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Predation on adult moose *Alces alces* by European brown bears *Ursus arctos*

Bjørn Dahle, Kjell Wallin, Göran Cederlund, Inga-Lill Persson, Line S. Selvaag & Jon E. Swenson

Several North American studies have reported significant predation rates on moose *Alces alces* by brown bears *Ursus arctos*. We documented predation on moose by brown bears in south-central Sweden, where brown bears and moose occurred at estimated densities of 10-30 and 400-1,340/1,000 km², respectively. Bears killed 0.8% of radio-collared adult female moose (i.e. ≥ 1 year old) annually and no male moose (≥ 1 year old). Bear predation was the least important mortality factor we documented. Based on tracking brown bears on snow during spring we recorded one successful hunt for every 372 km of tracks and documented attacks only by adult bears and successful attacks only by adult males. Autopsy of moose older than calves that were killed by brown bears revealed that yearlings were more prone to predation than older moose, and that older (i.e. ≥ 2 years) cows were more vulnerable to predation than older bulls. Our study suggests a lower tendency for Scandinavian brown bears to prey on moose compared to most of the North American studies.

Key words: Alces alces, brown bear, kill rate, moose, predation, Ursus arctos

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In North America, the brown bear *Ursus arctos* is an important predator on moose *Alces alces* (see Ballard 1992, Ballard & Van Ballenberghe 1998 and Boertje et al. 2010 for reviews) and other ungulates, such as caribou *Rangifer tarandus* (Adams et al. 1995, Young & McCabe 1997) and elk *Cervus elaphus* (Singer et al. 1997, Barber-Meyer et al. 2009). North American studies have reported predation rates on moose calves (% of calves killed) by brown bears in the range of 2-52%, and that each adult brown bear kills an average of 0.5-2.2 adult moose (> 1 year old) annually. Moose might be important prey for brown bears also in Eurasia, especially in the north (e.g. Zavatskii 1978, Danilov 1983, Dahle et al. 1998, Persson et al. 2001), although Haglund (1968) snow-tracked Swedish brown bears in spring and concluded that brown bears were rarely successful hunters on moose. None of these studies used methods that allowed the estimation of predation and kill rates of adult moose. We have found that brown bears killed 26% of the moose calves born and that each adult bear killed about 7-8 calves in our Swedish study area (Swenson et al. 2007, Rauset et al. 2012).

In Sweden, moose are hunted on an area of 370,000 km², and legal moose harvest increased from about 2,000-3,000 in the beginning of the 20th century and peaked in 1982 with 175,000 being shot that year (Lavsund & Sandegren 1989). The present harvest averages 100,000 annually. The Swedish brown bear population is recovering after previous attempts to exterminate the population (Swenson et al. 1995), and it is important to document the rates of predation by bears on an extensively human-exploited moose population. Our objective with this study was to document the proportion of adult moose killed by brown bears annually in south-central Sweden.

Material and methods

Study area

Our study area was in the northeastern part of the county of Dalarna and the neighbouring counties of Gävleborg and Jämtland, south-central Sweden (61°N, 18°E). The area is hilly with elevations ranging from about 200 to 950 m, but only a very small part of the area is above the timberline, which occurs at approximately 750 m a.s.l. Lakes and bogs cover large areas, but most of the area is covered by coniferous forest dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*.

The brown bear density in the area where moose were radio-marked was estimated to be 30/1,000 km² by a combination of a mark-recapture technique and faecal DNA sampling (Solberg et al. 2006), but bear density was lower (10/1,000 km²) in some of the areas where bears were tracked on snow in spring (Bellemain et al. 2005). The moose density in winter averaged 920/1,000 km², based on aerial sampling in the area where moose were radio-marked (Cederlund & Wallin 1998) and varied from 400 to 1,340/1,000 km² in the areas in which bears were tracked on snow in spring and necropsies of dead moose were conducted (Persson 1998).

Capture and radio-marking of moose

We immobilised adult and yearling male and female moose from a helicopter during February to mid-March (1994-1996) using a dart gun injecting a mixture of an anesthetic and a sedative (Ethorphine and Xylazine; Sandegren et al. 1987) and followed them through 1997. We equipped each animal with a numbered radio-collar (VHF transmitters, Televilt model TXH-3) and uniquely numbered ear tags. We first estimated the age of moose according to tooth wear during the marking event (Skuncke 1949). From moose which later died, we retrieved the jaw, sectioned the first permanent molar and counted the *cementum annuli* using a 20-40X 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 (Djuretiska nämnden in Uppsala).

Predation on radio-marked adult moose and necropsy of moose

We monitored adult moose from the air every third to fourth week outside the calving season and females from the ground about every third day during the calving season (late May - late June). Moose were visited on the ground if they remained at the same position for two consecutive trackings. If the moose was dead, we determined the cause of death according to methods described in Myrberget & Sørensen (1981). We calculated cause-specific mortality for an annual interval using the Kaplan-Meier method (Kaplan & Meier 1958). We chose this method, because it is still a recommended method (Millspaugh et al. 2012), it allows the inclusion of newly marked animals and it is compatible with the relatively long intervals between locations that we used in this study. We used this method only to

obtain estimates of mortality resulting from various causes. To evaluate whether some age and sex categories were more vulnerable than others to predation by brown bears, we inspected carcasses of moose that were reported to us and that we verified had been killed by brown bears. We assigned date of death to early spring (1 April - 15 May), moose calving period (16 - 31 May), summer (1 June - 31 August) and fall (1 September - 1 November).

Tracking brown bears on snow in spring

We followed 35 bears, of which 30 were radio-marked. Of the 35 bears, 15 were males > 3 years old (five of them unmarked), nine males ≤ 3 years old, eight females > 3 years old and three females ≤ 3 years old. We followed the tracks as long as it was practically feasible, given the snow conditions, day-length and weather conditions. We followed the bears for > 5 km in a given spring and each bear was followed on average 21.2 km. We located the tracks by driving on roads or off-road using vehicles. We used radio-telemetry to locate areas where tracks of radio-marked bears could be found. All bears were back-tracked to avoid influencing their behaviour.

Results

Predation on adult moose

We monitored 32-57 moose each year for a total of 180 moose years. Annual mortality rates were $0.185 (\pm 0.060)$ and $0.295 (\pm 0.112)$ for female and male moose, respectively, and bear predation was the least important of the factors documented, with estimated annual mortality rates of $0.008 (\pm 0.015)$ for females and 0 for males (Table 1). Using a winter density of 920 moose/1,000 km², and a bear density of 30 bears/1,000 km², we calculated a mean annual kill rate of about 0.5 moose ≥ 1 year old for adult bears (≥ 4 years old), assuming that all bear-killed moose were killed by adult bears and that 50% of the bears were adults (Swenson et al. 2007).

We followed bear tracks on snow in spring during 1992 and 1995-1998 for a total of 743 km and recorded 15 attacks on moose. Two of the attacks were successful (i.e. one successful hunt/372 km) and three moose were killed of which an older female (≥ 2 years) was killed by a 5-year-old male bear and two yearlings were killed in one occasion by a 9-year-old male bear. Adult male bears were followed for a total of 335.5 km and conducted nine attacks, two of which were successful (i.e. 2.7 attacks/100 km of

Table 1. Cause-specific mortality rates of radio-marked female and male moose > 1 year old calculated using the Kaplan-Meier (1958) method for estimating survival and cause-specific mortality rates in south-central Sweden during 1994-1997.

	Annual mortality rate (+ SE)	
	For females	For males
Mortality factor	133 moose years	47 moose years
Overall mortality	$0.185 (\pm 0.060)$	$0.295 (\pm 0.112)$
Hunting	$0.131 (\pm 0.054)$	$0.279 (\pm 0.112)$
Other mortality	$0.062 (\pm 0.040)$	$0.022 (\pm 0.042)$
Traffic accident	$0.024 (\pm 0.026)$	$0 (\pm 0)$
Train accident	$0.017 (\pm 0.022)$	$0 (\pm 0)$
Unknown	$0.015 (\pm 0.020)$	$0.022 (\pm 0.042)$
Bear predation	$0.008 (\pm 0.015)$	$0 (\pm 0)$

which 0.6/100 km were successful). On an individual basis, we found a mean of 4.54 attacks/100 km of tracks ($N = 14$, 95% CI = 0.42-8.66) and a mean of 1.48 killed moose/100 km (95% CI = 0-2.13). Adult female bears were followed for a total of 83.1 km and conducted five attacks, none of which were successful (6.0 attacks/100 km). On an individual basis, we found a mean of 3.16 attacks/100 km of tracks ($N = 8$, 95% CI = 0-6.39). Mann-Whitney ranked-sums tests showed no statistical difference between adult male and female bears in individual rates of attacks on moose ($T = 91.0$, $P = 0.973$) or individual kill rates ($T = 84.0$, $P = 0.603$). Subadult males were followed for 125 km and subadult females for 46 km, but neither group was observed to attack moose.

We necropsied 32 adult moose that were verified as killed by brown bears within our study area during 1995-1997. Brown bears tended to kill yearlings disproportionately to their occurrence, because yearlings made up 30% of the kills, but only 16% of the population (Cederlund & Wallin 1998; Fisher's exact test: $P = 0.08$). Among older moose, females were killed more often than males (88% of the killed adults, compared to 60% females and 40% males in this age group in the population; Fisher's exact test: $P = 0.024$).

Predation on adult moose was not distributed evenly throughout the year ($\chi^2_3 = 34.1$, $P < 0.001$; Fig. 1). Of the moose, 24 (75%) were killed during April-May; thus, adult moose were most prone to be killed during early spring (April) and during the moose calving season (May).

Discussion

Our study is the first study to report kill and predation rates on adult moose by brown bears

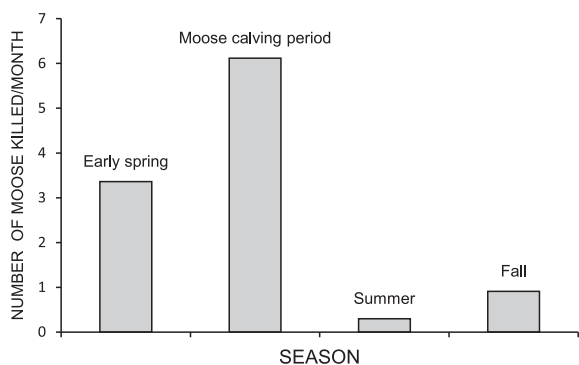


Figure 1. Seasonal brown bear predation on moose older than calves, given as the average number of moose verified as killed by brown bears per month in the study area in south-central Sweden during 1995-97. Early spring is 1 April - 15 May, moose calving period is 16 - 31 May, summer is 1 June - 31 August and fall is 1 September - 1 November.

outside North America and in an area without other moose predators as no other studies of mortality of radio-marked moose in areas holding bears in Eurasia have been published. We found that brown bear predation was an uncommon mortality factor for radio-marked adult moose in our study area. It was the least important mortality factor we recorded, accounting for only a 0.8% annual mortality rate for females and no observed mortalities for males. Our tracking results supported this and were consistent with Haglund's (1968) conclusion that bears were not generally effective predators on adult moose in spring. He recorded eight attacks on moose (none of them successful) by brown bears tracked for 503 km during spring in the mid-1960s in Sweden, which at that time had a much lower density of moose than during our study period. Although our spring tracking suggested that adult bears most often attacked adult moose in the spring and that only adult males were documented killing adult moose, there were no significant differences in attack and kill rates between individual adult male and adult female bears, perhaps resulting from our small sample sizes. Predation on adult moose may be locally important when snow conditions are favourable for bears (e.g. crusty snow). Hellgren (1967) reported that a medium-sized brown bear killed nine adult moose under favourable snow conditions in less than two weeks in Sweden, and Swenson et al. (2001) noted that a radio-marked four-year-old male bear killed five adult female moose during a spring in central Norway.

Kill rates on adult moose on our study area were in the lower part of the range previously reported for North American populations of brown bears.

Boertje et al. (1988) reported that adult brown bears killed on average 3-4 adult moose annually, and Ballard et al. (1990) reported that adult bears killed one adult moose per 44 bear days during spring and early summer. However, data presented by Larsen et al. (1989) suggest that each adult bear (> 5 years) killed about 0.5 adult moose annually in southwestern Yukon, which is similar to our estimated annual kill rates of moose by brown bears.

To our knowledge, we are the first to report that yearling moose tend to be more vulnerable to brown bear predation than adults, a pattern commonly reported for wolf predation (Ballard & Van Ballenberghe 1998). From North America, Boertje et al. (1988), Ballard et al. (1990) and Bertram & Vivion (2002) reported that adult moose are most often killed by brown bears during spring and during the calving season, which was also observed during our study in Sweden. Overall, rates of bear predation on moose indicate that bear predation had a relatively small effect on annual survival of yearling and adult moose in south-central Sweden during 1994-1997, which agrees with the conclusions of Gervasi et al. (2012).

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