Swenson, J. E., F. Sandegren, A. Söderberg, A. Bjärvall, R. Franzén, and P. Wabakken. 1997. Infanticide caused by hunting of male bears. **Nature** 386:450-451.

Infanticide caused by hunting of male bears

With few exceptions[1], models used to predict the effect of harvesting on animal populations disregard males[2]. However, the killing of adult males can reduce population growth if, for example, immigrant males that replace a removed resident male kill the young[1,3]. In a field study of brown bears, *Ursus arctos*, we have found that killing one adult male had a population effect equivalent to killing 0.5 to 1 adult females. This may be a general phenomenon in species showing this type of infanticide.

Biologists rarely consider the population consequences of a disrupted social structure when adult males die[4]. But an immigrating male replacing a dead individual may increase his reproductive success by killing existing cubs, as this can shorten the interval to a female's next conception[3]. We observed that young were lost primarily during the breeding season in May–June (15 of 20 cubs lost, $\chi^2_c = 15.96$, d.f. = 1, $P = 0.0001$). This loss shortens the time to next conception — 8 of 10 females that lost all young gave birth the following year, compared with none of 40 that successfully raised cubs ($\chi^2_c = 32.37$, d.f. = 1, $P < 0.0001$).

The sexually selective infanticide hypothesis[3] predicts that survival of cubs less than 1 year old would be lower after a resident adult male bear is killed. We tested this using a retrospective experiment in two study areas in Sweden[5] between 1985 and 1995. In the treatment area (south), hunters killed adult (at least 5 years old) males in 4 of the 11 years: 1989 (1 male), 1990 (1), 1991 (2), and 1992 (1). They killed none in the control area (north). We documented disappearance, assumed to mean death, among 124 unmarked cubs accompanying radio-tagged females during the period 1988–95. Bears commonly kill cubs[6] — we observed one death by a male, and suspected another on the basis of tracks. The hunting season was in autumn, so immigration of a new male and lowered cub survival would be first observed during the next spring.

Cub survival was lower in the treatment area (0.72, $N = 74$) than the control area (0.98, $N = 50$; $\chi^2_c = 12.48$, d.f. = 1, $P = 0.0004$). Also in the treatment area, cub survival was lower both 0.5 and 1.5 years after adult males had been killed, but not after 2.5 years (Fig. 1). This indicates that the social organization of adult males was unstable for 1.5 years after losing a resident male. Cub survival was 1.00 in the treatment area and 0.98 in the control area when no adult male had been killed 1.5 years earlier, suggesting that established adult males killed few cubs.

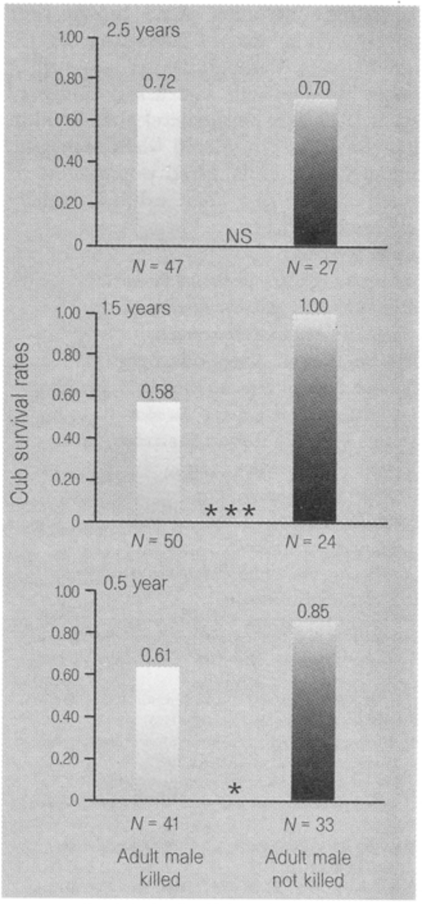

Figure 1 **Comparison of brown bear cub survival rates in their year of birth in relation to whether adult males were killed (yellow bars) or not killed (green bars) in the area 0.5, 1.5 and 2.5 years before the birth of the cubs. Annual survival is indicated at the top of each bar. N = sample size; *, $P = 0.016$ ($\chi^2_c = 5.78$, d.f. = 1); ***, $P = 0.0005$ ($\chi^2_c = 12.08$, d.f. = 1); NS, not significant.**

Our results cannot be explained by bear density or female condition. Cub survival was not correlated with year in this increasing bear population (logistic regression, $R = 0.000$, $\chi^2 = 0.084$, d.f. = 1, $P = 0.77$) and, unexpectedly, was negatively correlated with spring body mass of adult females ($R = -0.18$, $\chi^2 = 5.32$, d.f. = 1, $P = 0.02$).

We used computer modelling to show that the lowered cub survival reduced the population growth rate (λ) by 3.4%, from 1.18 to 1.14, and net reproductive output by 30%, in spite of a shortened litter interval. The 25–60 adult females on the 11,200 km^2 treatment area produce 25–60 cubs annually. A survival rate of 0.58 (Fig. 1) means that 11–25 cubs were lost, or 45–100% of the net reproductive output per female (24.6 cubs at $\lambda = 1.18$).

Bear populations are sensitive to loss of adult females[2,7,8]. However, the effect of shooting adult males on cub survival is controversial[8,9] and poorly documented[10]. We show that the population consequence of harvesting one adult male brown bear corresponds to that of harvesting 0.5–1.0 adult females, although the per capita effect would decline with increasing killing of males. This may be a general phenomenon and should be considered when managing threatened or endangered populations of other species that may exhibit sexually selected infanticide.

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