

Predation on Moose Calves by European Brown Bears

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ABSTRACT In North America, brown bears (*Ursus arctos*) can be a significant predator on moose (*Alces alces*) calves. Our study in Sweden is the first in which brown bears are the only predator on moose calves. Bears and moose occurred at densities of about 30/1,000 km² and 920/1,000 km², respectively, and bears killed about 26% of the calves. Ninety-two percent of the predation took place when calves were <1 month old. Bear predation was probably additive to other natural mortality, which was about 10% in areas both with and without bears. Females that lost their calves in spring produced more calves the following year (1.54 calves/F) than females that kept their calves (1.11 calves/F), which reduced the net loss of calves due to predation to about 22%. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1993–1997; 2007)

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In North America, the brown bear (*Ursus arctos*) is an important predator on calves of moose (*Alces alces*) and other ungulates, with reported predation rates on moose calves ranging from 2% to 52% (reviewed by Ballard 1992, Ballard and Van Ballenberghe 1998, Zager and Beecham 2006). Moose might be important prey for brown bears in Eurasia, especially in the north (e.g., Zavatskii 1978, Danilov 1983, Dahle et al. 1998, Persson et al. 2001), but estimates of predation and kill rates are unavailable. In Sweden, moose are hunted on an area of 370,000 km², and legal moose harvest increased from 2,000 to 3,000 in the beginning of the 20th century to a peak in 1982, when 175,000 were harvested (Lavsund and Sandegren 1989). Present harvest averages 100,000 annually. An estimated 2,350–2,900 brown bears occur in about two-thirds of Sweden, with an annual population growth rate of 5.5% (Kindberg and Swenson 2006). The authorities plan to allow a continued slow increase in numbers and distribution (Regeringen 2000). Although brown bear predation on moose is probably not regulatory (Ballard 1992, Ballard and Van Ballenberghe 1998, Zager and Beecham 2006), it is important to document possible limiting effects on an intensively human-exploited moose population that is also

experiencing a rapid brown bear population recovery after near extermination >100 years ago (Swenson et al. 1995, Kindberg and Swenson 2006). We are the first to document predation and kill rates on moose calves by brown bears outside North America and the first to document brown bear predation and kill rates in an area without other large carnivores that normally prey on moose (Zager and Beecham 2006). Our study of brown bear predation on moose calves aimed to document the proportion of moose calves killed by bears in south-central Sweden and to investigate whether the predation was additive or compensatory to other mortality.

STUDY AREA

Our study area was in northeastern Dalarna County and neighboring Gävleborg and Jämtland counties, south-central Sweden (61°N, 18°E). The area was hilly, with elevations ranging from about 200 m to 950 m, but only a very small part of the area was above timberline, approximately 750 m. Lakes and bogs covered large areas, but most of the area was covered with coniferous forest dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Besides moose, the major source of protein for the bears was ants (*Formica* spp. and *Componotus herculeanus*; Swenson et al. 1999a).

The last brown bears killed during the extermination campaign in Sweden were in 1897 in Dalarna County and 1895 in Gävleborg County. Following protection and effective conservation measures, bears returned to these counties in the 1920s and 1960s, respectively (Swenson et al. 1995). Bear density in the study area was estimated to be 30/1,000 km² by a combination of a mark-recapture technique and fecal DNA sampling (Solberg et al. 2006). Moose

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Table 1. Total mortality among unmarked calves of radiomarked female moose from birth to the beginning of the fall moose-hunting season in mid-September in south-central Sweden, 1988–1998.

Yr	No. of calves	Disappeared	% mortality
1988	22	6	27
1994	9	2	22
1995	13	6	46
1996	16	7	44
1997	13	2	15
1998	18	10	55
Total	91	33	36

density in winter averaged 920/1,000 km², based on aerial sampling in the area where moose were radiomarked (Cederlund and Wallin 1998).

METHODS

During February to mid-March (1988 and 1994–1996), we immobilized adult and yearling moose from helicopters using a dart gun injecting a mixture of an anesthetic and a tranquilizer (ethorphine and xylazine; Sandegren et al. 1987). We equipped each animal with a numbered radio-collar (very high frequency transmitters, model TXH-3; Televilt, Lindesberg, Sweden) and uniquely numbered ear tags. We estimated the age of moose according to tooth wear during the marking event (Skuncke 1949). From females that later died, we retrieved the jaw, sectioned the first permanent molar, and counted the cementum annuli with a 20–40× magnifier (Bubenik 1998). All animal experimentation reported in this paper complied with the current laws regulating the treatment of animals in Sweden and was approved by the appropriate ethical committee (Umeå djurförsöksetiskanämnd, protocols DNR A-11-91, A-12-91, A-102-93, A-103-93, A-17-94; Göteborgs djurförsöksetiskanämnd, protocol DNR 212-97).

We followed 20–35 adult moose females by radiotelemetry each year during 1988 and 1994–1998. We tracked them every third day during the moose calving season (until we confirmed birth) and documented birth rate. In 1994–1997, we captured a random sample of calves by hand (using gloves). We determined the sex of captured calves, weighed them with a spring scale, and measured skull length with a caliper. We determined age of calves by the frequency of observations of moose females, the condition of the umbilicus, and behavioral characteristics (Larsen et al. 1989). Handling time was <5 minutes, even for twin calves. In 1994 and 1995, we equipped captured moose calves with a 29-g ear-mounted radiotransmitter (Televilt Model TXP-1). In 1996, we equipped the captured calves with a 100-g radiotransmitter attached to an expandable neck collar (Model 305; Telonics, Mesa, AZ). The radiotransmitters had a mortality sensor with a 2.5-hour delay. We investigated mortality sites on the ground to determine the cause of death when we detected a mortality signal. We monitored radiomarked moose calves once a day during the first 5 weeks after marking, every second day during the sixth week, and thereafter once per week for 10 weeks until

Table 2. Causes of mortality among radiomarked moose calves from birth to onset of the fall moose-hunting season, south-central Sweden, 1994–1996.

Calves	1994	1995	1996	Total
Marked	12	18	17	47
Abandoned	2	4	3	9
Followed	10	14	14	38
Dead	8	9	6	23
Accident	1	0	1	2
Unknown ^a	1	3	2	6
Unknown predator ^b	0	1	0	1
Bear	6	5	3	14
Max. bear ^a	7	8	3	18

^a The max. unknown mortality possibly caused by bears was 1 in 1994 and 3 in 1995.

^b Not bear; possibly a lynx (*Lynx lynx*).

mid-September, the onset of the moose-hunting season. Unmarked calves with radiomarked mothers made up a control group, and we tracked their mothers to determine the presence or absence of the calves: once per week during the first 4 weeks of life, once after 6 weeks, and thereafter every third week until mid-September. In 1997, we did not equip moose calves with a radiotransmitter but did mount a uniquely numbered 2-g plastic ear tag (Busk 1998). We observed both the marked and unmarked calves after 4 weeks and 8 weeks after birth to determine their survival. In 1998, we registered only the number of calves born and the number that survived until the start of the moose-hunting season. We used S-Plus 6.2 (Insightful Corp., Seattle, WA) for statistical analyses.

RESULTS

Calf mortality, based on 91 unmarked calves of radiomarked females, averaged 36% annually (95% CI = 23–46) over 6 years (Table 1) and did not differ among years ($\chi^2_5 = 7.83$, $P = 0.17$). We marked 47 moose calves with ear-mounted transmitters in 1994–1995 and neck collar-mounted transmitters in 1996. We excluded from further calculations 9 (19%) marked calves that were abandoned by their mothers after handling. The abandoned calves had a lower birth weight ($\bar{x} = 9.5 \pm 2.1$ [SD] kg) than calves that survived ($\bar{x} = 13.2 \pm 3.8$ kg, $n = 15$, $t_{22} = -2.69$, $P = 0.014$). Of the remaining 38 calves, 23 (61%) died. Brown bear predation accounted for 61% of the mortality and might have been responsible for an additional 4 calves with unknown cause of mortality (17%; Table 2). Thus, bears were responsible for between 61% and 78% of the total mortality of radiomarked calves. Mortality among the radiomarked moose calves (61%) was higher than among unmarked calves (36%; $\chi^2_1 = 5.47$, $P = 0.02$). However, a comparison of mortality among marked and unmarked calves in 5 areas in Sweden, including our area, showed that there was no interaction between marking with ear-tag-mounted transmitters and the presence of bears in the pattern of calf mortality (Swenson et al. 1999b). Thus, we could estimate the real predation rate on moose calves by bears to be the total mortality rate among unmarked calves times the

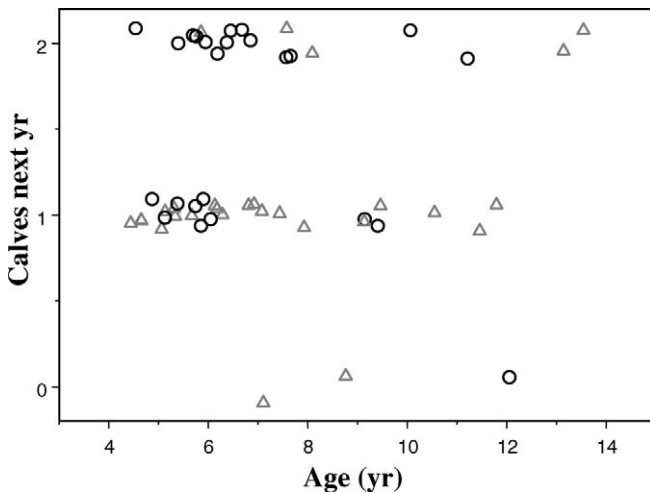


Figure 1. The number of calves born to female moose in south-central Sweden, 1995–1998, in relation to age of female (yr) and whether they lost (open circle) or kept (open triangle) their calves the previous year. Symbols are jittered to reduce overlap.

proportion of mortality among the marked calves documented to be caused by bears. This gave an estimated predation rate between 21% (0.36×0.61) and 28% (0.36×0.78). Assuming that bears killed 61% of calves with unknown cause of death (the documented predation rate among marked calves), the most likely estimate was 26%. As the total average mortality was 36%, we estimate that 10% of the moose calves died of causes other than bear predation.

Of the prehunt mortality, 92% took place during the first 4 weeks of life, and none of the calves died after the age of 13 weeks. Age of death did not differ between calves that were killed by bears and calves that died of other causes ($\chi^2_2 = 1.85$, $P = 0.40$). Mortality did not differ between control calves we observed once a week during first 4 weeks of age and calves that we first reobserved at the age of 4 weeks ($\chi^2_1 = 0.10$, $P = 0.75$). Birth weight did not differ between moose calves that were killed by bears ($\bar{x} = 11.2 \pm 3.1$ kg, $n = 14$) and calves that survived ($\bar{x} = 13.2 \pm 3.8$ kg, $n = 15$, $t_{27} = -1.60$, $P = 0.122$).

Based on the population density of bears, the age distribution in the bear population (Swenson et al. 1994, Sæther et al. 1998, Bellemain et al. 2005), the number of moose calves born (Cederlund and Wallin 1998), and the proportion of calves killed by bears, each bear ≥ 4 years old (assuming that bears < 4 yr kill no moose calves and that about 50% of the population is ≥ 4 yr old) in our study area killed on average 6.8 moose calves annually (no. of calves killed by bears/no. of bears ≥ 4 yr old that were present). This corresponds to one calf every sixth day during the 6-week period when moose calves were preyed upon efficiently by bears (2-week calving period and 92% killed within 4 weeks of age).

When 92% of the calf mortality occurred during the first 4 weeks after birth, and no calves > 13 weeks old died, moose females that lost their calves (to bear predation or other causes) invested fewer resources in their calves.

Females that lost their calves produced 39% more calves the following year ($\bar{x} = 1.54 \pm 0.59$ [SD] calves/F, $n = 24$) than females that raised calves that survived to the moose hunting season ($\bar{x} = 1.11 \pm 0.50$ [SD] calves/F, $n = 28$, $t_{50} = 2.89$, $P = 0.006$; Fig. 1). The proportion of moose females without calves and twinning rate seem to be rather stable from the age of 4 years (Andersen and Sæther 1996). Our sample of moose females only included females ≥ 4 years of age ($\bar{x} = 7.17 \pm 0.33$ [SE] yr). Moose females that lost their calves were not significantly younger ($\bar{x} = 6.92 \pm 1.98$ [SD] yr) than those that kept their calves ($\bar{x} = 7.54 \pm 2.63$ [SD] yr, $t_{50} = 0.95$, $P = 0.349$), so the higher reproduction for females that lost their calves than for females that kept their calves was not explained by age of females. This higher reproduction associated with loss of young reduced the net loss of calves due to bear predation from 26% to 22%.

DISCUSSION

This is the first study to report kill and predation rates on moose calves by brown bears outside North America and in an area without other moose predators. We found a predation rate that lies within the range reported in North America. This relatively high kill rate is supported by the results from scat analysis in our study area, which showed that moose calves are an important food resource for bears during late May–June (Opseth 1998). The timing of predation was also similar to that reported in North America (Ballard et al. 1981, Larsen et al. 1989).

Brown bears have been reported to prey disproportionately on smaller ungulate calves in caribou (*Rangifer tarandus*; Whitten et al. 1992) and elk (*Cervus elaphus*; Singer et al. 1997). Except for Keech et al. (2000), who reported that calf moose survival was positively related to birth mass where predation by bears and wolves was the major cause of mortality, most studies on calf moose mortality have not reported mass of calves, which is necessary to determine whether lighter calves are killed disproportionately more often than heavier ones. On our study area, birth weight did not differ statistically between calves that were killed by bears and calves that survived, suggesting that bears did not selectively prey on weaker calves. Also, mortality among control calves and calves marked with only an ear tag in 3 study areas in Sweden without brown bears averaged 10% ($N = 320$) and did not vary among areas (Swenson et al. 1999b). That 10% mortality is similar to the mortality rate caused by other than bear predation in our study, suggesting that predation by bears was additive.

Marking moose calves with an ear-tag-mounted radio-transmitter was associated with an increased mortality rate among calves. We do not know the reason for this elevated mortality among radiomarked calves, but it is possible that the transmitter somehow affected calf behavior or the calf–female relationship (Swenson et al. 1999b). Without a control group of unmarked calves, we would have overestimated the predation rate by brown bears and total calf mortality rate by 68% and 69%, respectively. However, corresponding studies on other cervids have not found

elevated mortality rates due to marking calves with radio-transmitters (Linnell et al. 1995).

Our results showed reproductive compensation in moose females following loss of calves. This has also been reported in Alaskan moose by Testa and Adams (1998) and Keech et al. (2000), who proposed the apparent mechanism: the body condition of moose females in fall is correlated positively with pregnancy rates and calving rates, and females with greater rump fat thickness in spring give birth to more twins. Rearing calves is costly; female moose accompanied by a calf in fall had less rump fat, a lower pregnancy rate, and smaller embryos. Therefore, lower calf survival may result in subsequent higher reproductive rates (Testa 1998). This seems to be a general phenomenon. Managers should expect partial compensation through higher reproduction the year after a moose female has lost her calves, especially when this happens early in the calves' lives.

MANAGEMENT IMPLICATIONS

Haglund (1974) concluded that brown bear predation was not an important factor in the population dynamics of moose in Sweden, and consequently predation has not been included in harvest plans. However, the brown bear population is expanding in size and range (Swenson et al. 1995, Kindberg and Swenson 2006) and is now found in most of the moose's range in Sweden. Our findings show that it is important that Swedish wildlife managers include the effects of brown bear predation in their moose population models, at least where bears are common.

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LITERATURE CITED

- Andersen, R., and B.-E. Sæther. 1996. Elgi Norge: biologi, atferd og forvaltning. Teknologisk forlag, Oslo, Norway. [In Norwegian.]
- Ballard, W. B. 1992. Bear predation on moose: a review of recent North American studies and their management implications. *Alces Supplement* 1:162-176.
- Ballard, W. B., T. H. Spraker, and K. P. Taylor. 1981. Causes of neonatal moose calf mortality in southcentral Alaska. *Journal of Wildlife Management* 45:335-342.
- Ballard, W. B., and V. Van Ballenberghe. 1998. Predator/prey relationships. Pages 247-273 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington, D.C., USA.
- Bellemain, E., J. E. Swenson, D. Tallmon, S. Brunberg, and P. Taberlet. 2005. Estimating population size of elusive animals using DNA from hunter-collected feces: comparing four methods for brown bears. *Conservation Biology* 19:150-161.
- Bubenik, A. B. 1998. Evolution, taxonomy and morphophysiology. Pages 77-124 in A. Franzmann and C. C. Schwartz, editors. *Ecology and management of the North American moose*. Smithsonian Institution Press, Washington, D.C., USA.
- Busk, H. 1998. Brown bear (*Ursus arctos*) predation on moose (*Alces alces*) calves in a Swedish boreal forest. Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Cederlund, G., and K. Wallin. 1998. Orsaprojektet, en slutrapport från populationsundersökningarna på älg. Grimsö forsknings station, Riddarhyttan, Sweden. [In Swedish.]
- Dahle, B., O. J. Sørensen, H. Wedul, J. E. Swenson, and F. Sandegren. 1998. The diet of brown bears in central Scandinavia: effect of access to free-ranging domestic sheep. *Wildlife Biology* 3:147-158.
- Danilov, P. I. 1983. The brown bear (*Ursus arctos* L.) as a predator in the European taiga. *Acta Zoologica Fennica* 174:159-160.
- Haglund, B. 1974. Moose relations with predators in Sweden, with special reference to bear and wolverine. *Naturaliste canadien* 101:457-466.
- Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management* 62:450-462.
- Kindberg, J., and J. Swenson. 2006. Populationsberäkning av björnstammen i Sverige 2005. Rapport 2006-2 från Det Skandinaviska Björnprojektet till Naturvårdsverket, Noppikoski, Sweden. [In Swedish.]
- Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in southwest Yukon. *Journal of Wildlife Management* 53:548-557.
- Lavsund, S., and F. Sandegren. 1989. Swedish moose management and harvest during the period 1964-1989. *Alces* 25:58-62.
- Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed Bambi?: the role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* 1:209-223.
- Opseth, O. 1998. Brown bear (*Ursus arctos*) diet and predation on moose (*Alces alces*) calves in the southern taiga zone in Sweden. Thesis, Norwegian University of Science and Technology, Trondheim, Norway.
- Persson, I. L., S. Wikan, J. E. Swenson, and I. Mysterud. 2001. The diet of the brown bear in the Pasvik Valley, northeastern Norway. *Wildlife Biology* 7:27-31.
- Regeringen. 2000. Sammanhållen rovdjurspolitik. Proposition 2000/01:57, Stockholm, Sweden. [In Swedish.]
- Sæther, B. E., S. Engen, J. E. Swenson, and F. Sandegren. 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos* populations: the effects of uncertain parameter estimates. *Oikos* 83:403-416.
- Sandegren, F., L. Pettersson, P. Ahlqvist, and B. O. Röken. 1987. Immobilization of moose in Sweden. *Swedish Wildlife Research Supplement* 1:785-791.
- Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management* 61:12-25.
- Skuncke, F. 1949. Älgen, studier, jakt och vård. P. A. Nordstedts och Söners, Stockholm, Sweden. [In Swedish.]
- Solberg, K. H., E. Bellemain, O.-M. Drageset, P. Taberlet, and J. E. Swenson. 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. *Biological Conservation* 128:158-168.
- Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999a. Bears and ants: myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology* 77:551-561.
- Swenson, J. E., F. Sandegren, A. Bjärvall, A. Söderberg, P. Wabakken, and R. Franzén. 1994. Size trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biological Conservation* 70:9-17.
- Swenson, J. E., 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 in Norway and Sweden. *Wildlife Biology* 1:11-25.
- Swenson, J. E., K. Wallin, G. Ericsson, G. Cederlund, and F. Sandegren. 1999b. Effects of ear-tagging with radiotransmitters on survival of moose calves. *Journal of Wildlife Management* 63:354-358.
- Testa, J. W. 1998. Compensatory response to changes in calf survivorship: management consequences of a reproductive cost in moose. *Alces* 34: 107-115.
- Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to

- reproductive effort in female moose (*Alces alces*). *Journal of Mammalogy* 79:1345–1354.
- Whitten, K. R., G. W. Garner, F. J. Mauer, and R. B. Harris. 1992. Productivity and yearly calf survival in the Porcupine caribou herd. *Journal of Wildlife Management* 56:201–212.
- Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. *Ursus* 17:95–108.
- Zavatskii, B. P. 1978. Feeding of brown bears in the central Yenesei taiga. *Ekologiya* 2:96–98. [In Russian.]

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