

INTRASPECIFIC PREDATION IN SCANDINAVIAN BROWN BEARS OLDER THAN CUBS-OF-THE-YEAR

JON E. SWENSON, Department of Biology and Nature Conservation, Agricultural University of Norway, Box 5014, N-1432 Ås, Norway and Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway, email: jon.swenson@ibn.nlnh.no
BJØRN DAHLE, Department of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway
FINN SANDEGREN, Research Unit, Swedish Association for Hunting and Wildlife Management, Bäcklösavägen 8, SE-756 51 Uppsala, Sweden

Abstract: Intraspecific predation of bears >1 year old is observed occasionally, but the mechanisms behind it are poorly understood and often debated. We documented 13 cases of intraspecific predation in brown bears (*Ursus arctos*) in 2 Scandinavian study areas during 668 bear-years of radiotracking 238 brown bears. We found area differences in the rates of intraspecific predation only for yearling females. Annual yearling female mortality due to intraspecific predation was higher (0.162, 6 of 38) in the south than in the north (no mortality recorded, 28 yearlings followed). No older subadult females were killed by other bears. Annual mortality rates due to intraspecific predation for males, areas combined, were: 0.032 for yearlings, 0.040 for 2-year-olds, and 0.061 for 3-year-olds, for a combined rate from age 1 through 3 years of 0.127. One adult female was killed. Staying with their mother did not significantly reduce intraspecific predation among yearlings. Neither population density, at the levels we observed, nor reduced food abundance influenced rates of intraspecific predation on yearlings in our areas. In our study areas, intraspecific predation on yearling females was correlated positively with the number of adult males that had died 3 years previously and whether any adult male had died 2 years previously. In an earlier study, we found that cub mortality was elevated during the breeding season 2 years after the death of adult males. As we found a similar pattern for intraspecific predation on yearling females, we speculate that infanticidal males may be prone to kill subadult bears. Although based on a relatively small sample of mortalities, our results strengthen our earlier conclusion that the killing of adult males may have a population consequence that managers should consider.

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Key words: brown bear, intraspecific predation, management, population dynamics, Sweden, *Ursus arctos*

Bears kill other bears, both cubs-of-the-year (called “cubs” in this paper) and older bears, but most authors consider the killing of bears older than cubs by conspecifics to be rare (Rogers 1983, Mattson et al. 1992, Garshelis 1994, McLellan 1994). However, McLellan et al. (1999) found that 5 of 12 natural mortalities among subadult and adult female brown bears in the Rocky Mountains were apparently due to conspecifics. Garshelis (1994) reported that about 2 North American black bears (*U. americanus*) per year were reported killed by conspecifics during the last 20 years, which is a low number considering the multitude of telemetry studies that have been conducted on this species. Intraspecific predation has also been reported occasionally in polar bears (*U. maritimus*; Lunn and Stenhouse 1985, Derocher and Wiig 1999). Two attempts have been made to quantify intraspecific predation in brown bears using scat analysis. Mattson et al. (1992) found that 0.17% of 6,976 brown bear scats in Yellowstone National Park, USA, contained remains of conspecifics (meat or >50% indigestible remains). Zhiryakov (1993) found that a similar proportion, 0.1%, of brown bear feces contained bear hair in and near the Alma-Ata State Reserve, Tian-Shan Mountains, Kazakhstan. McLellan et al. (1999) found that 5 of 34 total known mortalities of radiomarked subadult and adult female brown bears were due to conspecifics, but did not report whether the 2 natural mortalities of 25 total mortalities of males were due to intraspecific predation. In some areas of Russia, intraspecific predation is much more common among brown bears in years when the major food crops, usually berries and the very important seeds of stone pines (*Pinus sibirica*

and *P. pumila*), fail simultaneously. Smirnov and Shurygin (1991) wrote that intraspecific predation and cannibalism is a typical feature of brown bears in lean years in Tuva, central Siberia. Intraspecific predation during starvation years was reported to reduce adult survival and population size in central Siberia (Zavatskii 1993) and the Baikal region (Ustinov 1993), although these conclusions were not based on studies of radiomarked bears. In addition, Bunnell and Tait (1981) hypothesized that the killing or evicting of subadult males by adult males could be important in the regulation of bear populations.

Mattson et al. (1992) encouraged bear researchers not only to report instances of intraspecific predation, but also to report sample sizes and effort, such that mortality rates could be analyzed with respect to demographic and environmental parameters. Here we report mortality rates due to intraspecific predation in 2 brown bear populations in Scandinavia based on 13 instances of intraspecific predation during 668 bear-years (1 bear-year is the equivalent of 1 bear followed for 12 months, $n = 238$ bears) of radiotelemetry tracking during 1984–99. We use the term “intraspecific predation” to mean intraspecific killing. Because we usually recovered the carcass quickly, we are unsure how much of it would finally have been consumed by the perpetrator. We only considered bears >1 year old here; we considered mortality of cubs earlier (Swenson et al. 1997, 2001). Beyond reporting rates, we addressed the following questions:

Are bears in certain age or sex categories particularly vulnerable to intraspecific predation?—Mordosov (1993) stated that adults killed yearlings in spring, and Mattson

et al. (1992) suggested that young males might be especially vulnerable, but this was based only on 1 dead young male.

Do yearlings that stay with their mothers survive better than those that separate as yearlings, as predicted by Stringham (1983)?

Who are the perpetrators?—The general pattern from literature reviews in North America seems to be that adult males kill other bears of all age and sex classes, but adult females kill few adult males (Garshelis 1994, McLellan 1994), although there is not sufficient evidence to make a definite conclusion.

When does the mortality occur?—Mattson et al. (1992) found a tendency for brown bear feces to contain more bear remains (both brown and black bear) in March–May than later in the year in Yellowstone National Park. Zyryanov (1991) and Mordosov (1993) reported that intraspecific predation among brown bears in Siberia takes place in spring and autumn. There are several reports of bears being killed by conspecifics while in or at the den for American black bears (Rogers 1983, Tietje et al. 1986, Davis and Harestad 1996) and brown bears (Zetterberg 1951, Pearson 1975, Smirnov and Shurygin 1991, Zyryanov 1991, Mordosov 1993).

What is the reason for intraspecific predation?—No universal reason has yet been found, but several explanations have been proposed. (1) The Russian authors cited above have proposed that bears kill conspecifics for food when other food is scarce. This has also been suggested by some North American authors (Tietje et al. 1986, Olsen 1993), although data from Yellowstone National Park did not support this explanation (Mattson et al. 1992). Tietje et al. (1986) hypothesized that a male could improve his breeding success by killing and eating other bears to improve his condition during the breeding season in years of poor food availability. (2) Both adult males and females could benefit from killing unrelated conspecifics of the same sex, usually older bears killing younger ones. This would reduce the number of offspring of competitors, and thus remove future competitors to themselves and their own offspring for space, food, and mates (Rogers 1983, Tietje et al. 1986, LeCount 1987, Garshelis 1994, Helsing and Aumiller 1994). (3) Several authors have suggested that higher density or concentration of bears in of itself leads to increased intraspecific predation (Stringham 1983, Tietje et al. 1986, Davis and Harestad 1996). The pattern of intraspecific predation in Yellowstone did not contradict this hypothesis (Mattson et al. 1992).

These explanations were usually based on a few observed cases of intraspecific predation. There are certainly other valid explanations and it is reasonable to believe that there are actually several reasons for intraspe-

cific predation and that there may be different reasons in different circumstances.

STUDY AREAS

The study areas were located in northern Sweden and central Sweden–southeastern Norway, as 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. The northern study area was about 8,000 km² in central Norbotten County in northern Sweden, around Kvikkjokk (66°–68° N, 16°–20° E). It included alpine vegetation in the mountains, which were up to 2000 m high, in the western part of the area. Birch (*Betula pubescens*) formed the timberline at about 800 m. Boreal forest dominated and consisted primarily of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) in the U-shaped valleys and the lower (down to 300 m) and more rolling terrain in the eastern part of the study area. The southern study area was about 13,000 km² in northern Dalarna County and western Gävleborg County in Sweden and eastern Hedmark County in Norway (60°–61° N, 11°–16° E). The area was dominated by gently rolling terrain between 200 and 1000 m in elevation. Only a small part of the study area was above timberline. Intensively managed boreal forest dominated the study area, and the important tree species were Scots pine, Norway spruce, and the exotic lodgepole pine (*Pinus contorta*). The study populations belong to separate mitochondrial 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 Scandinavia (Waits et al. 2000). An analysis of reproductive and mortality data indicated rapid growth in both populations during 1984–95: $\lambda = 1.14$ in the north and $\lambda = 1.16$ in the south (Sæther et al. 1998).

Bear hunting was generally allowed during the autumn in both areas, but the northern area included 3 national parks, where bear hunting was forbidden throughout the study period. Hunting pressure has increased in the southern study area in recent years, from an average of 2.8 bears killed legally per year in the 2 provinces encompassing the study area (Dalarna and Gävleborg) during 1985–95, to 23 in 1998. There was evidence of considerable illegal killing of bears, especially in the northern area (Swenson and Sandegren 1999). Illegal killing appeared to be less on the study areas than in the surroundings, and it appeared to have a major limiting effect on the population in the north. We have documented this in the north through the loss of radiomarked bears, especially males leaving the study area, and changes in the distribution of females, as determined from the distribution of legally killed fe-

male bears (Sandegren and Swenson 1997, Swenson and Sandegren 1999). Swenson *et al.* (2001) concluded that a higher immigration rate of newly recruited males occurred in the southern study area than in the northern area after adult males died. This was based on an apparent stable population trend for adult males in the south, in spite of the loss of adult males, and the decline in number of adult males in the north after adult males died.

METHODS

During 1984–99, 101 bears were marked in the northern study area and during 1985–99, 137 were marked in the south. All were immobilized early in the spring from a helicopter and marked with radiotransmitters (Telonics, Mesa, Arizona, USA). Most of the subadult bears captured after 1994 were equipped with a transmitter with a mortality sensor, which changed the pulse rate of the transmitter after it had not been moved for 4.7 hours. Growing bears were recaptured each spring to provide them with larger collars, although in the latter years of the study, yearlings received a transmitter that was implanted into the body cavity. Except for yearlings of radiomarked females, we collected a premolar tooth, which we sent to Matson, Inc., Milltown, Montana, USA, for age estimation based on the cementum annuli (Craighead *et al.* 1970). Bears were weighed every time they were captured. During 1988–91, 86% of the females observed in the company of radiomarked males during the breeding season in the north had functioning radiotransmitters. The corresponding value in the south, based on this type of observations made in 1988, 1989, and 1993, was 47% (Swenson *et al.* 1994, 1995). Judging from observations of males with radiomarked females in the breeding season, Swenson *et al.* (2001) concluded that virtually all adult males in the north and about 56% of them in the south were marked.

As marking occurred only during one short period each year, we calculated annual survival rates using the Kaplan–Meier procedure (Kaplan and Meier 1958). In this method, survival is calculated each month based on the number of radiomarked bears alive each month, and the monthly survival rates are multiplied to obtain an annual survival rate. Because we were only interested in intraspecific predation, we censored other causes of mortality, as recommended by Pollock *et al.* (1989). The rates of intraspecific predation reported here are 1 minus the censored annual survival rates. All bears were located at least once a week from the ground or from an aircraft, weather permitting. When a mortality pulse was received or death was suspected, the site was visited as soon as possible, usually within a day in the south and a few days in the north. All carcasses were examined by veterinarians at the National Veterinary Institute of Sweden. Determining intraspecific

predation was based on bite marks, particularly in the skull. Most carcasses were found so quickly that there was no question as to the cause of death. However, some dead bears in the north were found later, due to the wilderness character of the study area and poor weather that often hindered telemetry work from aircraft and access to the carcass with a helicopter. In cases where decomposed carcasses were found, judgment regarding cause of death was based on bite marks on the bones, particularly the skull. Thus, our estimate of mortality due to intraspecific predation may have been somewhat low in the north, although we do not believe it caused a major bias. During this study we documented 12 cases of intraspecific mortality of radiomarked subadult bears, 1 of a yearling that had been ear-tagged but had no radiotransmitter, and 1 of an adult (>3 years old).

Almost half of the bears in the north (43%, $n = 35$ to 1998) and almost all in the south (89%, $n = 57$) separated from their mothers as yearlings (Swenson *et al.* 1994). It can be difficult to decide whether a yearling killed by another bear in the spring had separated from its mother before being killed. We attempted to locate bears at least once a week, and we considered a yearling to have been with its mother when killed if it had been with her during the last time it was located alive.

Following Garshelis (1994) and Swenson *et al.* (2001), we used yearling body mass as a surrogate measure of food abundance the previous year. Yearlings were weighed to the nearest 0.5 kg shortly after den emergence ($n = 62$ in the north and 80 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 that sex and area. Thus, body masses from both sexes in an area were standardized and could be combined. The yearling body mass index was termed “fall condition index”, because most of the body mass was gained during the previous fall season. The body mass index was also considered to provide a “spring condition index” for the year in which yearlings were weighed. Thus for example, a body mass index obtained in early spring 1997 was used as a “spring condition index” for 1997 and as a “fall condition index” for 1996.

Loss of cubs has been correlated with the death of adult males in our study areas (Swenson *et al.* 1997, 2001). We therefore examined for this effect among subadult bears. The locations where adult males (>5 years old) were known to have died were compared with the locations of radiomarked females with cubs for a given year, called a “cub area”. A high proportion of the adult males were radiomarked: almost all (>90%) in the north and about 56% in the south (Swenson *et al.* 2001). In addition, 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 must be turned in, including a tooth. We tallied the number of adult males known to have died within each cub area and within 1 male home-range diameter from it at time lags of 1, 2, and 3 years. This method is described in more detail and data are presented elsewhere (Swenson et al. 2001).

Indices of the trend in density of all adult females were derived by estimating the densities of breeding adult females and correcting these estimates for the proportion of radiomarked adult females that were breeding that year. Density of breeding adult females was estimated from the ratio of marked and unmarked females seen in the company of marked adult males during the breeding season using a simple Petersen estimate (Swenson et al. 1994). This was expanded to all adult females using the observed proportion of adult females that were breeding that year. We calculated a mean density from the years we have estimates (6 years in the north, 3 years in the south) and assigned this density to the year that was the mid-point of the years for which we had obtained estimates. With this starting point, we calculated annual density estimates before and after that year using the rates of population growth found from a demographic analysis of our data, $\lambda = 1.14$ in the north (1984–95) and $\lambda = 1.16$ in the south (1985–95; Sæther et al. 1998).

We also estimated the relative bear density in the home ranges of the subadults in a spatial manner, not temporally as above. In Sweden, female bears are concentrated in four geographically isolated areas termed female core areas (Swenson et al. 1994). These core reproductive areas are defined as the 90% harmonic mean areas (Dixon and Chapman 1980) of hunter-killed female bears during 1981–93 (Swenson et al. 1998a). In general, the relative density of bears is halved about every 24 km from the center of a core reproductive area toward the edge (Swenson et al. 1998a). This density gradient is a result of a sustained increase in population size, both in density and in distribution (Swenson et al. 1995, 1998a). In the south, our field station is located approximately in the center of the southernmost core reproductive area in Sweden. For practical reasons, to reduce the effect of a mismatch between the location of the center of the core reproductive area and the location of our field station, bear density was considered to be constant within 15 km from our field station. Outside this area, the relative density of bears was estimated as $0.5^{(x-10)/24}$, where x = the distance (in km) of a home range center from our field station (Swenson 1998a). We were not able to obtain this relative spatial density for the northern study area.

Estimated survival functions from radiomarked bears were compared using the z test recommended by Pollock

et al. (1989). Pollock et al. (1989) recommended a sample size of 40–50 animals to obtain a mortality estimate with good precision. This exceeds our sample sizes for every age–sex–area category, so we accepted an ∞ level of 0.10 for statistical significance.

We used stepwise multiple logistic regression to investigate correlates of annual rates of intraspecific predation mortality among radiomarked yearlings. Yearling fate (killed by another bear or not) was treated as the dependent variable. The independent variables were: area, sex, spring body mass of the yearling, annual spring condition index, annual fall condition index, adult female bear density, number of adult males known to have died in or near the cub areas (with time lags of 1, 2, and 3 years), and whether or not adult males were known to have died in or near the cub areas (with time lags of 1, 2, and 3 years). Independent variables were entered into the model, and removed by backward elimination using the Wald χ^2 statistic for removal (Norusis 1997). Statistical tests were carried out in SPSS.

RESULTS

Are Bears in Certain Age or Sex Categories More Vulnerable to Intraspecific Predation?

Yearlings—The mortality rate due to intraspecific predation was not significantly different for yearling males in the north and south ($z = 0.17$, 1 df 1, $P = 0.91$, Table 1). The combined mortality rate for yearling males in all areas was 0.032 (SE = 0.022, $n = 64$). In yearling females,

Table 1. Mortality rates of radiomarked brown bears in Scandinavia due to intraspecific predation by age, sex, and study area (north and south), 1984–98.

Age (years)	Sex	Area	Mortality (SE)	N ^a
1	M	N	0.037 (0.036)	30 (1)
		S	0.029 (0.029)	34 (1)
	F	N	0	28 (0)
		S	0.162 (0.061)	38 (6)
2	M	N	0.082 (0.056)	31 (2)
		S	0	28 (0)
	F	N	0	23 (0)
		S	0	26 (0)
3	M	N	0	18 (0)
		S	0.096 (0.064)	25 (2)
	F	N	0	21 (0)
		S	0	22 (0)
>3	M	N+S	0	179 ^b (0)
		F	0.0037 (0.004)	268 ^c (1)

^a Number of radiomarked bears for subadults and number of years and partial years the bears were followed for adults. The number in parentheses is the number documented as killed by another bear.

^b The actual time was 136.9 bear-years.

^c The actual time was 251.0 bear-years.

however, the bear-caused mortality was higher in the south than in the north ($z = 2.66$, 1 df, $P = 0.008$, Table 1). When comparing sexes of yearlings within an area, we found no statistical difference in mortality rate between males and females in the north ($z = 1.00$, 1 df, $P = 0.32$). In the south, however, females had a mortality rate due to intraspecific predation that was over 5 times higher than males ($z = 1.97$, 1 df, $P = 0.049$, Table 1). Female yearlings were 25% smaller than males in the north and 18% smaller in the south (Swenson *et al.* 2001).

Subadult bears.—Intraspecific predation was also observed in 2- and 3-year-old bears, but only in males (Table 1). In both areas combined, the annual rate of intraspecific predation was 0.040 (SE = 0.028, $N = 59$) among 2-year-old males and 0.061 (SE = 0.042, $N = 43$) among 3-year-old males. Thus, the cumulative rate of intraspecific predation for male bears from age 1 through 3 years (i.e., the second through fourth years of life) in both areas combined was 0.127. No radiomarked female 2-year-olds ($N = 49$) or 3-year-olds ($N = 43$) were killed by other bears. When combining areas and ages (2- and 3-year-olds), we found a significantly higher intraspecific predation rate among males (0.048, SE = 0.024, $N = 102$) than females (0 mortalities, 92 females followed, $z = 2.03$, 1 df, $P = 0.042$).

Adult bears—We followed bears older than 3 years for a total telemetry time of 388 bear-years and recorded only a single death due to another bear. This was a 12-year-old female with 3 cubs. The annual mortality rate for females older than 3 years due to intraspecific predation was 0.0037 (SE = 0.0037, based on 251 bear-years of radiotelemetry (Table 1).

Who Are the Perpetrators?

As with most studies of bear mortality, identifying the perpetrator was difficult. We identified 3 potential perpetrators, but do not have conclusive evidence for any of them: (1) an adult male likely killed a male yearling; (2) a 5-year-old female with 3 cubs may have killed a female yearling, who was her half-sister; and (3) an 11-year-old resident male probably killed a 12-year-old female, who had 3 cubs. Details of these incidents are given below.

Case 1.—An adult male was the most likely killer of yearling male (W9405). The yearling was located with its mother on 27 May 1994, but was located alone and inactive on 28 and 29 May at the site where the partially eaten bear carcass later was found. A large Scots pine tree at the kill site had many fresh claw marks from what appeared to be a large bear and a smaller bear, suggesting that a large bear had dragged a smaller bear out of the tree. We assume that the smaller bear was W9405, but his littermate (W9404, female) was also in the vicinity at the time. Tracks from a large male bear and a female with

cubs were observed in mud on a road about 400 m from the kill site. These indications suggest that an adult male may have killed W9405, although the female with cubs or other bears can not be ruled out. We concluded that this bear had been with its mother when killed, but it is possible that it had separated from her less than a day before it was killed.

Case 2.—Some evidence suggests that a female with cubs may have killed yearling female W9805. This yearling was observed alone on 11 June 1998. The next day, a radiotelemetry position was obtained at 21:30 and was, according to the activity sensor on the transmitter, inactive at the site where it was later found dead; it may have already been dead at this time. Another bear, W9404, a 5-year-old female with 3 cubs, was recorded, using radiotelemetry, to have passed this site about 20:30 on the same day. No other radiomarked bears were located in the area, but an unmarked bear can not be excluded as the killer. The kill site was visited on 13 June. It was evident that W9805 had been chased for about 50 m, based on torn up moss and tufts of hair. The bite marks suggested that she had been killed by an adult bear and the carcass was partially consumed. W9404 and W9805 were half-sisters born in separate litters to the same mother.

Case 3.—An adult male most likely killed adult female W8905. The 12-year-old female was observed with 3 cubs 300 m from their den on 21 May 1999. At 05:25 on 25 May, she was located at the same site with a passive signal (her transmitter did not have a mortality function), together with an 11-year-old male (W9807), who had an active signal. The site was checked by airplane the same day. The activity signals were the same; one adult bear was seen (probably W9807) and 2 cubs were observed in a tree. A visit to the site in the evening revealed that the adult female was dead, covered with moss, and the posterior portions had been eaten. The site showed evidence of a fight. Two of the young were found alive in a tree. They were kept alive by providing dog food at the den site, but were killed by an unknown bear on 11 June. They were in good condition when killed.

Do Yearlings that Stay with their Mothers Survive Better?

In the south, where 89% of the yearlings separated from their mothers during the spring, we were unable to reject the hypothesis of no difference in the rate of intraspecific predation among yearlings with their mothers (0.200, SE = 0.179, $N = 5$) and those separated from their mothers, sexes combined, (0.090, SE = 0.035, $N = 68$, $z = 0.60$, 1 df, $P = 0.55$). Likewise, in the north, where 43% of the yearlings separated from their mother, there was no statistical difference in intraspecific predation between those with their mother (no mortalities, $N = 26$) and those sepa-

rated from their mother (0.037, SE = 0.036, $N = 31$, $z = 0.96$, 1 df, $P = 0.30$). Similarly, for both areas combined, yearlings with their mother had an intraspecific predation rate (0.032, SE = 0.032, $N = 31$) that was not significantly different from those not with their mother (0.074, SE = 0.027, $N = 99$, $z = 1.00$, 1 df, $P = 0.32$).

When Does the Mortality Occur?

Of the 14 bears identified as killed by conspecifics, 13 of which were radiomarked and 1 earmarked, 86% were killed during May–July (Table 2). This pattern seemed to hold for all age and sex classes of victims. One bear, a 3-year-old male, was killed at his den site. He was located there alive in October; we thought that the subsequent mortality signal was due to hibernation, but he was found dead outside the den the following spring. He had obviously been killed there before the snow arrived, i.e. be-

Table 2. Months in which brown bears were killed by conspecifics in Scandinavia, according to age and sex, 1984–99. Data from both study areas are combined.

Month	Females		Males			Total
	Yearling	Adult	Yearling	2-yr old	3-yr old	
May	1	1	1	1		4
Jun	4 ^a					4
Jul	2		1		1	4
Aug					1	1
Sept						0
Oct				1		1

^a One of these bears was ear-tagged but not radiomarked and was found without the help of radiotelemetry.

fore he had entered the den.

Factors Correlated with Intraspecific Predation

In the stepwise multiple logistic regression, using yearlings of both sexes and areas and including sex and area as independent variables, 3 independent variables were statistically significant: the number of adult males known dying in the area 3 years earlier, sex, and fall condition index. A positive relationship was found between intraspecific predation and the 2 continuous variables (Table 3). Because sex was a significant variable, similar regressions were performed on the sexes separately. No significant independent variables were found for yearling males. However for yearling females, a positive relationship was found between intraspecific predation and both the number of adult males known dying 3 years previously and the fall condition index (Table 4). In the south, the relative density of bears within the yearlings' home ranges did not influence the probability of being killed by another bear for males (Wald $\chi^2 = 0.004$, 1 df, $P = 0.95$) or females (Wald $\chi^2 = 0.165$, 1 df, $P = 0.68$). The data, including the independent variable and the selected dependent variables, are presented in Table 5.

Because we earlier found a relationship between cub mortality and whether any adult males had died (Swenson et al. 2001), we also compared intraspecific predation rates for yearlings where any adult male had died (using time lags of 1, 2, and 3 years) to those where no adult male was known to have died. No significant results were found

Table 3. Results of a stepwise multiple logistic regression with whether a radiomarked yearling brown bear was killed by another bear in two study areas in Sweden as the dependent variable. Independent variables were study area, sex of the yearling, spring body mass of the yearling, annual spring condition index, annual fall condition index, bear density (based on adult females), number of adult males known to have died in or near the cub areas, with time lags of 1, 2, and 3 years, and whether or not adult males were known to have died in or near the cub areas, with time lags of 1, 2, and 3 years.

Variable	Slope	SE	Wald χ^2	df	P
Constant	-8.149	2.668	9.33	1	0.002
Number of adult males dying 3 years earlier	0.671	0.322	4.35	1	0.037
Sex	2.584	1.352	3.66	1	0.056
Fall condition index	1.320	0.699	3.56	1	0.059
Entire model			10.29	3	0.016

Table 4. Results of a stepwise multiple logistic regression with whether a radiomarked yearling female brown bear was killed by another bear in two study areas in Sweden as the dependent variable. Independent variables were study area, spring body mass of the yearling, annual spring condition index, annual fall condition index, bear density (based on adult females), number of adult males known to have died in or near the cub areas, with time lags of 1, 2, and 3 years, and whether or not adult males were known to have died in or near the cub areas, with time lags of 1, 2, and 3 years.

Variable	Slope	SE	Wald χ^2	df	P
Constant	-3.476	0.955	13.24	1	0.000
Number of adult males dying 3 years earlier	0.891	0.378	5.57	1	0.018
Fall condition index	2.209	1.053	4.40	1	0.036
Entire model			9.83	2	0.007

for males (Table 6). For yearling females, however, the rate of intraspecific predation was higher when adult males had died than if none were known to have died 2 years previously and a tendency in that direction was found with a 3-year time lag (Table 7).

In a similar test, we examined whether a 2- or 3-year-old male being killed by another bear was related to any of the same dependent variables used for the test for yearlings, except that age was included and sex excluded. Body mass was also excluded, as it was not available for several individuals. None of these variables entered into the final model. In the south, the relative density of bears within the subadult males' home ranges did not influence the probability of being killed by another bear (Wald $\chi^2 = 0.062$, 1 df, $P = 0.80$). There may have been too few instances of intraspecific predation in these subadult males in our data set to adequately test the effects of the independent variables.

DISCUSSION

In our 2 study areas, intraspecific predation was almost entirely confined to yearlings and subadults, as also reported by Mordosov (1993) and suggested by Mattson et al. (1992). The probability of being killed by another bear from our sample was 0.127 for males during ages 1 through 3 years (both areas), 0.162 for yearling females in the south, and 0 for yearling females in the north. Thus, intraspecific predation can be an important demographic factor in some populations. Yearling females were the most vulnerable to intraspecific predation. As they were

the smallest subadult bears, it is possible that they were the easiest to kill.

In spite of our relatively large sample sizes, we were unable to demonstrate a survival advantage to yearlings of staying with their mothers, contrary to that predicted by Stringham (1983). Furthermore, we found that 3 orphaned cubs from 2 litters experienced normal growth in the north (Swenson et al. 1998b). We do not know why some females keep yearlings for an additional year, when it means also postponing reproduction for an additional year. Factors that may influence this situation are that our populations are growing rapidly (Sæther et al. 1998) and they are expanding in distribution, with no evidence that carrying capacity has been reached in any areas (Swenson et al. 1998a).

The one adult female that was killed by a conspecific most probably was killed by an adult male and likely was killed while defending her young, as has been recorded elsewhere for American black bears and brown bears (Garshelis 1994, McLellan 1994). The annual rate of intraspecific predation for females >3 years old in our relatively large sample (251 bear-years) was only 0.0037. No adult males were killed by conspecifics, as also found by McLellan et al. (1999).

Intraspecific predation was greatest during the spring breeding season, as also reported by Mattson et al. (1992). Although intraspecific predation may be associated with breeding behavior, it may also be associated with a greater probability for bears to encounter each other during the breeding season. At this time, adult males and adult females without cubs travel the greatest distances (Zakrisson 2001).

Table 5. Loss of radiomarked yearling female brown bears to intraspecific predation in the northern and southern study areas in Sweden, 1987–98, including the yearling masses (i.e., spring condition index) and number of adult (>5 years) males dying within the cub areas 1, 2, and 3 years previously. (One female yearling was followed in the north in 1984. She survived the year.)

Year	North					South				
	Yearling female loss ^b	Spring index ^c	No. males dying ^a			Yearling female loss ^b	Spring Index	No. males dying		
			-1 yr	-2 yr	-3 yr			-1 yr	-2 yr	-3 yr
1987	0/0	—				0/2	—	0	0	0
1988	0/0	—	0	0	0	0/0	—	0	1	0
1989	0/2	-0.17	2	0	0	0/1	-0.39	0	0	3
1990	0/0	+0.17	0	1	0	0/1	+0.60	0	0	0
1991	0/0	+2.07	0	0	1	0/2	-1.68	1	2	0
1992	0/1	+0.69	0	0	0	1/4	-0.46	4	1	2
1993	0/3	+0.19	0	0	0	0/3	-0.48	2	4	1
1994	0/4	-0.28	0	0	0	2/5	-0.34	0	2	4
1995	0/8	+0.27	0	0	0	0/4	-0.21	1	0	2
1996	0/2	-0.98	0	0	0	1/1	-0.19	0	1	0
1997	0/1	-0.47	1	0	0	0/1	+2.01	3	1	1
1998	0/2	+0.35	0	1	0	1/6	+0.41	0	3	0
1999	0/4	-0.38	0	0	1	1/8	+0.52	4	3	3

^a Adult males. Numbers can change when tracked diagonally because the cub areas were different each year.

^b Number killed by intraspecific predation/total number followed with radiotelemetry.

^c Spring condition index in 1989 corresponds to fall condition index in 1988.

Table 6. Annual rate of intraspecific predation in yearling male brown bears in Scandinavia, in relation to whether adult (>5 years) males were known to have died within the cub areas at various time lags, 1984–99. Data are combined from both study areas.

Time before the mortality of yearlings	Following known adult male death			No known adult male death			<i>z</i>	<i>P</i>
	Mortality	SE	<i>N</i>	Mortality	SE	<i>N</i>		
1 year	0.029	0.029	36	0.037	0.036	27	0.17	0.86
2 years	0.027	0.027	37	0.044	0.042	26	0.34	0.73
3 years	0.039	0.038	26	0.029	0.029	37	0.21	0.83

^a Two-tailed *z* test as described in Pollock et al. (1989).

Table 7. Annual rate of intraspecific predation in yearling female brown bears in Scandinavia, in relation to whether adult (>5 years) males were known to have died within the cub areas at various time lags. Data are combined from both study areas.

Time before the mortality of yearlings	Following known adult male death			No known adult male death			<i>z</i>	<i>P</i>
	Mortality	SE	<i>N</i>	Mortality	SE	<i>N</i>		
1 year	0.114	0.054	36	0.069	0.047	30	0.63	0.53
2 years	0.182	0.067	33	0	0	33	6.14	0.007
3 years	0.132	0.055	38	0.037	0.036	28	1.45	0.15

^a Two-tailed *z* test as described in Pollock et al. (1989).

We did not find an unequivocal reason for intraspecific predation. However, it is probably not possible to find one explanation for all intraspecific predation in bears. In our study areas, we only found significant relationships, among the factors we tested, for intraspecific predation on yearling females. In a multivariate analysis, positive relationships were found between this and the number of adult males known to have died in the area 3 years previously and the fall condition index. In a univariate analysis, a positive relationship was found between intraspecific predation and whether any adult male was known to have died 2 years earlier, with a tendency in that direction after 3 years. As both variables had been included in the multivariate analysis, the number of males dying 3 years previously was the factor that best explained the observed variation. However, both results suggest that disruption of the adult male social organization, perhaps resulting in the immigration of new males (Swenson et al. 1997, 2001), may have been involved in elevating the rates of intraspecific predation.

The pattern of intraspecific predation of yearling females in relation to mortality of adult males was similar to the pattern we observed for loss of cubs in our 2 study areas (Swenson et al. 2001). Mortality of cubs was also considerably higher in the south, where mortality of adult males was higher, than in the north, and cub mortality in the south was correlated with number of adult males dying 2 years earlier in a multivariate analysis. Cub mortality was also higher when any adult males had died 2 years earlier in a univariate analysis. Swenson et al. (2001) concluded that there was a higher immigration rate of new males in the south than in the north. This was based on a high emigration rate of radiomarked subadult males and no significant change in the number of adult males, de-

spite an annual mortality rate of about 10%. The conclusion was that infanticide caused by these immigrating males was probably the most important cause of cub loss. Intraspecific predation on yearling females was correlated with the number of adult males dying 3 years earlier in the multivariate analysis, in contrast to the 2-year time lag found for cubs. However, the same result, higher mortality after 2 years, was found in the univariate analyses. Based on these results, we speculate that infanticidal males might be more prone to kill young bears, including subadults. Also, the 2-year time lag for cub mortality and 3-year time lag for yearling mortality means that the cohort that experiences an elevated mortality rate as cubs following the loss of adult males on the area, also experiences a higher mortality the following year, at least the females in the cohort. Subadult bears were also killed by conspecifics most often in the breeding season, which is the same pattern we observed regarding cub loss (Swenson et al. 2001).

A higher loss of subadults with a time lag following high adult mortality also appears to have occurred in grizzly bears in the Yellowstone Ecosystem. Stringham (1983) analyzed data from the Yellowstone brown bear study during 1959–79 and found that the mean number of adult males censused before and after a cohort was born was negatively correlated with the cohort sizes at ages 0.5 years ($r^2 = 0.31$), 1.5 years ($r^2 = 0.50$), and 2.5 years ($r^2 = 0.82$). The highest numbers of censused adult males were in 1968–70 (Stringham 1983). The known mortality of adult males in the Yellowstone Ecosystem was also highest during these 3 years, mean of 9/year, compared to 1959–67, with a mean of 2.7/year (Craighead et al. 1995:278). Thus, low cohort size may also have been correlated with high losses of adult males with the reported time lags. The

elevated losses of cubs and subadults apparently continued for 2 or 3 years after many adult males were killed. Again, the high losses may have been related to a disruption of the adult male social organization, and perhaps occurred after new males entered the studied subpopulation of bears using the garbage dumps.

A second factor that was correlated with intraspecific predation in yearling females was fall condition. However, it was difficult to interpret this result, because the relationship was positive. It is not intuitively obvious why better condition in the fall should lead to higher intraspecific mortality, especially when most of the mortality occurs in the spring. A similar relationship was found for cubs (Swenson et al. 2001). Thus, there may be a factor involved here that we have not identified. Loss of cubs and intraspecific predation on yearling females may be correlated with a factor or factors other than intraspecific predation that is also correlated with the death of adult males 2 or 3 years earlier. We have not identified such a factor, but our results suggest that it is not poor food availability.

Relative population density was not found to influence the probability of intraspecific predation in either yearlings of both sexes or subadult males. We tested for density effects both temporally and spatially. We conclude that population density, within the range of densities observed in our study, was not an important factor influencing intraspecific predation. We earlier failed to find evidence that brown bears had reached carrying capacity in any areas in Sweden (Swenson et al. 1998a).

MANAGEMENT IMPLICATIONS

There has been considerable debate in the scientific literature about potential negative or positive effects on population growth of killing adult males. After reviewing the evidence and presenting his own data, Miller (1990) recommended that managers should not assume that the killing of adult males would have a positive effect on cub survivorship. Wielgus and Bunnell (1994, 2000) went even further, suggesting that killing adult males might even decrease cub survival. Our studies of cub survival (Swenson et al. 1997, 2001) have led us to agree with Wielgus and Bunnell (1994, 2000). However, this debate has only been concerned with cub survival.

The similarity of the results for cubs and yearling females leads us to speculate that the killing of adult males and disruption of the resident adult male social organization, with presumed immigration of new males, has even a greater demographic effect on a bear population than we proposed previously (Swenson et al. 1997, 2001). Loss of cubs was 0.35 in the south and 0.04 in the north (Swenson et al. 2001). Loss of female yearlings due to

intraspecific predation was 0.162 in the south and 0 in the north. Assuming that many of the cubs were killed by other bears, we conclude that intraspecific mortality can be an important demographic factor in some bear populations. As the level of intraspecific predation can be related to the killing of adult males, we repeat the caution we have given earlier (Swenson et al. 2001): "Until this question is adequately resolved, managers should act conservatively and assume a population consequence of harvesting adult male bears."

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