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Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland

Ilpo Kojola[1]*, Otso Huitu[2], Katri Toppinen[3], Kalevi Heikura[3], Samuli Heikkinen[1] and Seppo Ronkainen[4]

[1] Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, Tutkijantie 2 A, FIN-90570 Oulu, Finland
[2] University of Turku, Department of Biology, FIN-20014 University of Turku, Finland
[3] University of Oulu, Department of Biology, Zoological Museum, Box 3000, FIN-90014 University of Oulu, Finland
[4] Finnish Game and Fisheries Research Institute, Taivalkoski Game and Fisheries Research, Ohtaojantie 19, FIN-93400 Taivalkoski, Finland

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Abstract

It is generally accepted that predation by wolves *Canis lupus* is one of the major factors limiting densities of woodland caribou *Rangifer tarandus caribou* in North America. Conversely, little is known about the role of European wild forest reindeer *R. t. fennicus* as wolf prey, or about the influence of wolf predation on populations of this rare subspecies. This relationship was examined in east-central Finland, where wild forest reindeer coexist with moose *Alces alces* at a numerical ratio of *c*. 1 reindeer to 1.5 moose. During the study, moose were clearly the primary prey of wolves. Reindeer were, however, an important part of wolf diet in summer, autumn and early winter, when their remains comprised roughly 20–50% of all food items identified in wolf scats. Wolves exhibited a slight preference for reindeer over moose as prey during early winter (November–December) when the reindeer were moving towards their wintering ranges. Virtually no reindeer were killed by wolves during midwinter (January–March). This held also for a pack whose territory was located in the middle of the wintering range of reindeer, where reindeer outnumbered moose during the winter months. After the approximate ratio of wolves to reindeer increased from 0.004 (1998) to 0.02 (2000), wolf predation became the most common source of mortality (50%) for reindeer. The annual net increase in the reindeer population decreased from 13% to 7% because of increased wolf predation. The results indicate that wolf predation was an important factor limiting reindeer population growth. Wolves were, however, unable to prevent entirely the number of reindeer from increasing, partly owing to behavioural traits used by reindeer during winter and calving times.

Key words: *Rangifer tarandus*, *Canis lupus*, predation, Finland

INTRODUCTION

Populations of sedentary woodland caribou/wild reindeer *Rangifer tarandus* have been declining in many areas both in North America and Eurasia (Bergerud, 1988; Edmonds, 1991; Seip, 1992; Quellet, Ferron & Sirois, 1996; Danilov *et al*., 1998). It is generally accepted that wolf predation is one of the main factors limiting the growth of populations of woodland caribou in North America (Bergerud & Eliot, 1986; Bergerud, 1988; Rettie & Messier, 2000). Predation on caribou populations has been observed to intensify following increasing wolf population sizes (Bergerud & Ballard, 1988). Increasing wolf numbers, on the other hand, have been linked to increasing densities of moose, which in turn are favoured by habitat disturbance from logging (Bergerud & Ballard, 1988; Seip, 1992; Heikkilä & Härkönen, 1996; Rempel *et al*., 1997).

*All correspondence to: I. Kojola.
E-mail: ilpo.kojola@rktl.fi

Reindeer and moose are the recent Holocene ungulate species in the midboreal coniferous zone of north-western Europe (Okarma, 1995; for vegetation zones see Ahti, Hämet-Ahti & Jalas, 1968). In Finland, wild forest reindeer became extinct in the early 1900s, but reappeared in the late 1950s by expanding their population range into east-central Finland from Russian Karelia (Montonen, 1974; Heikura, Pulliainen *et al*., 1985). In 2001, 1800 wild forest reindeer *R. t. fennicus* were estimated to exist in east-central Finland (K. Heikura, 2003, pers. obs.)). At present, the majority of wild forest reindeer of Finland and Russian Karelia (Hakala *et al*., 1996) inhabit Finland (K. Heikura, pers. comm.).

Large herbivores are the primary prey of wolves in northern Europe (Pulliainen, 1965; Pulliainen, 1974; Olsson *et al*., 1997; Gade-Jørgensen & Stagegaard, 2000). When moose is the only wild ungulate, they may constitute $>90\%$ of the biomass ingested by wolves (Gade-Jørgensen & Stagegaard, 2000). Practically nothing is known about the role of European wild reindeer as

wolf prey, or about the role of wolf predation in the population dynamics of this deer. Among 30 dead wild forest reindeer examined during the 1970s in east-central Finland, only two were identified as being killed by wolves (Pulliainen, 1980*a*). Wolves were, however, rare at that time (Pulliainen, 1980*b*). Here we report on a study of wolf predation on wild forest reindeer in the same area, where the subspecies currently coexists with moose and where the number of wolves increased substantially during the late 1990s. Population trends of wild forest reindeer under different rates of wolf predation are examined, and seasonal differences in wolf predation on reindeer and moose for the identification of prey species is considered. The results are discussed in the context of the efficiency of anti-predator behavioural traits adopted by reindeer.

METHODS

Study area and species

Our 8000-km^2 study area was located in the province of Kainuu, east-central Finland (Fig. 1), and belongs to the mildly continental part of the mid-boreal coniferous forest zone (Ahti *et al*., 1968). The topography is flat, with elevations (a.s.l.) ranging from 160 to 307 m. Forests cover *c*. 80% of the land area. Lakes and swamps are common; 93% of forested land area is commercial forest, and about half of the swamps have been drained. Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* are the dominant tree species. As a result of extensive logging, particularly during the 1970s and 1980s, young successional mixed forests are common. The mean density of humans is 2 people km^{-2}, but < 1 km^{-2} within wolf territories. Permanent snow usually appears in mid-November and melts in early May. Snow depth usually exceeds 80 cm and peaks in March.

Wild forest reindeer (hereafter reindeer) and moose are the 2 most numerous ungulate species in the area (Okarma, 1995). The mean density of moose in the study area was estimated by the local Game Management District, using reports given by hunters, as 375 moose/1000 km^2 before and 250 moose/1000 km^2 after the hunting season, without remarkable differences between the study years (Kojola, 2000) The mean density of reindeer in the Finnish part of the distribution range was *c*. 200/1000 km^2. In January–March, as reindeer aggregated into wintering ranges, densities rose to 700–900 individuals/1000 km^2.

Reindeer were counted from a helicopter in 1996, 1999 and 2001. These surveys were each performed within a week in late February and early March. The counts were based on preliminary information collected by the local Game Management District on the location of the main herds. The route was designed to cover the whole region where reindeer were present. Sightings were recorded using a GPS navigator and a computer connected to a map plotter. The total area was divided into sub-areas that could be scanned in 2–3 h. The distance between adjacent sighting lines was *c*. 500 m. Flight speed was 50 knots and altitude 100 m.

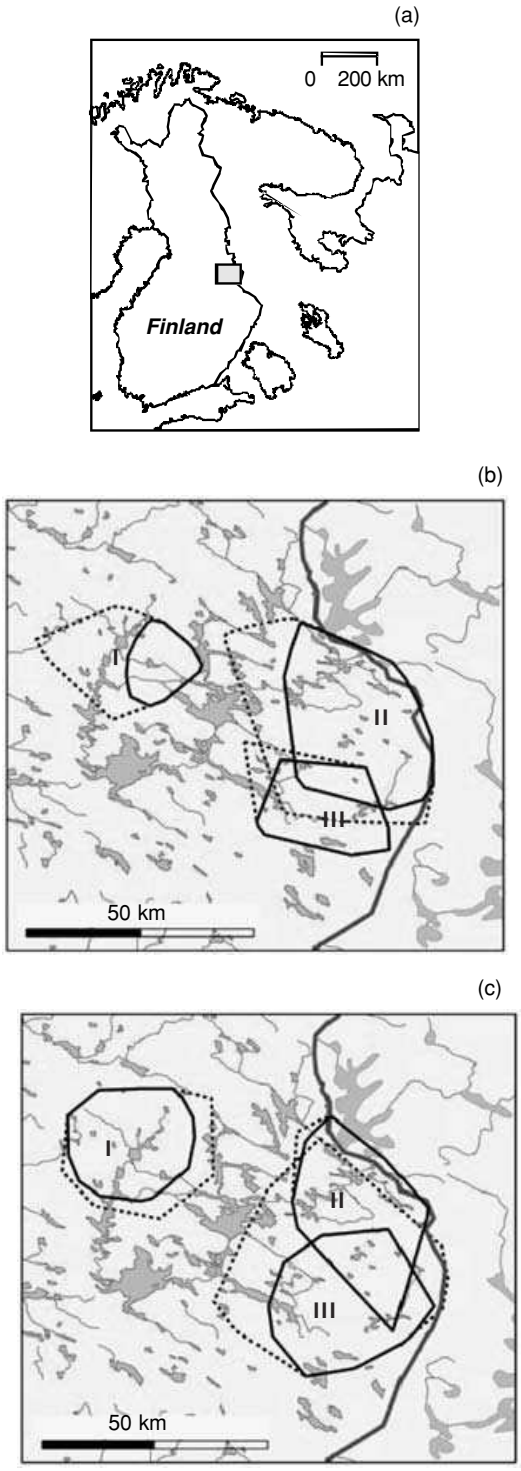

Fig. 1. Location of study area (a) (shaded) and territories of wolves *Canis lupus* in study area: (b) 1999; (c) 2000. Home ranges as 80% (solid line) and 100% (dashed line) minimum convex polygons.

Eight wolves from the 3 study packs (all 3 alpha couples and 2 pups) were radio-collared in 1998–2000. The wolves were captured using snowmobiles in February–March when the snow was soft and at least 80 cm deep. The

snowmobiles were driven alongside wolves, which were captured using a neckhold noose attached to a pole. The restrained animals were put in a wooden box strengthened with metal grating from the outside and with doors at both ends. They were kept for 30 min before an anaesthetic (a mixture of medetomine and ketamine) was injected intramuscularly (Jalanka & Roeken, 1990). Once the wolf was radio-collared, marked with ear-tags and measured for size parameters, it was put back into the box. After an antagonist (atimepazole) was injected, the wolf was allowed to recover before release. After the study period each wolf was either recaptured and equipped with a collar with drop-off option or they were shot in legal licensed-based wolf hunting performed in the area during 2001–2002. No injury was inflicted to wolves as a result of our study. All radio-collared wolves were located regularly throughout the year, 2–5 per week by means of ground-tracking.

Dietary analyses

During radio- and snow-tracking in 1998–2000, a total of 467 fresh wolf scats were collected. Scats were frozen until analysis. Before analysis, scats were autoclaved under 1 bar pressure to kill zoonotic parasites. The scats were then washed through a sieve with a mesh size of 0.5 mm to retain macro-components for further analysis. The micro-components (< 0.5 mm) were discarded as insignificant for the analysis of wolf diet. The analysis of food types in the remaining macro-components of scats was based on the identification of mammalian guard hairs to species level using the technique described by Kennedy & Carbyn (1981), and by means of reference hairs provided by the Finnish Museum of Natural History in Helsinki, the Zoological Museum of Oulu University as well as written guidelines (Kennedy & Carbyn, 1981; Teerink, 1991). From scats collected in summer, calves of reindeer and moose were distinguishable from older animals.

The frequency of occurrence and the relative volume of remnant prey types were examined. The frequency of occurrence of a given prey type was calculated as the number of times the prey type was identified in all scats divided by the total number of prey items identified (Ciucci *et al*., 1996). Trace-amounts (proportion of given prey type in 1 scat $\leq 2.5\%$) were ignored in frequency of occurrence calculations, as they may represent remains from a previous meal (Ciucci *et al*., 1996). The relative volumes of the identified prey types were estimated visually for each scat from prey remains spread out on graph paper. The resultant proportions were then summed across all scats for each prey type, and these values were transformed into ingested biomass values by using Weaver's (1983) linear regression model ($y = 0.439 + 0.008x$ for mammalian prey, based on feeding trials with captive wolves and where y is the biomass ingested (kg) and x is the live mass (kg) of the prey (Siivonen & Sulkava, 1994; Olsson *et al*., 1997; Gade-Jørgensen & Stagegaard, 2000; Kojola, 2000) multiplied by its relative volume in scats). Scats collected in April ($n = 24$) were not included in seasonal comparisons because this month is unique owing to the rapid spring migration of reindeer.

Preference of wolves between reindeer and moose, pooled over pack territories, was estimated by using Jacobs (1974) electivity index $D_i = (r_i - p_i)/(r_i + p_i - 2r_ip_i)$ where i is a given prey species, r_i the percentage of the species in the diet (here the relative amount of biomass ingested) and p_i the proportion of the species in the environment. Positive values of the index indicate preference for the prey species, zero values indicate no preference, and negative values indicate avoidance of the species. Preferences were calculated only for summer (May–September) and early winter (November–December) because reindeer did not occur in territories II and III in late winter and because moose density estimates were available only as averaged across the whole study area. Two time periods were used because the winter density of moose was significantly lower than the summer density owing to the hunting of moose in autumn. Preferences were calculated from both the available numbers and the biomass of the 2 prey species. The mean body mass of reindeer was designated as 90 kg (Siivonen & Sulkava, 1974) and the mean mass of moose 200 kg for summer and 225 kg for early winter (Kojola, 2000). Mean masses of moose were calculated from the body mass of calves, yearlings, adult females and males in proportion to their prevalence among all moose killed by wolves (Kojola, 2000).

To estimate the role of wolf predation as a mortality factor in the wild forest reindeer population, data on reindeer found dead ($n = 60$) in 1998–2000 were used. To define the cause of death, all these reindeer were thoroughly examined by an expert working as a field technician on a wild reindeer research project; these data were obtained as a part of continuous daily fieldwork in which movement patterns of reindeer were studied using radio-telemetry (K. Kilpeläinen, pers. comm.). The cause of death could only be defined for fresh kills. For 7 (12%) reindeer the cause of death could not be assessed.

Estimation of the number of reindeer killed by wolves

Jedrzejewski, Schmidt *et al*. (2002) showed that observed kill rate by wolves in eastern Poland yielded 5.6 kg daily expenditure. Since food consumption is affected by body mass (Nagy, 1987), the age structure in the local wolf population was taken into account. Pups are born in mid-May and reach adult body mass in midwinter (I. Kojola, A. Hakala & S. Ronkainen, pers. obs.). The estimated daily consumption by an adult wolf was halved for pups-of-the-year. Thereby a rough estimate of the total number of reindeer consumed by wolves can be obtained from the formula $R = [P^*(A^*C^*365 + Y^*C/2^*195)]/(0.75^*B)$ in which R = number of reindeer killed by wolves during the calendar year, P = the overall proportion of reindeer in the food biomass consumed by wolves, A = number of wolves $>$ 6 months old, B = estimated mean body mass of reindeer, Y = number of pups born in the given year, and C is the estimated daily expenditure (5.6 kg). In 1999,

there were 7 wolves > 6 months old and 9 pups-of-the-year. In 2000, the study population consisted of 15 wolves > 6 months old and 20 pups-of-the-year.

RESULTS

Wolves were rare in the study area until 1999. When the first four wolves in the study were radio-collared in March 1998, only five wolves (a pack of two males and two females and a single female) inhabited the area. In early 1999, the pack of four wolves split into two neighbouring couples (occupying territories hereafter called territories II and III, Fig. 1). A third pack (occupying territory I) was formed after a roaming male joined the single female of the previous year. In 1999, there were seven wolves > 6 months old and nine pups-of-the-year. In 2000, the study population consisted of 15 wolves > 6 months old and 20 pups-of-the-year. In autumn 1999 each couple was observed with three pups and in autumn 2000 they had six or seven pups. The total number of wolves in the study area was 15 after the 1999 and 35 after the 2000 breeding seasons. During autumn 2000 and winter 2000–01 the number of wolves declined to 14–16, mainly as a result of removal by hunters and juvenile dispersal.

The number of counted reindeer was 1004 in 1996, 1474 in 1999 and 1687 in 2001, with annual growth rates being 0.128 between 1996 and 1999 and 0.068 between 1999 and 2001. If the population growth of reindeer was assumed to be linear, the reindeer–wolf ratio decreased to a low level when wolf numbers peaked, being about 210 reindeer/wolf in autumn 1998, 100 reindeer/wolf in autumn 1999 and 50 reindeer/wolf in autumn 2000.

Annual territory sizes as 100% minimum convex polygons varied from *c*. 600 to 1700 km^2. Territories II and III were overlapping (Fig. 1).

The primary prey of wolves was moose (Table 1). The year-round frequencies of occurrence of reindeer and moose remains among all food items identified in scats were 24.1% and 55.2%, respectively, in territory I ($n = 166$), 30.2% and 39.7% in territory II ($n = 134$) and 25.8% and 62.6% in territory III ($n = 167$). These frequencies did not differ between territories. The occurrence of smaller mammals was lower in territory III (18.7%) than in territories I (27.7%) and II (30.6%) ($\chi^2 = 6.62$, d.f. $= 2$, $P = 0.038$).

The overall proportion of reindeer in food biomass ingested by wolves was 21.1% (21.3%, 25.6% and 17.3% for territories I, II and III, respectively). For moose, the corresponding figures were 75.8% (76.2%, 69.2% and 80.6%).

The occurrence of reindeer and moose remains in wolf scats differed among seasons (Fig. 2; reindeer: $\chi^2 = 92.6$, d.f. $= 4$, $P < 0.001$; moose: $\chi^2 = 97.8$, d.f. $= 4$, $P < 0.001$). In mid and late winter (January–March) reindeer were practically absent from wolf scats, also in the territory that was situated within the wintering area of reindeer (territory I; Table 1). The overall frequency of occurrence of reindeer was higher in autumn and early winter than in summer (Fig. 2).

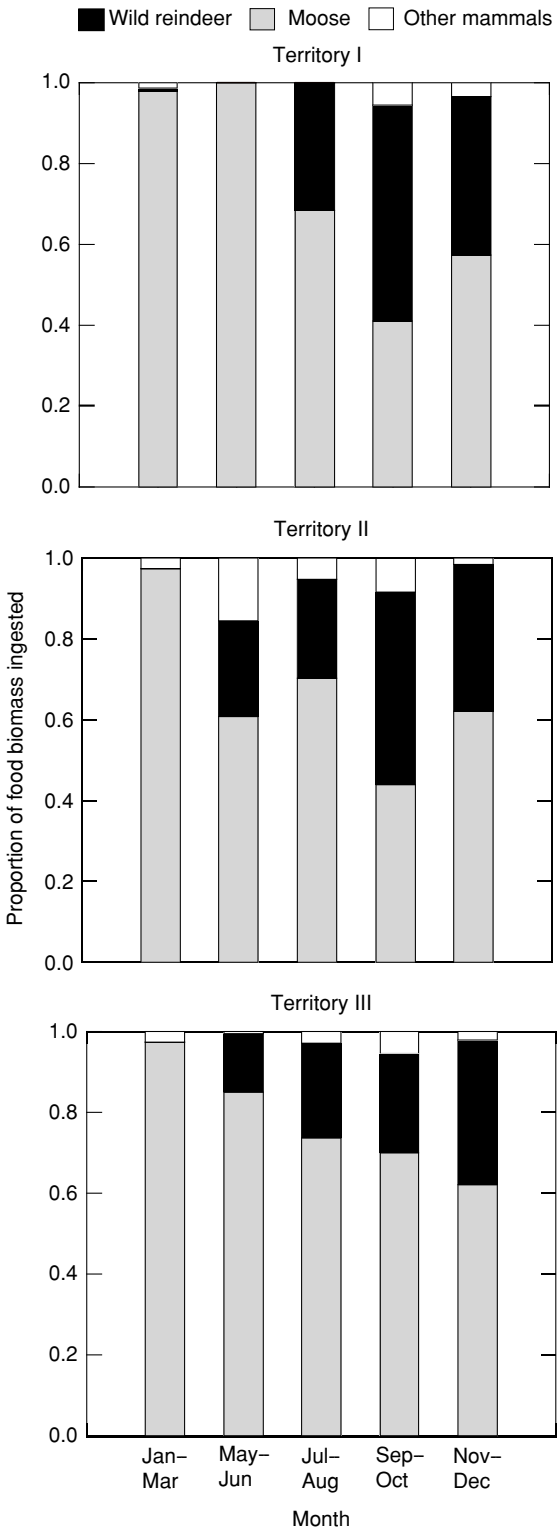

Fig. 2. The proportion of reindeer *Rangifer tarandus*, moose *Alces alces* and other mammals in food biomass ingested by wolves *Canis lupus* occupying three territories in east-central Finland, one with reindeer throughout the year (territory I), two without reindeer in January–March (territories II and III).

Overall proportions of reindeer and moose in food biomass ingested by wolves during May–September ($n = 175$ scats) provided evidence of a slight preference

Table 1. The relative frequencies of occurrence of wild reindeer *Rangifer tarandus*, moose *Alces alces* and smaller mammals in wolf *Canis lupus* scats found in three wolf pack territories in east-central Finland during 1998–2000. Samples from April are not included owing to small size

Territory	Month	Wild reindeer (%)	Moose (%)	Smaller prey (%)	*n*
I	Jan–Mar	1.5	92.4	6.1	67
	May–Jun	0.0	98.6	0.9	11
	Jul–Aug	46.6	36.7	14.3	15
	Sep–Oct	44.1	19.1	23.1	16
	Nov–Dec	48.3	40.1	9.9	58
II	Jan–Mar	0.0	90.5	9.5	21
	May–Jun	21.6	32.6	41.4	23
	Jul–Aug	40.0	40.0	15.0	20
	Sep–Oct	56.3	28.9	11.6	31
	Nov–Dec	45.9	44.5	9.6	22
III	Jan–Mar	0.0	93.2	6.8	38
	May–Jun	22.9	72.6	4.4	17
	Jul–Aug	21.6	37.5	24.1	28
	Sep–Oct	26.1	42.0	23.3	23
	Nov–Dec	45.3	44.7	6.2	53

Table 2. Proportion of animals killed by wolves *Canis lupus* among wild forest reindeer *Rangifer tarandus* found dead in 1998–2000 in east-central Finland

Year	Wolf-killed (%)	Traffic accident (%)	Other (%)	Sample size
1998	19.0	38.1	42.9	21
1999	33.0	23.8	43.2	21
2000	50.0	38.9	11.1	18

for reindeer (Jacob's (1974) index D 0.229 by biomass and 0.279 by number). During October–December ($n =$ 166 scats) reindeer were more clearly preferred (0.459 by biomass and 0.505 by number).

The proportion of reindeer killed by wolves among all reindeer found dead increased during the study (Table 2, Cochran's test for linear trend, $\chi^2 = 4.17$, d.f. $= 1$, $P = 0.041$). Wolf predation was the main cause of death of reindeer in 2000 (Table 2). The number of reindeer killed by wolves (see Methods) was estimated to have been 62 reindeer in 1999 and 137 reindeer in 2000.

DISCUSSION

Our results did not provide evidence for high vulnerability of European wild forest reindeer to wolf predation under the conditions prevailing in our study area, despite relatively high wolf–reindeer ratios in 1999 and 2000. Reindeer seemed to be able to avoid wolf predation efficiently in winter and at the time of calving. The short spring migration before calving dilutes the reindeer population into the entire distribution range. This is a spacing tactic that probably decreases the risk of wolf predation, even though the landscape in our study area does not enable movements into higher elevations or mountainous terrain, behaviour which has been observed to decrease wolf predation in some caribou populations (Oosenburg & Theberge, 1980; Bergerud, 1985; Seip, 1992; Quellet *et al*., 1996). Woodland caribou may find areas with a lower risk of wolf predation also by migrating to islands or shorelines at calving (Bergerud, 1985; Bergerud, Ferguson & Butler, 1990). In our study area wild reindeer preferred habitats composed of a mosaic of different environment types (Helle, 1980*a*). This kind of habitat may both reduce predation risk and enable optimal foraging (Helle, 1980*a*; Pulliainen, 1980*b*; Helle, 1982; Pulliainen & Leinonen, 1990; Rettie & Messier, 2000).

Caribou are both morphologically and behaviourally better adapted to snow than other boreal ungulates (Pruitt, 1959, 1979; Telfer & Kelsall, 1984). Caribou have large dewclaws and a foot loading 2.3 times smaller than moose (Telfer & Kelsall, 1984). Techniques of locomotion in snow are critical determinants of predation risk. Direct observations show that wolves usually fall behind when caribou escape into deep, soft snow (Telfer & Kelsall, 1984). Wild forest reindeer are well adapted to soft and deep taiga snow, with, for example, a shoulder height 15 cm greater than that of Scandinavian mountain reindeer *R. t. tarandus* L. (Nieminen, 1980). Wild forest reindeer also seem to be faster than wolves on hard surfaces, such as lake ice, which reindeer commonly use for resting (Montonen, 1974; Helle, 1982; Heikura, Pulliainen *et al*., 1985; Pulliainen & Leinonen, 1990). The making and use of trails is another behavioural adaptation that helps caribou cope better with snow (Telfer & Kelsall, 1984). The extensive use of trails is connected to gregariousness, which is typical for caribou that feed primarily on ground lichens, much like the wild forest reindeer in our study area (Helle, 1980*b*; Heikura, Lindgren *et al*., 1983; Sulkava *et al*., 1983). Reindeer are furthermore spatially very sedentary during winter in our study area; the mean size of the winter home range is only 155 km^2 (Pulliainen, Danilov *et al*., 1986).

Reindeer were most vulnerable to wolf predation during the autumn rut and in early winter, during the gradual migration toward wintering areas. During this time snow does not considerably hinder animal movements. Unfortunately little dietary data exist from the period of the short spring migration (April), during which reindeer disperse into summer ranges. The few scats that were collected in April contained mostly reindeer. This implies increased vulnerability of reindeer also after mid and late winter, when wolves had preyed exclusively on moose. These observations, together with the fact that reindeer mostly use traditional routes during migrations (Pulliainen, Sulkava *et al*., 1983; Pulliainen, Danilov *et al*., 1986; Pulliainen, 1989; Pulliainen & Leinonen, 1990), suggest that wolves are most effective in preying on reindeer during their biannual migration periods. Another reason why reindeer were preferred in early winter may be because of the *c*. 30% decline in moose densities during the autumn hunting season.

Wolf predation was an important, although not necessarily the main, limiting factor of population growth in reindeer. According to official statistics, the total

percentage of all reindeer reported to die in traffic collisions was 1.2% (18) in 1999 and 0.7% (11) in 2000 (Table 2 includes only carcasses examined by experts working in wild reindeer research). Reindeer were hunted in 2000 with a harvest rate of 0.9% of the population (14), but no hunting was carried out in 1999. In our study area, mean biomass of the primary winter forage of reindeer, ground lichens *Cladina* sp., did not decrease during 1985–96, largely owing to the gradual shift of the winter range over years (Heikura, 1998*a*). In that period wolves were rare and only 4% of reindeer was estimated to be killed annually by predators (wolf, brown bear and lynx), and the annual net increase of the reindeer population was 13% (Heikura, 1998*b*). If the population had still increased at this rate during 1999–2001, *c*. 400 animals more should be found in 2001 than in the 1999 helicopter count. The difference from the actual increase is *c*. 190 reindeer, which corresponds relatively well with the estimated number of reindeer killed by wolves. In central Finland, where predation is virtually non-existent, regular aerial surveys show that the size of an introduced wild forest reindeer herd has increased 20% per year on average (J. Bisi, pers. comm.). Because the reproductive rate for 1999–2001 is not known, we cannot firmly conclude whether wolf predation was the main limiting factor on the population growth of reindeer, although it was obviously the most common cause of death in 2000.

In the long run, an uncontrolled wolf population might limit wild reindeer population size more strongly because the hunting traditions of wolves potentially affect prey-catching efficiency of a given prey species (Okarma, 1995; Skogland, 1991). Our study area does not necessarily portray an established wolf–wild reindeer relationship, because wild forest reindeer exist within a very limited distribution range and wolves may have originated from packs hosting territories where reindeer do not exist.

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