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Predation by golden eagle *Aquila chrysaetos* on semi-domesticated reindeer *Rangifer tarandus* calves in northeastern Finnish Lapland

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Calf losses are an acute issue in Fennoscandian reindeer *Rangifer t. tarandus* management. We studied calf mortality in northeastern Finnish Lapland using 621 calves (304 in 1997 and 317 in 1998) marked with silent mortality transmitters and followed their survival during 2 July 1997 - 31 January 1998 and during 22 June 1998 - 31 January 1999. In total, we found 43 dead calves and investigated their causes of death. A Kaplan-Meier analysis indicated 91.5% survival during July-January in both study years. However, differences in the temporal distribution of survival between the two study years were found. A minimum of 53% of total mortality was attributed to predation, with golden eagle *Aquila chrysaetos* being the main predator. Mortality caused by golden eagle comprised 2.8 and 4.2% during the study periods in 1997/98 and 1998/99, respectively. Body weight of the calves at midsummer (all weights adjusted on 2 July) was a significant predictor for survival, whereas sex and pelt colour were not. We conclude that predation is a major source of calf mortality during July-January, and that golden eagle predation was prominent, especially during midsummer and in open alpine landscapes.

Key words: *Aquila chrysaetos*, landscape, mortality, predation, *Rangifer*, survival

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Two main factors influencing reproductive output and survival in ungulates are nutrition (Rognmo et al. 1983, Helle & Kojola 1993, Kojola et al. 1995, Kumpula et al. 1998, Kumpula et al. 2002) and predation (Bergerud & Ballard 1988, Björvall et al. 1990, Adams et al. 1995,

Linnell et al. 1995, Young & McCabe 1997, Nybakk et al. 2002, Norberg et al. 2005). The relative role of these two factors is spatially and temporally regulated by stochastic environmental conditions (e.g. climatic variables; Sæther 1997, Post & Stenseth 1999, Kumpula & Colpaert

2003, Tveraa et al. 2003) and local abundance of predators, varying from totally predator-free to multiple predator-prey systems. When present, predators contribute to the dynamics of ungulate populations (Skogland 1991), especially through offspring survival (Linnell et al. 1995). However, a compensatory relationship between food limitation and predation has been suggested, in which case the actual effect of predation on demography and population dynamics of ungulates may be limited (Tveraa et al. 2003).

Several studies have addressed the major role of large terrestrial carnivores on the neonate mortality of large and medium-sized ungulates (see review by Linnell et al. (1995)). In some studies, golden eagles *Aquila chrysaetos* have also been found to prey on juvenile ungulates such as semi-domesticated reindeer *Rangifer t. tarandus* (Nybakke et al. 1999), lambs *Ovis aries* (Bergo 1987, Warren et al. 2001) and even domestic calves *Bos taurus* (Phillips et al. 1996). Predation on adult reindeer has also been reported for golden eagles (Nybakke et al. 1999), although their diet consists mainly of smaller prey, such as grouse (Tetraoninae), hare (Leporidae) and other small mammals (Watson 1997, Sulkava et al. 1999). The current knowledge of the prey selection of golden eagle in northern Fennoscandia is mostly based on analyses of prey remains collected from nest sites (Tjernerberg 1981, Sulkava et al. 1999), and thus, is both temporally restricted and excludes the non-breeding portion of the eagle population.

According to local reindeer herders in northeastern Finnish Lapland, calf mortality between midsummer

ear-marking round-ups and subsequent winter round-ups (taking place in October-January) is extensive. Predation is assumed to account for a substantial part of this mortality. Brown bear *Ursus arctos*, wolverine *Gulo gulo*, lynx *Lynx lynx*, red fox *Vulpes vulpes* and golden eagle are all potential predators in the area. In this paper, we examine the factors affecting mortality among reindeer calves from the age of 2-6 weeks to 6-8 months, including the effect of landscape on predation risk.

Study area

Our study was conducted in the reindeer-herding cooperative of Lappi, managed by reindeer herders inhabiting the village of Vuotso, Finland (68°06'N, 27°08'E; Fig. 1). The total land area of the cooperative covers 4,002 km², and is the fourth largest among the 56 cooperatives in the Finnish reindeer husbandry. The area belongs to the northboreal vegetation zone (Ahti et al. 1968). The two main landscape types are alpine highlands in the northeast and boggy and flat woodland in the southwest (see Fig. 1). The study was carried out during two consecutive years in 1997 and 1998. In 1997, reindeer had access to the entire area, whereas in 1998, a pasture rotation fence (completed in late 1997) separated the area into two parts. The southwestern section was reserved for summer grazing and the northeastern for winter grazing (see Fig. 1). There were approximately 7,400 adult (> 1 year old) reindeer during both years, and we estimated that altogether 4,200 and 4,700 calves

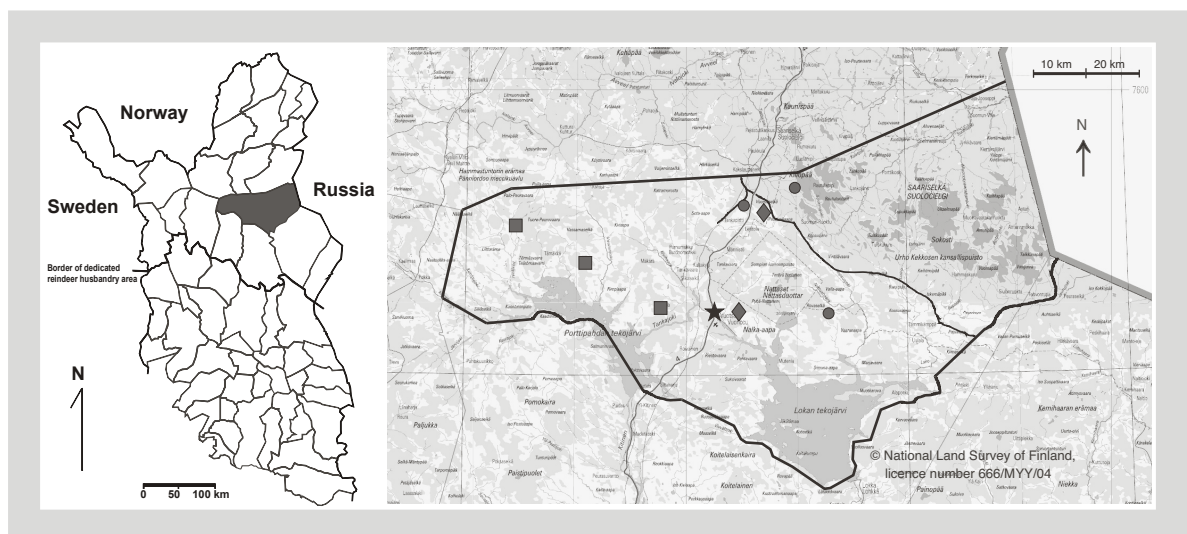


Figure 1. Study area, i.e. the reindeer-herding cooperative of Lappi, where reindeer calves were fitted with radio-collars at the round-up sites in 1997 and 1998 (■) in 1997 only (●) and in 1998 only (◆). The village of Vuotso is shown (★). In 1997, calves had access to alpine highland areas in the northeastern section of the study area, whereas in 1998, access was impeded due to a new pasture rotation fence which was completed in November 1997.

were born in 1997 and 1998, respectively. According to the Finnish Forest and Park Service (T. Ollila, pers. comm.), 12-15 golden eagle territories (breeding pairs) were occupied in the study area during both years. Most territories were situated in the northeastern alpine highlands.

Material and methods

In 1997 and 1998, we fitted 304 and 317 calves (ca 7% of all calves in the study area), respectively, with mortality indicating radio-transmitters (Televilt Inc., Lindesberg, Sweden; frequency 230 MHz) attached to expandable collars (Björvall & Franzén 1981). Marking took place during the first half of July in 1997 and the last week of June and the first week of July in 1998. Consequently, calves were 2-6 weeks old at the time of marking. The study period was terminated in late January of the following year, as the majority of calves were selected for slaughter during the winter round-ups conducted during October-January. In addition to radio-collared calves, we marked 92 calves in 1997 and 189 calves in 1998 with plastic ear-tags to control for the effect of radio-collaring on growth and survival. Each calf was sexed and weighed, and pelt colour was recorded with a five-step scale (1 = white, 2 = light, 3 = normal brown, 4 = dark brown and 5 = black). Subsequent to fitting calves with radio-collars, radio-tracking both from the air (fixed-wing aircraft and helicopter) and by ground triangulation was carried out to locate dead calves. Tracking flights were performed in 2-5 day intervals until the end of September. During October-December, we conducted 1-2 flights per month, supplemented with additional ground triangulations. The width of the scanning strip was approximately 50 km in flat bog and woodland areas, and 20-30 km in the more rugged and alpine northeastern part of the cooperative. Flight altitude during tracking was 500-1,000 m a.s.l.

After locating the activated transmitters from the air, we found them at ground level using hand receivers (Televilt RX-8910®, Televilt Inc., Lindesberg, Sweden, and hound radar modification by Tracker Inc., Oulunsalo, Finland). Cause of death was first investigated in the field (e.g. evidence supporting presence of predator/scavenger species, such as tracks, scats and feathers/downs) and then supported by necropsies conducted in the laboratory. All eagle feathers found near the carcass were collected and subsequently analysed to assess the age class of the individual eagle possibly responsible for the kill. The lines of drop-off feathers observed at some sites were deduced to have been formed in the course of the killing event,

and were thus regarded as evidence of an eagle attack. However, the presence of haemorrhages and perforations, both in the skin and soft tissues of the dead calf, were critical for determining the cause of death when depredation was suspected (Wiley & Bolan 1971, Björvall et al. 1990). Of the 43 calves found dead combined for both years, 36 (84%) were subjected to post-mortem examination. In seven cases, too few or no carcass remains were left for necropsy. Of the 36 necropsies, 53% were conducted in cooperation with the National Veterinary and Food Research Institute, while project staff participated in assessment of all cases. If the combined evidence from the field site and the necropsy was inadequate, for example due to late discovery of the carcass, the cause of death was classified as unknown.

Statistical analysis

We calculated daily survival estimates for the radio-collared calves using the Kaplan-Meier product/limit method (Kaplan & Meier 1958, Cox & Oakes 1984, Hosmer & Lemeshow 1999) modified by Pollock et al. (1989). This method allows a staggered entry of study animals at different times of the study period and accounts for daily changes in the number of animals at risk. We used the computer program 'Kaplan-Meier survivorship analysis version 1.0' (Pollock et al. 1989) to obtain daily and total survival estimates for the study periods. As marking began earlier in 1998 than in 1997, we first calculated the survival estimates for the comparable time periods (2 July - 31 January) in both study years, and then also for the total period between 22 June 1998 and 31 January 1999. The daily survival estimates were used to present survivorship curves between July and January in both years. For calculating monthly survival estimates, cause-specific mortality rates and 95% confidence limits, we used the program 'Micromort version 1.3' (Heisey & Fuller 1985). Differences in monthly survival rates between the two consecutive study years were tested using the program 'Contrast' (Sauer & Williams 1989).

Calculation of survival estimates was based on documented cases; i.e. in the survival analysis, we included only the calves that 1) were found dead, 2) had dropped their radio-collars during the study or 3) were recovered in the winter round-ups (survivors) when radio-collars were eventually taken off. In case a calf dropped its radio-collar during the study, that individual was excluded from survival analysis at the date when the collar was found. Although the observation time for the calves that dropped their collars ($N = 8$ in 1997/98 and $N = 56$ in 1998/99) was incomplete regarding the total study period (see Hosmer & Lemeshow 1999), we know that these calves survived at least until the day their collar was

dropped. Furthermore, 59% of the calves that lost their collars in 1998/99 were later recorded in the winter round-ups (by their ear-tags). We assume that the majority of the remaining 41% also survived, but we were unable to detect them in the round-ups by their ear-tags only. In total, we controlled for 290 calves in 1997/98 (95.5% of all radio-collared) and 296 in 1998/99 (93.4%).

In addition to estimates based on documented cases, we also calculated the minimum and maximum survival estimates as suggested by Heisey & Fuller (1985) and Pollock et al. (1989). For minimum survival, all non-documented calves ($N = 14$ in 1997/98 and $N = 21$ in 1998/99) were assumed to be dead at the end of the year (31 December), whereas for maximum survival, all were assumed to be alive. It is important to note that assuming that all missing radio-collared calves are dead has a greater effect on the survival estimate than assuming that missing calves are alive (Heisey & Fuller 1985, Pollock et al. 1989).

As we weighed and marked calves during 13 (2–15 July) and 18 (22 June–10 July) day periods in 1997 and 1998, respectively, we aimed to adjust the weight of all calves to correspond to the same day (2 July). To get the daily weight increase during the calf-marking period, we regressed the weights for radio-marked, ear-tagged and all weighed calves in 1997–1998 on weighing date. However, despite the relatively large number of calves weighed ($N = 394$ in 1997 and $N = 506$ in 1998), the regression models only explained 5–33% of the variation in weight gain within different groups and years, the average daily weight increase ranging within 197–353 grams. Thus, we decided to use the average daily weight gain of 270 grams as suggested by Timisjärvi et al. (1982), and adjusted the weight of a calf according to the number of days deviating from the 2 July.

To evaluate random selection of the radio-marked calves, we compared the average body mass of radio-collared calves with that of calves marked with ear-tags only. To control for possible effects of radio-collars on growth and survival, we compared the daily and absolute growth (Equations 1 and 2) of radio-collared and ear-tagged calves from the time of marking to slaughtering (only data from 1998 were used as slaughter data for ear-tagged calves in 1997 were not available).

$$\text{Daily growth rate (kg/day)} = (M_s - M_m)/(D_s - D_m) \quad (1),$$

$$\text{Absolute growth (kg)} = M_s - M_m \quad (2),$$

in which M_s is live weight at time of slaughtering (= slaughter weight * 2), M_m is live weight at marking (adjusted on 2 July), D_s is cumulative date of slaughtering

(from 1 May) and D_m is cumulative date of marking (from 1 May).

We tested the effects of adjusted weight at ear-marking, sex, pelt colour, study year and the possible interaction between weight and sex on calf survival probabilities using stepwise logistic regression with enter command (SPSS 1993). We also compared the weights of the calves killed by golden eagles with the weights of calves that a) survived and b) died from any cause other than eagle predation. We compared means using ANOVA (one-way) when variances did not differ between groups and t-test if there was a significant difference in variances between groups (Levene's test for the homogeneity of variances). All statistical tests were two-tailed and considered significant at $P < 0.05$.

Results

For 1997/98 and 1998/99 combined, 43 out of 621 radio-collared calves were recovered dead. Survival of radio-collared calves between 2 July and 31 January was 0.915 (SE = 0.029) in the 1997 cohort (Table 1A, Fig. 2) and 0.914 (SE = 0.036) in the 1998 cohort (see Fig. 2). In 1998, survival during the total study period starting from 22 June was 0.877 (SE = 0.041; see Table 1B). Indeed, survival was lowest during the 9-day period in June 1998, when altogether five radio-collared calves were found dead (see Table 1B). The maximum survival estimates during both study years differed only 0.4–0.5% from the estimates for controlled (i.e. documented) calves, whereas the minimum estimates differed 6% in 1997/98 and even 17–18% in 1998/99 (Table 2). When comparing the monthly survival estimates between the two years, survival was significantly lower in August 1997 ($\chi^2 = 5.609$, df = 1, $P = 0.018$) and slightly lower in September

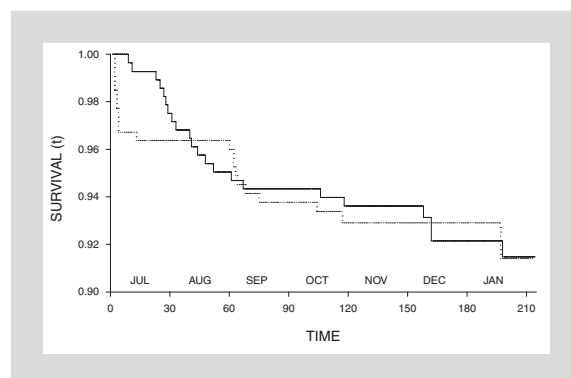


Figure 2. Survivorship curves for radio-collared reindeer calves in northeastern Finnish Lapland in cohorts of 1997 (—) and 1998 (.....), related to time expressed as days after 2 July (day 1 = 2 July).

Table 1. Monthly survival estimates and mortality agents of radio-collared reindeer calves in northeastern Finnish Lapland during 2 July 1997 - 31 January 1998 (A) and during 22 June 1998 - 31 January 1999 (B). After marking in summer 1997, calves had free access to the entire area of the cooperative, whereas in 1998 access to mountainous habitat was impeded during study period.

A) Period: 2 July 1997 - 31 January 1998				Interval rates			
Interval	No. of days	Radio days	Survival	Mortality			
				Eagle (N)	Other predation (N)	Other causes (N)	Unknown (N)
July	30	7594	97.3	0.0 (0)	0.0 (0)	0.0 (0)	2.7 (7)
August	31	8406	97.1	2.2 (6)	0.0 (0)	0.0 (0)	0.7 (2)
September	30	7999	99.6	0.0 (0)	0.4 (1)	0.0 (0)	0.0 (0)
October	31	8197	99.2	0.8 (2)	0.0 (0)	0.0 (0)	0.0 (0)
November	30	7584	100	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
December	31	5648	98.4	0.0 (0)	1.6 (3)	0.0 (0)	0.0 (0)
January	31	3800	99.2	0.0 (0)	0.0 (0)	0.8 (1)	0.0 (0)
Total period	214	49225	91.5 ^a	2.8 (8)	1.9 (4)	0.7 (1)	3.4 (9)
95% confidence limits:			Lower	87.5	0.9	0.04	0.0
			Upper	94.8	4.8	3.7	2.2
B) Period: 22 June 1998 - 31 January 1999							
June ^b	9	1065	95.9	1.7 (2)	0.8 (1)	1.7 (2)	0.0 (0)
July	31	7868	97.7	1.2 (3)	0.4 (1)	0.4 (1)	0.4 (1)
August	31	8192	99.6	0.0 (0)	0.0 (0)	0.0 (0)	0.4 (1)
September	30	7541	97.6	1.6 (4)	0.0 (0)	0.4 (1)	0.4 (1)
October	31	6978	99.1	0.0 (0)	0.0 (0)	0.9 (2)	0.0 (0)
November	30	5392	100	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
December	31	3058	100	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
January	31	2039	98.5	0.0 (0)	0.0 (0)	1.5 (1)	0.0 (0)
Total period	224	42133	87.7 ^a	4.2 (9)	1.2 (2)	4.6 (7)	1.1 (3)
95% confidence limits:			Lower	84.0	1.3	0.0	0.8
			Upper	94.1	7.2	3.0	8.3

^a Survival estimate for the total study period calculated using Kaplan-Meier survivorship analysis ver. 1.0 (Pollock et al. 1989), which takes into account the daily changes in calves at risk. Interval rates and 95% confidence limits derived from monthly data were processed with Micromort version 1.3 (Heisey & Fuller 1985).

^b In 1998, the first calves were radio-collared on 22 June. Thus, there were only nine days within the June interval.

1998 ($\chi^2 = 3.622$, $df = 1$, $P = 0.057$; see Fig. 2). There was no annual difference in survival for any other month or for the entire study period.

The average adjusted (2 July) weight (\pm SD) of the calves during midsummer ear-marking was significantly lower in 1997 (13.0 kg; SD = 2.6 kg, $N = 394$) than in 1998 (13.5 kg; SD = 2.5 kg, $N = 506$; $t = -3.046$, $df = 819$, $P = 0.002$). The average weight of the radio-tagged study calves did not differ from the average weight of calves marked with plain ear-tags in the pooled data for 1997/98 ($F = 1.743$, $df_1 = 1$, $df_2 = 898$, $P = 0.187$) or in

1998 ($F = 1.847$, $df_1 = 1$, $df_2 = 504$, $P = 0.175$), whereas in 1997, radio-collared calves weighed significantly less (12.8 kg; SD = 2.6 kg, $N = 302$) than ear-tagged calves (13.7 kg; SD = 2.6 kg, $N = 92$; $F = 9.476$, $df_1 = 1$, $df_2 = 392$, $P = 0.002$). Radio-collars did not affect the growth of the calves, as there was no statistical difference in either daily or absolute weight gains between radio-collared and ear-tagged calves. The daily weight gain for radio-collared calves was 0.149 kg (SD = 0.047 kg, $N = 115$) and for ear-tagged calves 0.147 kg (SD = 0.046 kg, $N = 64$), while absolute weight gain was 20.5 kg

Table 2. Minimum and maximum survival estimates (\pm SE) for radio-collared calves in northeastern Finnish Lapland during the two consecutive study years. In 1998, tagging started 10 days earlier than in 1997, so estimates for 1998 were calculated both for the same period as in 1997 and for the total study period. In minimum survival estimates all radio-collared calves missing were assumed to be dead, whereas in maximum estimates all missing calves were assumed to be alive.

Period	Radio-collared calves missing	Minimum survival (\pm SE)	Maximum Survival (\pm SE)
2 July 1997 - 31 January 1998	14 (4.6%)	0.855 (0.036)	0.919 (0.029)
2 July 1998 - 31 January 1999	21 (6.6%)	0.730 (0.050)	0.919 (0.035)
22 June 1998 - 31 January 1999	21 (6.6%)	0.703 (0.051)	0.885 (0.040)

(SD = 4.2 kg, N = 115) in radio-collared calves compared with 20.8 kg (SD = 4.6 kg, N = 64) in ear-tagged calves.

According to the stepwise logistic regression, the adjusted midsummer weight of a calf significantly predicted the survival probability of radio-collared calves (Wald = 11.723, df = 1, $P = 0.001$), whereas sex (Wald = 0.405, df = 1, $P = 0.525$), pelt colour (Wald = 2.266, df = 4, $P = 0.687$) or study year (Wald = 0.175, df = 1, $P = 0.676$) did not. The weights of male and female calves did not affect survival differently, as there was no significant interaction between weight and sex on calf survival (Wald = 0.540, df = 1, $P = 0.463$). From measurements taken during radio-collaring in midsummer, calves that survived until winter round-ups weighed on average 13.3 kg (SD = 2.6 kg, N = 542), while those that did not survive until winter weighed on average 11.6 kg (SD = 2.4 kg, N = 41).

Predation comprised 55 and 52% of total mortality (predation out of total number of dead radio-collared calves recovered) in 1997/98 and 1998/99 (see Table 1), respectively. Golden eagle was found to be the single most significant mortality factor in the study area, comprising at least 40% of total mortality and 74% of predation (combined data from 1997/98 and 1998/99). Other predation comprised 14% of the total mortality, and was caused by lynx (7% of total), brown bear (5% of total) and red fox (2% of total). Causes not associated with predation comprised 19% of total mortality, and included traffic accidents (N = 1 in 1997 and N = 2 in 1998), other accidents (N = 2 in 1998), pathological condition (N = 1 in 1998) and stress caused by the combined effects of ear-marking, heat and insect harassment (N = 2 in 1998). In 28% of the dead calves recovered, the cause of death remained unknown, a fact that has to be accounted for in the distribution of mortality factors. Excluding the deaths with unknown cause (N = 12), predation comprised 74%, and eagle predation 55% of the total mortality. During July-January, calf mortality caused by golden eagle comprised 2.8 and 2.7% in 1997/98 and 1998/99, respectively (see Table 1).

The adjusted midsummer weight of calves killed by golden eagles (12.6 kg; SD = 2.7, N = 17) was on average 0.8 kg less than that of calves that survived until winter round-ups ($F = 1.425$, df₁ = 1, df₂ = 557, $P = 0.233$). When comparing the original (non-adjusted) weights at the time of ear-marking, the calves preyed upon by golden eagle weighed on average 12.0 kg (SD = 3.4 kg, N = 17), and were 1.6 kg lighter than calves that survived until the winter round-ups (13.6 kg; SD = 2.8 kg, N = 542; $F = 5.047$, df₁ = 1, df₂ = 557, $P = 0.025$). The average adjusted weight of calves that succumbed due to all

other causes combined (besides eagle predation) was statistically lower (11.0 kg; SD = 2.1 kg, N = 24; $F = 4.764$, df₁ = 1, df₂ = 39, $P = 0.035$) than the average weight of calves killed by golden eagles.

Most calves killed by golden eagles were found in the northeastern highland area (N = 6 of 8) in 1997, while just two eagle-killed calves (25% of all eagle kills) were found in the western bog and forested areas. In 1998, the northeastern section was separated from the rest of the study area by pasture rotation fencing to prevent reindeer from grazing there during summer (see Fig. 1). Consequently, most kills were concentrated close to the fence adjacent to open alpine landscape and occurred either directly after marking or later in September (see Table 1B).

Discussion

The mortality curve in most mammal species is typically U-shaped, with the neonates and juveniles suffering the highest mortality, which then gradually decreases towards the prime-aged individuals at the bottom of the 'U' (Caughley 1966). Indeed, several studies on reindeer and caribou *Rangifer* sp. demonstrate that calf mortality is generally highest within the first few days postpartum, after which mortality decreases considerably (e.g. Eloranta & Nieminen 1986, Whitten et al. 1992, Adams et al. 1995). Since the majority of semi-domesticated reindeer calves in northern Finland are born in May (peak calving taking place on 15-25 May; Eloranta & Nieminen 1986), the mortality pattern between parturition and midsummer was not accounted for in our study.

A great deal of early calf mortality may be associated with the body size and condition of parturient females (Eloranta & Nieminen 1986, Lenvik & Aune 1988, Tveraa et al. 2003), both of which are retrospectively affected by resource limitation through density-dependent and/or density-independent processes (Skogland 1985, Helle & Kojola 1993, Saether 1997). However, it has been shown that the importance of extrinsic factors (e.g. climate and food availability), as well as factors such as female condition on calf survival, decrease after calves have survived their first few weeks post-calving (Adams et al. 1995, Tveraa et al. 2003).

In our study, calves were minimum two weeks old when radio-collared. Therefore, we assume that the factors related to climate or food availability prior to calving did not play a significant role in our survival data. Interestingly, however, we found that the lowest survival estimate was associated with the 9-day initial period at the end of June 1998, followed by a gradual increase in

survival during subsequent months (see Table 1B and Fig. 2). Though comparable to mammalian mortality patterns in general, the high mortality observed in late June (in total five dead calves/nine days) was influenced by the two calves that succumbed due to exhaustion from the combined stress associated with ear-marking, heat and insect harassment. The cause of death for these calves may therefore be considered partly anthropogenic. Three other calves found in June 1998 were killed by golden eagle ($N = 2$) and brown bear ($N = 1$).

In 1997, calves had access to alpine highland area in the northeastern section of the cooperative, whereas in 1998, access was impeded due to a new pasture rotation fence (see Fig. 1). This was probably reflected in the survivorship curves from the two study years, especially in July and August (see Fig. 2), when reindeer attempt to find relief from insect harassment by seeking alpine or otherwise windy and open areas (Helle & Tarvainen 1984, Mörschel 1999, Colman et al. 2003, Weladji et al. 2003). In 1997, the radio-collared calves entered the alpine habitat directly after release from the ear-marking corrals and were consequently exposed to predation by golden eagle, which eventually comprised the major part of their summer mortality. In addition to the calves determined as golden eagle kills in 1997 ($N = 8$), the same number of calves were probably killed by eagles, but were classified as having died from unknown causes due to lack of evidence (see also Nybakk et al. 1999). However, the observations for these cases suggested a typical prey pattern of the golden eagle. If all potential golden eagle kills from the 1997 cohort were included, then the calf mortality caused by eagles would comprise in total 5.9% (73% of total mortality) for 1997/98, whereas eagle-caused mortality would be 2.8% if only the cases with adequate, substantiated evidence were included (see Table 1A). In 1998, when calves could not enter the alpine highlands, mortality ceased for nearly one and a half months from mid-July to the end of August, the next dead calves being found during the first week of September (see Table 1B and Fig. 2).

The observed rates and temporal distribution of eagle-caused mortality during the two study years suggest that access to alpine highlands was associated with an increased risk of golden eagle predation. In a mortality study conducted in central Norway, Nybakk et al. (1999) also found that most of the radio-collared reindeer killed by golden eagles were discovered in open alpine terrain. Similar risks related to open landscapes have also been demonstrated for lambs of free-ranging domestic sheep in northern Norway (Warren et al. 2001). In addition to the fact that most of the golden eagle territories were situated in the northeastern part of our study area, the rug-

ged and open terrain formed an ideal hunting habitat for the eagles, irrespective of individual eagles' breeding status (Watson 1997). The latter was demonstrated by the fact that in several golden eagle kills, the feathers found at the scene indicated that the individuals responsible for the kills were subadults.

Predators killed a minimum of 55 and 52% of all calves found dead in 1997/98 and 1998/99, respectively. Including cases in which the probable cause of death was predation, the potential figures in our study totalled 91 and 62% for 1997/98 and 1998/99, respectively. Similar proportions of predation in reindeer and caribou calf mortality have been reported in radio-telemetry studies carried out in Sweden, Norway and Alaska (Björvall et al. 1990, Adams et al. 1995, Kvam et al. 1998, Nybakk et al. 2002). Based on a review of 111 papers and reports on neonatal (first summer) mortality of 10 species of northern ungulates, also Linnell et al. (1995) concluded that predation is the most significant factor affecting the mortality of neonates in environments where predators occur. However, the relative importance of predation and different predator species as mortality factors varies greatly in time and space, and with predator densities. In our study area, we could not observe the early calf mortality between parturition and midsummer, during which predation by brown bear is usually peaking (Adams et al. 1995, Young & McCabe 1997, Norberg et al. 2005). Thus, our results do not illustrate the full mortality pattern between parturition and subsequent winter.

In addition to our study, only Kvam et al.'s (1998) study in Nord-Trøndelag, central Norway, found predation by golden eagle to be the main cause of mortality. According to Kvam et al. (1998), reindeer calves killed by golden eagles comprised 40% of total calf mortality. Their total mortality rate (8.1%) was also relatively similar to the one found in our study. In another Norwegian study (Nybakk et al. 1999), golden eagles killed 1-2% of all radio-collared calves, which was less than what was found in our study (3-4%). Furthermore, the share of golden eagle predation in the total mortality was substantially smaller (5-7%) compared with the results of our study (at least 40%) and that of Kvam et al. (1998), whereas other large carnivores (lynx and wolverine) accounted for most of the mortality (Nybakk et al. 1999, 2002).

Several studies (e.g. Haukioja & Salovaara 1978, Elovanta & Nieminen 1986, Tveraa et al. 2003) show that the body mass of reindeer calves at calving and during summer is associated with survival. Our results concur with findings that body mass is of crucial importance for the future survival of a calf. Although we could not associate the tagged calves with their mothers, we assume

that the mothers of the calves that succumbed were both younger and smaller than the mothers of the calves that survived. The association between maternal life-history traits (age and size) and calf-rearing success (mediated by calf body mass) has been extensively studied in many ungulate species (see e.g. Eloranta & Nieminen 1986, Ozoga & Verme 1986, Lenvik & Aune 1988, Tveraa et al. 2003). However, we did not find any direct documentation in the literature on the relationship between maternal life-history traits and antipredator behaviour, a feature rarely pointed out in survival studies (but see Lingle & Pellis 2002, Jarnemo 2004). Nevertheless, we assume that the age and size of the mother, and hence calf body mass, are also related to mothers' experience and ability to avoid predation and to defend offspring against predators.

In most studies addressing golden eagle predation on livestock, depredated calves have been shown to weigh less at marking than surviving calves (e.g. Nybakk et al. 1999, Norberg et al. 2005). However, the time of tagging and weighing (i.e. marking) appears to influence the significance of the weight difference between calves that survived and calves that were depredated, leading to a more complex association between calf body mass and predation risk. In a radio-collar study conducted in central Norway (Nybakk et al. 1999), calves were marked on 6 August 1995 and 23 July 1996, and the calves subsequently killed by golden eagles weighed on average 4.1 and 2.7 kg less than surviving calves at marking for each year, respectively. In our study, the weights of calves were adjusted to 2 July, and the weight difference (eagle kills vs survivors) was only 0.8 kg. On the other hand, in subsequent calf mortality studies conducted in the northern part of the Finnish reindeer herding area during 1999–2004, the average body weights at marking (weights also adjusted to the beginning of July) were on average 3.5–5.8 kg higher than in our study. Due to the higher weights at marking, the calves subsequently killed by golden eagles weighed on average 3.8–6.3 kg less than survivors, the differences being statistically significant (Norberg et al. 2005).

Accordingly, it seems apparent that when average calf size is larger, depending on either the time of marking or annual as well as spatial variation in calf body masses, golden eagles have to select for smaller calves disproportionately, while within a sample of smaller average calf size, selection may not be as strong. The suggested association between average prey body mass and selectiveness of golden eagle is supported by Temple (1987), who stated that “the degree to which substandard individuals of a particular prey species are taken disproportionately by a predator seems to be a direct function of

how difficult it normally is for the predator to capture and kill individuals of that species”. In addition to all summer months, we also found eagle-killed calves in September and October, when the body mass of reindeer calves in our study area was approximately 40 kg. These findings concur with those of Bergo (1987), who suggested that golden eagle is capable of killing prey individuals of up to 50 kg of body mass. Furthermore, in a study by Nybakk et al. (1999) three 60–70 kg adult reindeer (5–9 year old females) killed by golden eagle were also found.

When comparing the weights of eagle-killed calves with those of calves that died from any other cause, we found that eagle-killed calves weighed significantly more than other dead calves. This, together with the non-significant 0.8 kg weight difference between the adjusted body masses of survivors and eagle-killed calves, also supports the conclusion that in our study, golden eagles did not prey on calves by significantly disproportionately selecting for substandard individuals. We also conclude that access to alpine highlands affected the risk of predation by golden eagle, and subsequently the temporal survival distribution and mortality in our study area. In general, our study confirmed earlier findings on the major role of predation in the mortality of semi-domesticated reindeer calves. We also emphasise the relative importance of golden eagle as a mortality factor in the northern part of the Finnish reindeer herding area, where the proportion of open alpine landscape is higher than in the more southern reindeer management areas in Finland.

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