998), and in nonsocial mammals, such as the collared lemming (*Dicrostonyx groenlandicus*, Mallory and Brooks 1978), house mouse (*Mus musculus*, vom Saal and Howard 1982) and white-footed mouse (*Peromuscus leucopus*, Wolff and Ciciello 1989). The list also includes birds, such as the barn swallow (*Hirundo rustica*, Crook and Shields 1985; Møller 1988), house wren (*Troglodytes aedon*, Freed 1986), tree swallow (*Tachycineta bicolor*, Robertson and Stutchbury 1988), and house sparrow (*Passer domesticus*, Veiga 1990). Consistent with the SSI hypothesis, female birds can also kill another female's young, such as has been found in two species of polyandrous jaçanas (*Jacana spinosa* and *J. jacana*, Stephens 1982, Emlen et al. 1989)

and in the house sparrow (Veiga 1990). Documented infanticide is not always consistent with SSI, but the evidence for SSI has become so numerous as to be very convincing.

But should we really expect to see SSI in a nonsocial carnivore with a promiscuous mating system such as bears? Packer and Pusey (1984) examined the occurrence of SSI in carnivores and state that "…because of their carnivorous habits and because most bear altricial young, carnivores are more likely to exhibit infanticide than any other mammalian order." (Packer and Pusey 1984:31). Although SSI has been best documented in the social lions, they suspected that "infanticide as a male reproductive strategy may be confirmed eventually in many solitary carnivore species where the female's reproduction is accelerated by the death of her young." (Packer and Pusey 1984:42). It has been shown that the death of a female brown bear's young accelerates her reproduction (Swenson et al. 1997*a*). Female American black bears can breed within 48 hours of losing their cubs (LeCount 1983), and a female brown bear was observed apparently in estrus and with an adult male 4 days after her cubs were killed (Hessing and Aumiller 1994). We have also shown that the cubs in our study died mostly during the breeding season. This does not necessarily support the SSI hypothesis, but it is a requirement for it. In addition, mating with multiple males has been documented in brown bears (Craighead et al. 1995*a,b*, L. Waits, Scandinavian Brown Bear Research Project, University of Idaho, Moscow, Idaho, USA, unpublished data). Hrdy (1977) proposed that this is an infanticide-avoidance behavior, whereby females mate with likely perpetrators because they are less likely to kill potential offspring. Thus, there is no biological reason to expect that the SSI hypothesis is inappropriate for bears.

MANAGEMENT IMPLICATIONS

Much has been written about the potential effects on the survival of cubs of hunting adult male bears. Miller (1990) has recommended that managers do not assume that the killing of adult males will positively effect cub survivorship, because there is no evidence for such a relationship and such an assumption could lead to overharvest. Wielgus and Bunnell (1994*a*) went further, and suggested that the hunting of adult males could actually be depensatory. We agree with Wielgus and Bunnell (1994*a*). Our results suggest that the death of about 20% of the adult males in a local area significantly reduced cub survival. We do not recommend that adult males not be harvested, but we recommend that the potential consequences be considered when modeling the effects of hunting on bear populations and when considering the fate of

problem adult males in control actions in threatened and endangered populations. Our study was correlational, not experimental, and other factors, unexamined or autocorrelated with those we found to be important, may be the true mechanism behind our observed results. Until this question is adequately resolved, managers should act conservatively and assume a population consequence of harvesting adult male bears.

We recommend that other researchers investigate SSI in bear populations. Our results are based on presumed infanticide; we have not marked any cubs and have documented infanticide in only 2 litters. Also, replication is important to determine the generality of the pattern we have observed. In future research, it is important to focus on the loss of adult males and subsequent immigration, not just the proportion of adult males in a population, as was reported in some earlier studies (McCullough 1981, 1986; Stringham 1983; Clark and Smith 1994). We have started an experiment in the southern study area to test the SSI hypothesis. The Swedish Environmental Protection Agency has agreed to keep the harvest level for several years at a constant and high enough level to stop population growth. We predict that cub survival will decrease with the increase in harvest rate, including adult male harvest.

ACKNOWLEDGMENTS

LITERATURE CITED

BARTOS, L., AND J. MADLAFOUSEK. 1994. Infanticide in a seasonal breeder: the case of red deer. Animal Behaviour 47:217–219.

BJÄRVALL, A., AND F. SANDEGREN. 1987. Early experiences with the first radio-marked brown bears in Sweden. International Conference on Bear Research and Management 7:9–12.

BUNNELL, F.L., AND D.E.N. TAIT. 1985. Mortality rates of North American bears. Arctic 38:316–323.

CLARK, J.D., AND K.G. SMITH. 1994. A demographic comparison of two black bear populations in the interior highlands of Arkansas. Wildlife Society Bulletin 22:593–603.

COULON, J., L. GRAZIANI, D. ALLAINÉ, M.C. BELL, AND S. POUDEROUX. 1995. Infanticide in the Alpine marmot (*Marmota marmota*). Ethology, Ecology and Evolution 7:191–194.

CRAIGHEAD, J.J., F.C. CRAIGHEAD, JR., AND H.E. MCCUTCHEN. 1970. Age determination of grizzly bears from fourth premolar tooth sections. Journal of Wildlife Management 34:353–363.

———, J.J., J.S. SUMNER, AND J.A. MITCHELL. 1995a. The grizzly bears of Yellowstone, their ecology in the Yellowstone Ecosystem, 1959–1992. Island Press, Washington, D.C.

CRAIGHEAD, L., D. PAETKAU, H.V. REYNOLDS, E.R. VYSE, AND C. STROBECK. 1995b. Microsatellite analysis of paternity and reproduction in Arctic grizzly bears. J. Heredity 86:225–261.

CROOK, J., AND W.M. SHIELDS. 1985. Sexually selected infanticide by adult male barn swallows. Animal Behaviour 33:754–761.

DEROCHER, A.E., AND I. STIRLING. 1995. Temporal variation in reproduction and body mass of polar bears in western Hudson Bay. Canadian Journal of Zoology 73:1657–1665.

———, AND ———. 1996. Aspects of survival in juvenile polar bears. Canadian Journal of Zoology 74:1246–1252.

———, AND M. TAYLOR. 1994. Density-dependent population regulation of polar bears. Pages 25–30 *in* M. Taylor, editor. Density-dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management, Monograph Series No. 3.

ELOWE, K.D., AND W.E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962–968.

EMLEN, S.T., N.J. DEMONG, AND D.J. EMLEN. 1989. Experimental induction of infanticide in female wattled jacanas. Auk 106:1–7.

FREED, L.A. 1986. Territory takeover and sexually selected infanticide in tropical house wrens. Behavioural Ecology and Sociobiology 19:197–206.

GARSHELIS, D.L. 1994. Density-dependent population regulation of black bears. Pages 3–14 *in* M. Taylor, editor. Density-dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management, Monograph Series No. 3.

HESSING, P., AND L. AUMILLER. 1994. Observations of conspecific predation by brown bears, *Ursus arctos*, in Alaska. Canadian Field-Naturalist 108:332–336.

HDRY, S.B. 1977. The langurs of Abu: female and male strategies of reproduction. Harvard University Press, Cambridge, Massachusetts, USA.

———. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethology and Sociobiology 1:13–40.

KAPLAN, E.L., AND P. MEIER. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistics Association 53:457–481.

KASBOHM, J.W., M.R. VAUGHAN, AND J.G. KRAUS. 1995. Food habits and nutrition of black bears during a gypsy moth infestation. Canadian Journal of Zoology 73:1771–1775.

KREBS, C.J. 1989. Ecological methodology. Harper & Row, Publisher New York, New York, USA.

LECOUNT, A.L. 1982. Characteristics of a central Arizona black bear population. Journal of Wildlife Management 46:861–868.

———. 1983. Evidence of wild black bears breeding while raising cubs. Journal of Wildlife Management 47:264–268.

———. 1987. Causes of black bear cub mortality. International Conference on Bear Research and Management 7:75–82.

LEWISON, R. 1998. Infanticide in the hippopotamus: evidence for polygynous ungulates. Ethology, Ecology and Evolution 10:277–286.

LINDSTEDT, S.L., AND M.S. BOYCE. 1985. Seasonality, fasting endurance, and body size in mammals. American Naturalist 125: 873–878.

LINDZEY, F.G., K.R. BARBER, R.D. PETERS, AND E.C. MESLOW. 1986. Responses of a black bear population to a changing environment. International Conference on Bear Research and Management 6:57–63.

MALLORY, F.F., AND R.J. BROOKS. 1978. Infanticide and other reproductive strategies in the collared lemming, *Dicrostonyx groenlandicus*. Nature 273:144–146.

MATTSON, D.J., AND D.P. REINHART. 1995. Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. Canadian Journal of Zoology 73:2072–2079.

MCCULLOUGH, D.R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173–196 *in* C.W. Fowler and T.D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.

———. 1986. The Craighead's data on Yellowstone grizzly bear populations: relevance to current research and management. International Conference on Bear Research and Management 6:21–32.

MCLEAN, I. 1983. Paternal behaviour and killing of young in Arctic ground squirrels. Animal Behaviour 31:32–44.

MCLELLAN, B. 1994. Density-dependent population regulation of brown bears. Pages 15–24 *in* M. Taylor, editor. Density-dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management, Monograph Series No. 3.

MILLER, S.D. 1990. Impact of increased bear hunting on survivorship of young bears. Wildlife Society Bulletin 18:462–467.

———. 1994. Black bear reproduction and cub survivorship in south-central Alaska. International Conference on Bear Research and Management 9(1):263–273.

MOHNOT, S.M. 1971. Some aspects of social changes and infant-killing in the Hanuman langur, *Presbytis entellus* (Primates: Cercopithecidae), in western India. Mammalia 35:175–198.

MØLLER, A.P. 1988. Infanticidal and anti-infanticidal strategies in the swallow *Hirundo rustica*. Behavioural Ecology and Sociobiology 19:365–371.

NORUŠIS, M.J. 1997. SPSS professional statistics 7.5. Statistical Package for the Social Sciences Inc., Chicago, Illinois, USA.

OLSON, T.L. 1993. Infanticide in brown bears, *Ursus arctos*, at Brooks River, Canada. Canadian Field-Naturalist 107:92–94.

OPSETH, O. 1998. Brown bear (*Ursus arctos*) diet and predation on moose (*Alces alces*) calves in the southern taiga zone in Sweden. Canditatum Scientarius Thesis, Norwegian University of Science and Technology, Trondheim, Norway.

PACKER, C., AND A.E. PUSEY. 1984. Infanticide in carnivores. Pages 31–42 *in* G.Hausfater and S.B. Hrdy, editors. Infanticide, comparative and evolutionary perspectives. Aldine, New York, New York, USA.

PATTERSON, I.A.P., R.J. REID, B. WILSON, K. GRELLIER, H.M. ROSS, AND P.M. THOMPSON. 1998. Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises? Proceedings of the Royal Society of London, Series B Biological Sciences 265:1167–1170.

PUSEY, A.E., AND C. PACKER. 1994. Infanticide in lions: consequences and counterstrategies. Pages 277–299 *in* S. Parmigiani and F.S. vom Saal, editors. Infanticide and parental care. Harwood Academic, Amsterdam, The Netherlands.

ROBBINS, M.M. 1995. A demographic analysis of male life history and social structure of mountain gorillas. Behaviour 132:21–47.

ROBERTSON, R.J., AND B.J. STUTCHBURY. 1988. Experimental evidence for sexually selected infanticide in tree swallows. Animal Behaviour 36:749–753.

ROGERS, L.L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monograph 97.

SÆTHER, B.E., S. ENGEN, J.E. SWENSON, Ø. BAKKE, AND F. SANDEGREN. 1998. Viability of Scandinavian brown bear *Ursus arctos* populations: the effects of uncertain parameter estimates. Oikos 83:403–416.

SANDEGREN, F., AND J. SWENSON. 1997. Björnen—viltet, ekologin och människan. Svenska Jägareförbundet, Spånga, Sweden. (In Swedish.)

SELLERS, R.A., AND L.D. AUMILLER. 1994. Brown bear population characteristics at McNeil River, Alaska. International Conference on Bear Research and Management 9(1):283–293.

STABELL, L. 1999. Use of ungulates by brown bears *Ursus arctos* in Scandinavia: effects of area, season, sex, age, and individual. Candidatum Scientarius Thesis, University of Oslo, Oslo, Norway.

STEPHENS, M.L. 1982. Mate takeover and possible infanticide by a female northern jacana (*Jacana spinosa*). Animal Behaviour 30:1253–1254.

STRINGHAM, S.F. 1980. Possible impacts of hunting on the grizzly/brown bear, a threatened species. International Conference on Bear Research and Management 4:337–349.

———. 1983. Roles of adult males in grizzly bear population biology. International Conference on Bear Research and Management 5:140–151.

SWENSON, J.E., A. JANSSON, R. RIIG, AND F. SANDEGREN. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology 77:551–561.

———, AND F. SANDEGREN. 1999. Mistänkt illegal björnjakt i Sverige. Pages 201–206 in Bilagor till Sammanhållen rovdjurspolitik; Slutbetänkande av Rovdjursutredningen. Statens Offentliga Utredningar 1999:146. Stockholm, Sweden. (In Swedish.)

———, ———, A. BJÄRVALL, A. SÖDERBERG, P. WABAKKEN, AND R. FRANZÉN. 1994. Size, trend, distribution and conservation of the brown bear *Ursus actos* population in Sweden. Biological Conservation 70:9–17.

———, ———, S. BRUNBERG, AND P. WABAKKEN. 1997b. Winter den sites abandonment by brown bears *Ursus arctos*: causes and consequences. Wildlife Biology 3:35–38.

———, ———, A. Söderberg, A. Bjärvall, R. Franzén, and P. Wabakken. 1997*a*. Infanticide caused by hunting of male bears. Nature 386:450–451.

———, P. Wabakken, F. Sandegren, A. Bjärvall, R. Franzén, and A. Söderberg. 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. Wildlife Biology 1:11–25.

Taberlet, P., J.E. Swenson, F. Sandegren, and A. Bjärvall. 1995. Localization of a contact zone between two highly divergent mitochondrial DNA lineages of the brown bear *Ursus arctos* in Scandinavia. Conservation Biology 9:1255–1261.

Taylor, M., editor. 1994. Density-dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management, Monograph Series No. 3.

Veiga, J.P. 1990. Infanticide by male and female house sparrows. Animal Behaviour 39:496–502.

Vom Saal, F.S., and L.S. Howard. 1982. The regulation of infanticide and parental behavior: implications for reproductive success in male mice. Science 215:1270–1272.

Waits, L., P. Taberlet, J.E. Swenson, F. Sandegren, and R. Franzén. 2000. Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (*Ursus arctos*). Molecular Ecology 9:421–431.

Wielgus, R.B., and F.L. Bunnell. 1994*a*. Dynamics of a small, hunted brown bear *Ursus arctos* population in southwestern Alberta, Canada. Biological Conservation 67:161–166.

———, and ———. 1994*b*. Sexual segregation and female grizzly bear avoidance of males. Journal of Wildlife Management 58:405–413.

———, and ———. 1995. Tests of hypotheses for sexually segregation in grizzly bears. Journal of Wildlife Management 59:552–560.

———, and ———. 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. Biological Conservation 93:145–154.

Wolff, J.O., and D.M. Ciciello. 1989. Field evidence for sexual selection and resource competition infanticide in white-footed mice. Animal Behaviour 38:637–642.

Young, B.F., and R.L. Ruff. 1982. Population dynamics and movements of black bears in east central Alberta. Journal of Wildlife Management 46:845–860.