DISPERSAL IN AN EXPANDING WOLF POPULATION IN FINLAND

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Dispersal influences distribution and genetic structure of animal populations. Dispersal in expanding wolf (*Canis lupus*) populations is not well documented, especially in Europe, where no studies of dispersal based on marked wolves are available. We studied the dispersal of wolves in Finland, where a peripheral wolf population (160–180 animals) increased and expanded during 1998–2004. We equipped 60 wolves from 8 neighboring wolf pack territories with radio or GPS transmitters in east-central Finland during 1998–2004, and at least 30 wolves (50%) dispersed from the home territory. Additional information was collected by detecting the natal pack of captured wolves with multilocus microsatellite genotyping and paternity analysis. In the study area, the directions formed a sun-ray pattern. Wolves usually departed their home territory as pups and yearlings, and in unimodal seasonal fashion. The dispersal distance (median 98.5, range 35–445 km) did not differ by sex ($P = 0.342$). Long-distance travelers (>200 km) were found only among wolves that departed at the age of 10–12 months. Survival was linked to the direction of dispersal. All marked wolves that dispersed to reindeer management areas in the north were shot before being able to reproduce, whereas elsewhere, the majority of dispersers (10 of 16) reproduced.

Key words: *Canis lupus*, dispersal, distance, expansion, Finland, radiocollar, reindeer, reproduction, survival, wolf

Dispersal plays an important role in the spatial distribution and genetic structure of animal populations (Taylor and Taylor 1977; Vilà et al. 2003); therefore, it may influence population viability (Boyce 1992; Nilsson 2003). However, there is no underlying theory that can predict all aspects of dispersal behavior needed for conservation and management (Macdonald and Johnson 2001; Woodroffe 2003). Dispersal patterns in animal populations vary for a variety of reasons and a multifactorial approach is needed to understand reasons underlying the variation (Ims and Hjermann 2001; Macdonald and Johnson 2001).

In the last few years, wolf populations in many European countries have been increasing and expanding (Boitani 2000; Lucchini et al. 2002), reinhabiting their former distribution range, but studies of dispersal based on marked wolves are not available. In Scandinavia, wolves exist as a fairly isolated population rooting from 3 founders that most likely originated from a Finnish–Russian population (Vilà et al 2003). The Scandinavian population is suffering from severe inbreeding depression (Liberg et al. 2005). In Finland, wolves have been reproducing regularly from the mid-1990 onward (Kojola and Määttä 2004). The latest population size estimate (2003) was 150–165 wolves, consisting of 13 packs that had denned solely in Finland and 5 additional packs extending their territories on the Russian side of the border (Kojola and Määttä 2004). Wolves are still strongly concentrated in eastern Finland and, in almost each case, only single, roaming animals live elsewhere in the country (Kojola and Määttä 2004). Some of us (IK, JA, SR) have confirmed 2 recent cases of reproduction in western Finland, 1 in 2002 and 1 in 2004.

Wolf dispersal has been studied in several North American populations by means of radiotelemetry (Ballard et al. 1983, 1987; Boyd and Pletscher 1999; Fritts 1983; Fritts and Mech 1981; Fuller 1989; Gese and Mech 1991; Mech 1987; Peterson et al. 1984; Van Camp and Cluckie 1979), although only 2 articles document dispersal in expanding populations (Boyd and Pletscher 1999; Fritts and Mech 1981). Dispersing wolves may travel over huge distances from their natal area, but recent
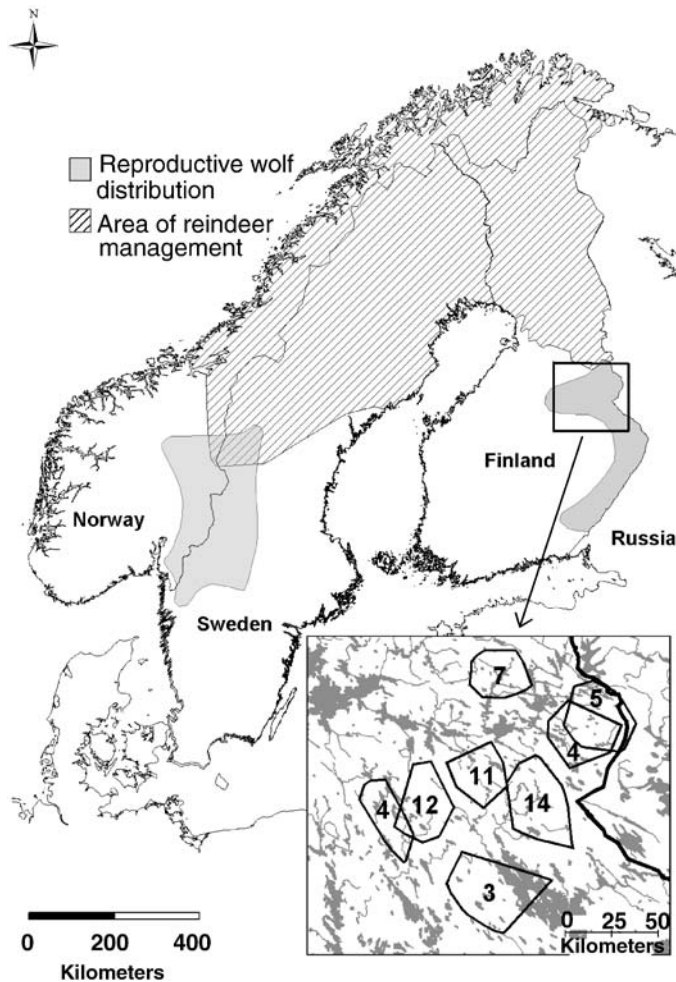

Fig. 1.—The range of reproductive wolf packs (Aronson et al. 2001) and reindeer husbandry region of Fennoscandia, and wolf territories (as 100% multiple convex polygons) in the study area with number of wolves radiocollared.

findings provide evidence that climate, habitat barriers, and prey specialization may influence gene flow across large geographical ranges (Carmichael et al. 2001; Geffen et al. 2004).

We examined the direction and distance of dispersal and fate of the dispersing wolves in a peripheral and colonizing wolf population in Finland. Dispersal may be correlated with population trend and density. In territorial species such as wolves, dispersal should be inversely density-dependent because territoriality at high densities may impede immigration and make it difficult for juveniles to leave their natal area (Wolff 1997). Because our study packs form a pack cluster mostly surrounded by unoccupied areas, such obstacles do not exist. The fate of the dispersing wolves, may, however, be influenced by the direction of the dispersal because in northern Finland, wolf harvest rates have been much higher due to considerable depredation of semidomesticated reindeer.

MATERIALS AND METHODS

Study area.—Our 15,000-km² study area was located in east-central Finland (Fig. 1). The area is coniferous boreal forest with Scotch pine

(*Pinus sylvestris*) and Norway spruce (*Picea abies*) as the dominant tree species. Forests cover about 80% of the land area. Elevation range is 160–307 m. Permanent winter snow usually appears in mid-November and melts in early May. The mean density of humans is 2 people km^{-2}, but <1 km^{-2} within wolf territories.

Methods.—Wolves were captured February–April in east-central Finland using snowmobiles when the snow was soft and at least 80 cm deep. Snowmobiles were driven alongside wolves, which were looped using a neck-hold noose attached to a pole. The wolves were placed in a wooden box that had been strengthened with metal grating around the outside and had doors at both ends. They were kept for 30 min before being injected with a mixture of medetomin and ketamine having a dose ratio of 1:20 (Jalanka and Roeken 1990).

We equipped 60 wolves from 8 territories in east-central Finland (Fig. 1) with radiocollars ($n = 40$; Telonics, Mesa, Arizona) or a collar with a global positioning system (GPS) and a radio ($n = 20$; Televilt, Lindesberg, Sweden and Vectronic, Berlin, Germany) during 1998–2004. Once the individual wolf was collared, marked with ear-tags, and measured for several morphological variables, it was placed back into the box, and the antagonist drug (atipamezole; dose 4-fold of the dose of medetomin) was injected so that the wolf could recover before being released. No harm or injury was inflicted on the wolves. The permit to capture wolves as described above was issued by the county veterinarian of Oulu, Finland. All radiocollared wolves were tracked regularly throughout the year, 2–5 times/week by means of ground-tracking. The data from VHF-GPS collars were downloaded through a cell phone (Global System for Mobile Communication, GSM) connection. Collars were programmed to collect locations 6 times/day.

The sex ratio of equipped wolves was 38 males (63.3%) and 22 females (36.7%), which deviated from parity ($\chi^2 = 4.23$, *d.f.* = 1, $n = 6$, $P = 0.039$). Alpha wolves were resident pairs that were reproducing in the study territories (cf. Mech and Boitani 2003). Females were assigned to a reproductive class when they constantly stayed for 3 weeks at the den site in early May and the presence of litter was later confirmed. Genetic parentage analysis (see below) showed that all other captured wolves in the territory were offspring of the captured alpha wolves. Age estimation of the wolves captured within their natal territory was based on several criteria. When the number of wolves in a pack corresponded to the known litter size, all except the alpha wolves were assumed to be pups. Moreover, during the capture season, pups also were distinguishable from older wolves on the basis of their softer and wavier hair. Teeth also were checked. No signs of tooth wear existed in pups. However, the classification of wolves into pups and older wolves was subjective because it was not based on unambiguous quantitative criteria. For example, amount and type of tooth wear is variable (Gipson et al. 2000). None of the animals estimated to be pups reproduced in the capture year, whereas 2 of 3 yearlings did. The ages of wolves that were harvested by hunters ($n = 6$) after their dispersal were estimated in Matson's Laboratory (Milltown, Montana) on the basis of cementum annuli in the roots of canine teeth (Ballard et al. 1995). In each case the estimated age corresponded to the age estimated at the time of capture. Animals with radiocollars consisted of 11 alpha wolves, 3 yearlings, and 46 pups. The number of individuals fitted with transmitters in the 8 territories varied from 3 to 14 (Fig. 1).

Dispersal rates were calculated only for radiocollared wolves but information on direction and distance of dispersal was achieved for 3 additional wolves (2 females, 1 male) by use of parentage analysis and microsatellite scoring of captured and harvested wolves. Tissue samples ($n = 104$) were taken from wolves that died between 1996 and 2004, and hair-bulb samples ($n = 23$) were taken from live-captured wolves. Each wolf was genotyped for allelic variation at
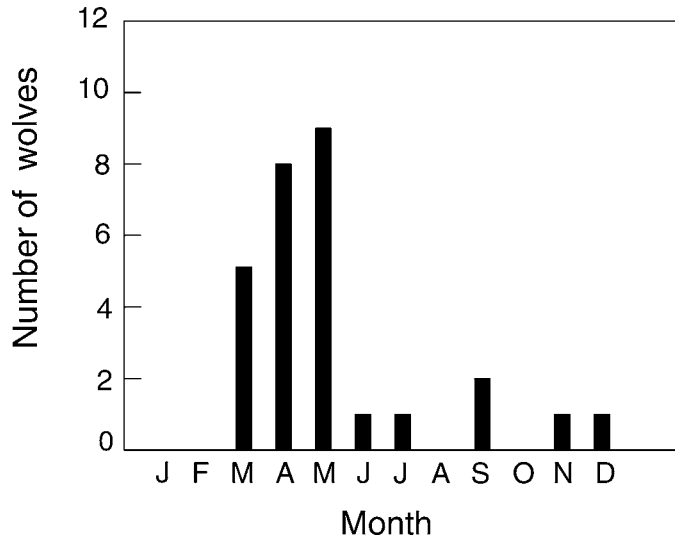
FIG. 2.—Month of wolf departures from their home territory, Finland, drawn for wolves that were estimated to be pups when captured (2000–2004).
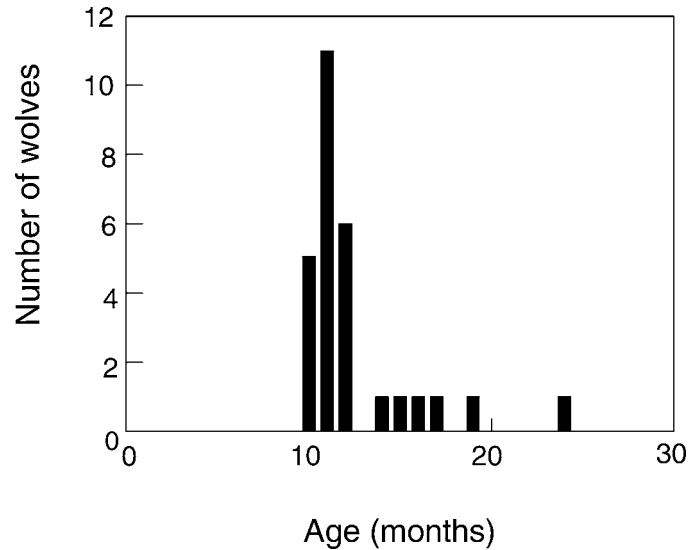

FIG. 3.—Estimated age of wolves at departure from home territory, Finland, drawn for wolves that were estimated to be pups when captured (2000–2004).

11 (tissue samples) or 10 (hair-bulb samples) autosomal microsatellite loci (Aspi et al., in press). This genotypic data allowed us to carry out parentage analysis (with resolving power of 97.1%), and thus we could detect dispersal of these 3 individuals from their home territories to new established ones.

We considered a wolf to be dispersed from its natal territory once it moved consistently outside the territory boundaries (Boyd and Pletscher 1999). The principal criteria for direction and distance were similar to those used in other extensive studies of wolf dispersal (Boyd and Pletscher 1999; Gese and Mech 1991). Dispersal distance was assessed differently for wolves for which the boundaries of the new territory could not be assessed during the lifespan of the transmitter ($n = 6$) than for wolves from which boundaries of their new territory were defined ($n = 14$ with radiocollar, and $n = 3$ from genetic analysis). New territories were detected by checking observations of collared wolves with aerial surveys and by following movements of GPS-collared wolves. When the new territory was known and its boundaries defined through radio- or GPS-tracking, the dispersal distance was defined as the distance between midpoints of the old and new territories. Without data on the boundaries of the new territory, the wolf was estimated to have established a new territory if at least 6 months had passed since departure from the home territory. This criterion has not been formerly used but was based on findings on the wolves for which the establishment of the new territory could be confirmed in our study population. For the rest of the wolves, dispersal distance was defined as the distance between midpoint of the home territory and the site of death (shot or traffic accident, $n = 4$) or the last known location ($n = 2$). The direction of movement was assessed using the geographic coordinates of the midpoints between the new territory and old territory, and if the new territory was not known, then the last known location outside the home territory or site of death was used.

We used chi-square tests when comparing observed to expected distributions (sex ratio, direction of dispersal). For the test of heterogeneity in direction, we divided the directions into 4 sectors (0–90°, 91–180°, 181–270°, and 271–360°). For dispersal distance, we used nonparametric tests (Spearman rank correlation for age effect, Kruskal–Wallis for direction effect, and Mann–Whitney U-test for

sex effect), because distance data did not meet the assumption of normality. All statistical tests were 2-tailed and considered significant at $P \leq 0.05$.

RESULTS

Dispersal rate.—At least 50% (30 of 60) of all marked wolves dispersed from their home territory. Zero of 11 marked alpha wolves dispersed, whereas most of the nonalpha wolves ($\geq 61.2\%$, $n = 49$) disappeared from their home territory. Among nonalpha wolves that disappeared, there were 15 wolves for which dispersal was not confirmed; this group may include some wolves that were killed within their natal territory. Therefore, the theoretical maximum for the dispersal rate of the nonalpha wolves was 88.2% ($n = 34$). Three wolves from the same litter stayed and divided their original territory after their mother was shot: 1 female mated with her father, the other female with her brother. A 4th wolf that stayed within the home territory was a female that also mated with her father after the alpha female had been shot. The sex ratio of the dispersed animals (19 males : 11 females) did not differ from the sex ratio of marked wolves (38:22, $\chi^2 = 0.70$, $d.f. = 1$, $P = 0.404$).

Timing and age of dispersal.—Dispersal peaked during April through June and did not take place during January and February (Fig. 2). The number of departures in quarterly periods (January–March, April–June, July–September, and October–December) varied significantly ($\chi^2 = 22.92$, $d.f. = 3$, $P < 0.001$). Mean estimated age at which wolves departed from their home territory was 13.5 months ($SD = 4.0$, range 10–24 months, calculated for the wolves that were captured during their 1st winter). Most departures occurred at the age of 11–12 months (Fig. 3). Average time from departure to settlement in the new area where the wolf later reproduced was 70 days ($SD = 58$, $n = 7$ wolves with GPS transmitters).
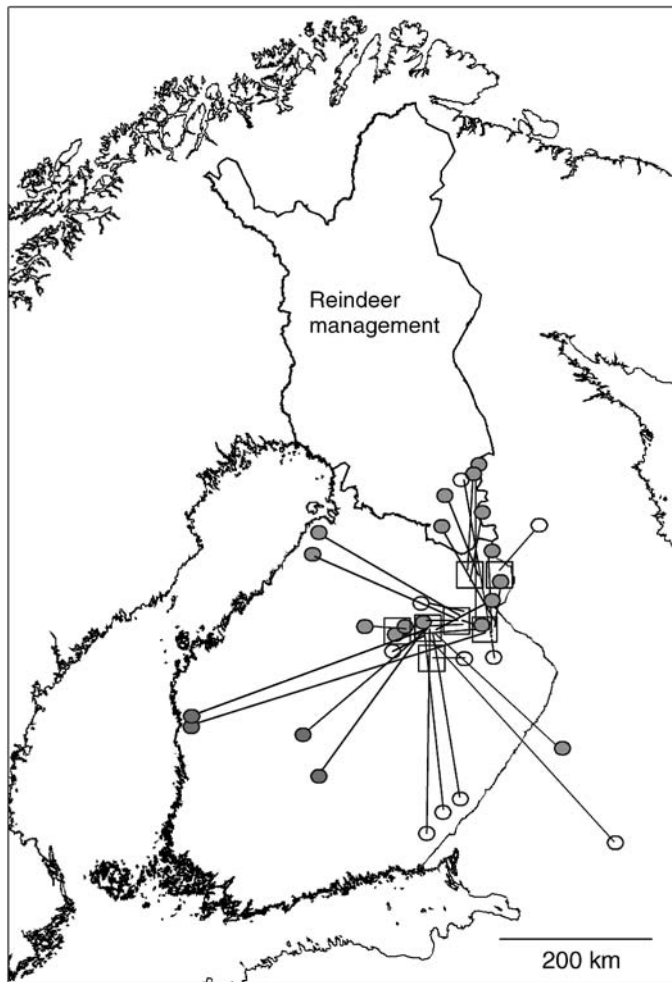
Fig. 4.—Dispersal of wolves in Finland, 2000–2004. Squares indicate territories where wolves were fitted with transmitters, black circles indicate defined and assumed new territories, and open circles delineate the last location or site of death for cases in which establishment of the new territory was not apparent.

Direction and distance of dispersal.—Directions in which study packs dispersed formed a sun-ray pattern (Fig. 4). The frequency of wolves dispersing in each directional sector did not vary ($\chi^2 = 1.3$, $d.f. = 3$, $P = 0.753$; Fig. 4). The median distance between midpoints of the original and new territories was 99 km ($n = 20$, range 35–445 km), with the median for males being 109 km (range 35–445 km) and for females 99 km (range 60–390 km). Distance did not differ between sexes (Mann–Whitney U-test, $U = 62$, $P = 0.342$). Dispersal distance was associated negatively with age (Spearman rank correlation, $r_s = -0.471$, $n = 17$, $P < 0.05$), whereas body mass at capture was not correlated with distance (females: $r = 0.342$, $P = 0.407$; males: $r = -0.170$, $P = 0.687$). Dispersal distance did not differ with the sector of the direction (Kruskal–Wallis test statistic $= 4.174$, $d.f. = 3$, $P = 0.243$).

Fate of dispersers.—Almost half (45%; 10 of 22) of dispersed wolves with known fates for at least 2 years after the departure survived until their 1st reproduction. Survival was not associated with dispersal distance (Mann–Whitney U-test,

$U = 40$, $P = 0.368$) or sex of the wolf ($\chi^2 = 0.023$, $d.f. = 1$, $P = 0.880$). All wolves ($n = 6$) dispersing into the reindeer management area were shot before the 1st reproduction, whereas 10 of the wolves that dispersed outside this area ($n = 16$) succeeded in reproducing at least once in the new area.

DISCUSSION

Dispersal rate in our study was similar to that of a colonizing wolf population in the central Rocky Mountains of North America (53%, $n = 58$; Boyd and Pletscher 1999) and higher than in many other North American studies where 24–35% of the marked wolves dispersed from their home territory (Ballard et al. 1987; Fritts and Mech 1981; Fuller 1989; Gese and Mech 1991; Peterson et al. 1984). Differences in dispersal rate are apparently influenced by the proportion of nondispersing alpha wolves among marked animals.

In some expanding wolf populations, a trend toward a female-biased sex ratio has been observed (Boyd and Pletscher 1999; Fritts and Mech 1981; Wyweden et al. 1995).

We did not find any difference between sexes in the proportion of dispersing individuals. Pulliainen (1965, 1980) reported a strong male bias among wolves shot in Finland about 40 years ago. There was a male bias among the wolves captured, but actual sex ratio in Finnish wolf population probably does not differ from unity because in the dataset where hunter-killed and marked wolves were pooled, and some of us (IK, JA) have found that the sex ratio did not deviate from unity (48 males and 58 females; $\chi^2 = 0.31$, $d.f. = 1$, $P = 0.579$). Male bias reported by Pulliainen (1965, 1980) might indicate that males outnumbered females among long-distance dispersers. Our data did not provide evidence of the sex difference with distance although the 2 wolves that traveled farther than 400 km were males. Our finding of the association between early dispersal and long-dispersal distance is in accordance with results presented by Gese and Mech (1991) from northeast Minnesota, where pups and yearlings dominated among long-distance dispersers.

The seasonal distribution of dispersal seems to be unimodal in several other populations (Ballard et al. 1987; Fritts and Mech 1981, Fuller 1989). A bimodal pattern also has been found (Gese and Mech 1991). However, seasonality of dispersal may be very slight (Boyd and Pletscher 1999) or dispersal can be quite even throughout the year (Van Ballenberghe 1983). The seasonality may vary even between geographically close wolf populations (Fuller 1989; Gese and Mech 1991).

Seasonal differences in the dispersal rate may be connected with several explanatory factors. Intrapack aggression is known to increase during the mating season (Packard et al. 1983), and one of us (SR) has observed it to be March in our study area. In the Montana Rockies, wolf population dispersal rates are lowest during March and April, and Boyd and Pletscher (1999) suggested that this could reflect an abundance of food resources because ungulates are most vulnerable to wolves during late winter and early spring. However, although an increased vulnerability among prey animals decreases food competition within packs, it also helps dispersing wolves find food in new

areas. This might explain the spring peak of dispersal in Finland where moose (*Alces alces*) is the only wild ungulate in most territories and the primary prey of wolf packs even within the range of wild forest reindeer (*Rangifer tarandus*; Kojola et al. 2004).

Dispersal by young wolves predominated also in the studies carried out in northwestern (Fritts and Mech 1981) and northeastern (Gese and Mech 1991) Minnesota, where most dispersers leave their home territory as yearlings. These studies portray examples of colonizing populations. Yearlings and 2-year-olds composed 61% of dispersers in Kenai, Alaska (Peterson et al. 1984). However, in some other populations the mean age of dispersal has been clearly higher than in our study (Ballard et al. 1987; Boyd and Pletscher 1999).

Our findings were consistent with Wolff's (1997) hypothesis that low population density enhances dispersal rate in territorial species. Some of us (IK, JA) found that, in our study area, wolf density was 3.0–3.5 wolves 1,000 km^{-2} , which is among the lowest reported from boreal forests in North America (Fuller et al. 2003). Mean density of moose was 0.3–0.4 moose km^{-2} km (Ruusila et al. 2005). This is below the threshold (0.5) under which wolf populations may be affected (Messier 1994). Some of us (IK, JA) observed that, due to low wolf density, ungulate biomass index per wolf (see Fuller 1989) was higher (460) than the mean index in North American studies (271; Fuller et al. 2003). Thus, we observed high dispersal rates under conditions of low density and relatively high food abundance. Conversely, Boyd and Pletscher (1999) presumed that low prey abundance and high wolf density promote early departure.

Our analysis of dispersal direction indicated that wolves dispersed relatively evenly to different directions, but it is possible that we do not have completely unbiased data to evaluate the effect of conspecific attraction because we lost contact with some wolves. They could have dispersed to Russia, where wolf density is at present much higher than in Finland (Linden et al. 2000). Dispersal to the reindeer management region in northern Finland was common and could be because of abundant food resources in that area. Free-ranging semidomesticated reindeer, which are the primary prey of wolves in the reindeer management area (Pulliainen 1965) may be as numerous as 300,000 before the autumn harvest and 200,000 in winter within the range of 114,000 km^2 (density 2.6 and 1.8 reindeer km^{-2}, respectively). Dispersal to the reindeer management area may partly be explained by exploratory movements during which the young wolves acquire information on the environmental quality outside the home territory before their final departure (Gese and Mech 1991; Messier 1985). The low survival of wolves in this area is due to wolf elimination through quota-based hunting and special licenses that result in harvesting rates being substantially higher than elsewhere.

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