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Source: *The Journal of Wildlife Management*, Apr., 2009, Vol. 73, No. 3 (Apr., 2009), pp. 309-313

Published by: Wiley on behalf of the Wildlife Society

Stable URL: https://www.jstor.org/stable/40208530

Dispersal Behavior and the Connectivity Between Wolf Populations in Northern Europe

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ABSTRACT The isolated gray wolf (*Canis lupus*) population of the Scandinavian Peninsular is suffering from inbreeding depression. We studied dispersal of 35 wolves fitted with very high frequency (20) or Global Positioning System–global system for mobile (15) radiocollars in the neighboring Finnish wolf population. The growing wolf population in Finland has high numbers of dispersing individuals that could potentially disperse into the Scandinavian population. About half (53%) of the dispersing wolves moved total distances that could have reached the Scandinavian population if they had been straight-line moves, but because of the irregular pattern of movements, we detected no wolves successfully dispersing to the Scandinavian population. Dispersal to the Scandinavian population was also limited by high mortality of wolves in reindeer (*Rangifer tarandus*) management areas and by dispersal to Bothnian Bay at times of the year when ice was not present. We suggest that when a small wolf population is separated from source populations by distance, barriers, and human exploitation, wildlife managers could promote the population's viability by limiting harvest in the peripheral areas or by introducing wolves from the source population. (JOURNAL OF WILDLIFE MANAGEMENT 73(3):309–313; 2009)

DOI: 10.2193/2007-539

KEY WORDS barrier, *Canis lupus*, connectivity, dispersal, distance, management, seasonality, travel route, wolf.

Functional bridges to other populations can be crucially important for long-term viability of small population fragments. The Swedish–Norwegian wolf (*Canis lupus*) population in Scandinavia has been isolated for 15 years from the neighboring Finnish population that is connected to a large Russian population (Vila et al. 2003, Liberg et al. 2005). Due to intensive persecution, the wolf was functionally extinct in Scandinavia in the mid-1960s but it returned in the late 1970s. In 1978 a reproduction was confirmed in northern Sweden (Wabakken et al. 2001), which was the last confirmed breeding there until 1983 when another litter was born 900 km to the south, starting the current Scandinavian population (Wabakken et al. 2001). In 1991, the population was complemented with a male (Wabakken et al. 2001, Vila et al. 2003). Genetic studies demonstrate that all 3 founders came from the Finnish–Russian population (Flagstadt et al. 2003, Vila et al. 2003). After the isolation a male reached the Scandinavian population from Finland in 2007, as determined by genetic analysis of a scat (O. Liberg, University of Umeå, unpublished data). Due to this bottleneck, the contemporary Scandinavian population, 140–150 wolves, is assumed to suffer from inbreeding depression (e.g., litter size [Liberg et al. 2005] and congenital anomalies [Räikkönen et al. 2006]).

Genetic material indicates that Finland's wolf population was about 1,000 animals before the decline that occurred during the late 19th century (Aspi et al. 2006). During the 20th century reproductions took place only occasionally until the late 1990s when wolves began to increase as a result of improved protection (Pulliainen 1965, 1980; Kojola et al. 2006). Wolves can disperse >1,000 km from their home territory (Wabakken et al. 2007). The narrowest dispersal distance between Finnish and Scandinavian wolf populations is about 700 km over the 75-km-wide area across Bothnian Bay, which is frozen for several months even in mild winters (Seinä and Palosuo 1996, Linnell et al. 2005). Wolves are able to cross substantial distances of sea ice (Linnell et al. 2005). Wolves must have crossed ≥20–30 km of ice to get to Isle of Royal in Lake Superior, Michigan, USA and the 70 km to Wrangel Island in Siberia, Russia (Peterson 1977, Hutt 2003). Wolves are found on most of the Canadian Arctic islands that, in some cases, demand for crossing ≥40–50 km of ice at the shortest points (Linnell et al. 2005). The shortest distance (800 km) across land for dispersing wolves would be through a reindeer (*Rangifer tarandus*) management area. Because of wolf predation on reindeer, wolf controls are more liberal in these areas and could cause high levels of wolf mortality (Ministry of Agriculture and Forestry 2005, Kojola et al. 2006). In Finland, legal harvest is much higher in the reindeer management area (>50% of estimated no. of wolves) than outside that area (about 10%; I. Kojola, Finnish Game and Fisheries Research Institute, unpublished data). Our goal was to improve the understanding of the interactions between dispersal distance and behavior and the importance of barriers like the seas and regions of high exploitation for successful dispersal between wolf populations.

STUDY AREA

The 15,000-km^2 study area located in east-central Finland included the bolt of coniferous boreal forest dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*; Kojola et al. 2006). Elevation ranged from 160 m to 307 m

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above sea level. Permanent snow cover usually lasted from mid-November to early May. Mean density of humans was 2 people/km, but <1/km within wolf territories. Number of wolf territories per unit area was higher than elsewhere in Finland (Kojola et al. 2006).

METHODS

We captured wolves in February–April using snowmobiles when the snow was soft and $\geq$80 cm deep. We drove snowmobiles alongside wolves, which we looped using a neck-hold noose attached to a pole (Kojola et al. 2006). We placed wolves in a wooden box, strengthened with metal grating around the outside and with doors at both ends. We kept wolves for $\geq$30 minutes in the box before injecting them with a mixture of medetomin and ketamin at a ratio of 1:20 (Jalanka and Roeken 1990). Capture, handling, and anesthetizing of wolves met the permits issued by the Animal Care and Use Committee at the University of Oulu and by the provincial government in Oulu (OYEKT-6-99, OLH-01951/Ym-23).

We fitted 82 wolves with collars. We received the distance to the new territory or to the last fix for 35 dispersed individuals, of which 20 were equipped with a very high frequency (VHF) radiocollar (Telonics, Mesa, AZ) and 15 with a transmitter including Global Positioning System (GPS) and mobile phone component global system for mobile (GSM; Televilt, Lindesberg, Sweden and Vectronic Aerospace, Berlin, Germany). We tracked radiocollared animals 2–5 times weekly by vehicle and foot in their home territory since they departed their home territory. If we found the wolf settled down we started radiotracking again in the new area. The GPS–GSM transmitters provided 6 radiolocations daily.

We assessed dispersal distance as the straight-line distance between the middle of the capture territory and the middle of the new territory (see Kojola et al. [2006] for details). Based on performance and tooth wear (Kojola et al. 2006), we assumed that all dispersing wolves were aged from 10 months to 24 months and were born in the capture territory. We assessed that a wolf established a new territory if it spent $\geq$8 months in a new home range. If wolves died or their transmitter stopped working before the new territory was established, we calculated minimum distance as the distance between the middle of the home territory and the last radiolocation. For wolves fitted with a GPS transmitter, we determined length of the dispersal route as the sum of the distances between consecutive radiolocations. From GPS transmitters we determined duration of dispersal, which was the number of days between the day of departure to the day of arrival into the area where the wolf settled down. We considered a wolf to be dispersed from its natal territory once it moved consistently outside the territory boundaries (Kojola et al. 2006). We assessed length of the dispersal route and the duration of dispersal only for GPS-collared wolves because we were not able to air-track VHF-collared dispersers comprehensively to assess the day of arrival to the new home range.

Based on the behavior of collared wolves and the pack size assessed by snow-tracking (Wabakken et al. 2001), we estimated the number of wolves that dispersed annually from the natal packs of the study area using the following formula: $Dn = N \times Dm$, where N is the proportion of subadult wolves (age 8–20 months at capture) that dispersed from the home territory during the capture year, and Dm is the number of subadult wolves in packs in our study area. Because there were no 2-litter packs, we assigned the number of subadult wolves as 2 wolves (breeding pair) less than the pack size. We estimated the annual number of wolves moving to Bothnian Bay by using the proportion of such wolves among collared dispersers.

To evaluate the potential for crossing the Bay, we examined how the timing of dispersal was related to the melting and thawing of ice. Finnish Institute of Marine Research provided us with data of the duration of ice cover.

RESULTS

During dispersal about half of the GPS-collared wolves (53%, $n = 15$) moved >800 km (Fig. 1), which would be enough for a wolf moving along the shortest routes to reach the Scandinavian Peninsula population (see Linnell et al. 2005). We were able to assess the location of the new territory for 26 wolves. Of those fitted with GPS–GSM transmitters, we could define the location of the new territory for 10 individuals. Most wolves moving toward new regions established new territory <200 km from their home territory (Fig. 1). Although dispersal distance and distance of dispersal route were correlated (Pearson $r = 0.730$, $P = 0.016$, $n = 10$; Fig. 2), the irregular pattern of movements (Fig. 3) resulted in dispersal distances that were too short for successful dispersal to the Scandinavian population. Only 3 wolves (9%) traveled >400 km from their natal territory, with the longest distances being 470 km, 455 km, and 405 km (Fig. 1). Mean duration of dispersal was 89.2 days (95% CI = 38.6–139.8 days, $n = 15$). The estimated number of wolves leaving their natal packs annually increased from 10 to 30 during 2000–2006, and 5–10 of these wolves moved to the shores of Bothnian Bay. The increase of reproducing packs was linear over the years (I. Kojola, unpublished data); consequently, we estimated the number of wolves traveling the Bothnian Bay to grow linearly. Dispersal distance was greater among wolves that departed later in spring (Pearson $r = 0.388$, $n = 22$, $P = 0.075$).

Overall mortality of radiocollared wolves during the first year following departure of home territory was 50% ($n = 28$). Mortality was far higher (100%, $n = 9$) in the reindeer management area than elsewhere (26%, $n = 19$). All wolves that traveled into the reindeer area were killed before they succeeded in reproducing. In all mortalities ($n = 14$) the wolf had been shot.

The ice of the Bothnian Bay melted during April and thawed in mid-January in our study years (J. Vainio, Finnish Institute of Marine Research, unpublished data). The 4 GPS-collared wolves that moved to the Bay arrived at the

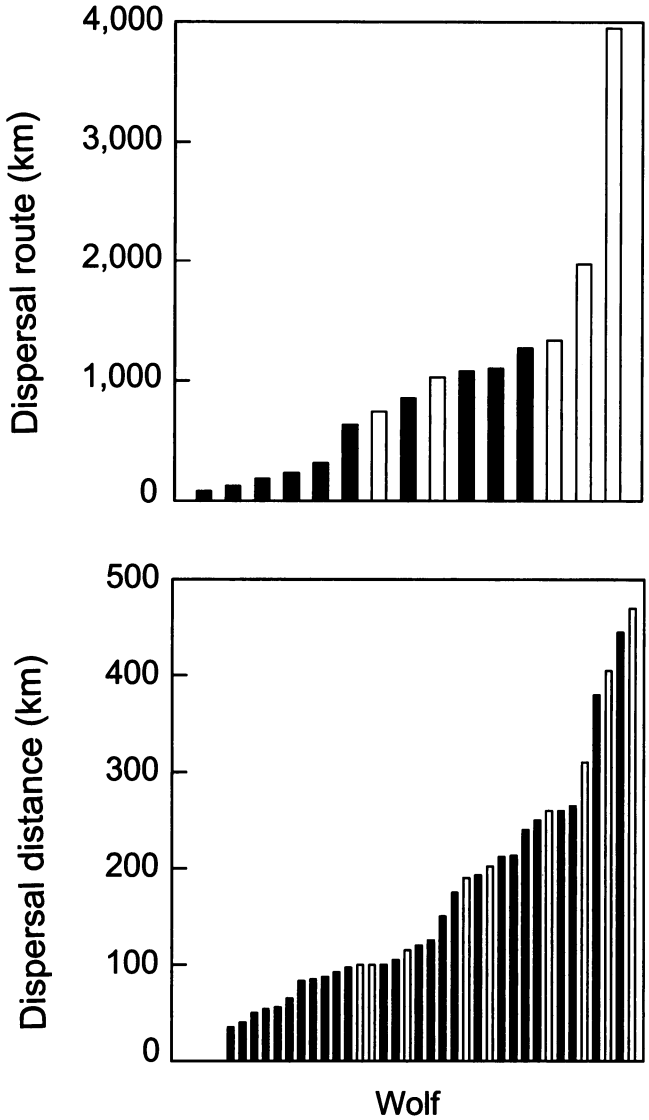

Figure 1. Dispersal distances and lengths of wolf dispersal routes in Finland, 1 April 2000–3 March 2007. Wolves with known location in new territories are shown in black, and those we followed to their last radio location are shown in white.

shore when the ice was already melted (Fig. 4). Two of these wolves established new territories in the coastal region and 2 wolves moved back from the shore.

DISCUSSION

Our study suggests that despite a recent expansion of the Finnish population of wolves and its potential to be a source for wolves inhabiting Scandinavia it is unlikely that the Finnish population can provide numerous immigrants to the Scandinavian population. We propose 3 explanations. First, the distance between these 2 populations is so big (700 km over the ice of Bohnian Bay and 800 km via the reindeer management area) that only a few of the dispersing wolves can be expected to immigrate to the Scandinavian population (Linnell et al. 2005). Second, the exploitation rate in Finland's reindeer management area is so high that wolves can only occasionally reach the Scandinavian

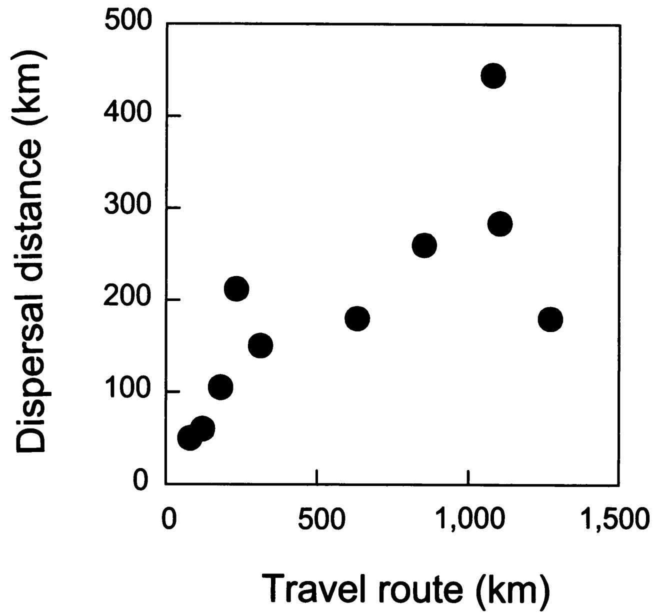

Figure 2. Relationship between wolf dispersal routes and dispersal distances in Finland, 15 April 2002–16 September 2005.

territory without being harvested. Third, our results provide some evidence that Bothnian Bay is a barrier because dispersing wolves arrived at the Bay after ice had melted.

Many wolf populations in the United States and Europe are separated from source populations by distances and barriers that restrict the exchange of animals (Haight et al. 1997). Wolf depredation of livestock usually occurs in peripheral ranges where human-caused deaths decrease exchange between core ranges (Musiani and Paquet 2004). Free-ranging, semi-domesticated reindeer are easy prey for wolves, and reindeer densities are far higher than those of wild ungulates. Wolves that traveled to the reindeer management area usually settled down near (<150 km) their home territory in the southern boundary of the reindeer management area (Kojola et al. 2006). Wolves cause considerable depredation in semi-domesticated reindeer herds (Norberg and Nieminen 2007); thus, intense lethal controls were applied to wolves that entered the reindeer management area.

Mortality of wolves was high in northern Sweden. Immigrant wolves were detectable by means of genetic analyses because a practically complete pedigree exists for much of the Scandinavian wolf population (Liberg et al. 2005). Seddon et al. (2005) found 4 wolves from the Finnish wolf population in Sweden during 2002–2005, but only one of these was still alive in 2005.

Despite that the gray wolf appears to be an incredible disperser (see Linnell et al. 2005 for a review), recent findings suggest that gene flow can be restricted, due to prey and habitat specialization (Pilot et al. 2007) and human-built obstacles, for example (Aspi et al. 2009). Observed seasonal dispersal, where wolves unimodally departed their home territories in spring (Kojola et al. 2006), probably decreased the chances of crossing the Bothnian Bay, which offers the shortest route from Finland to Scandinavia. The

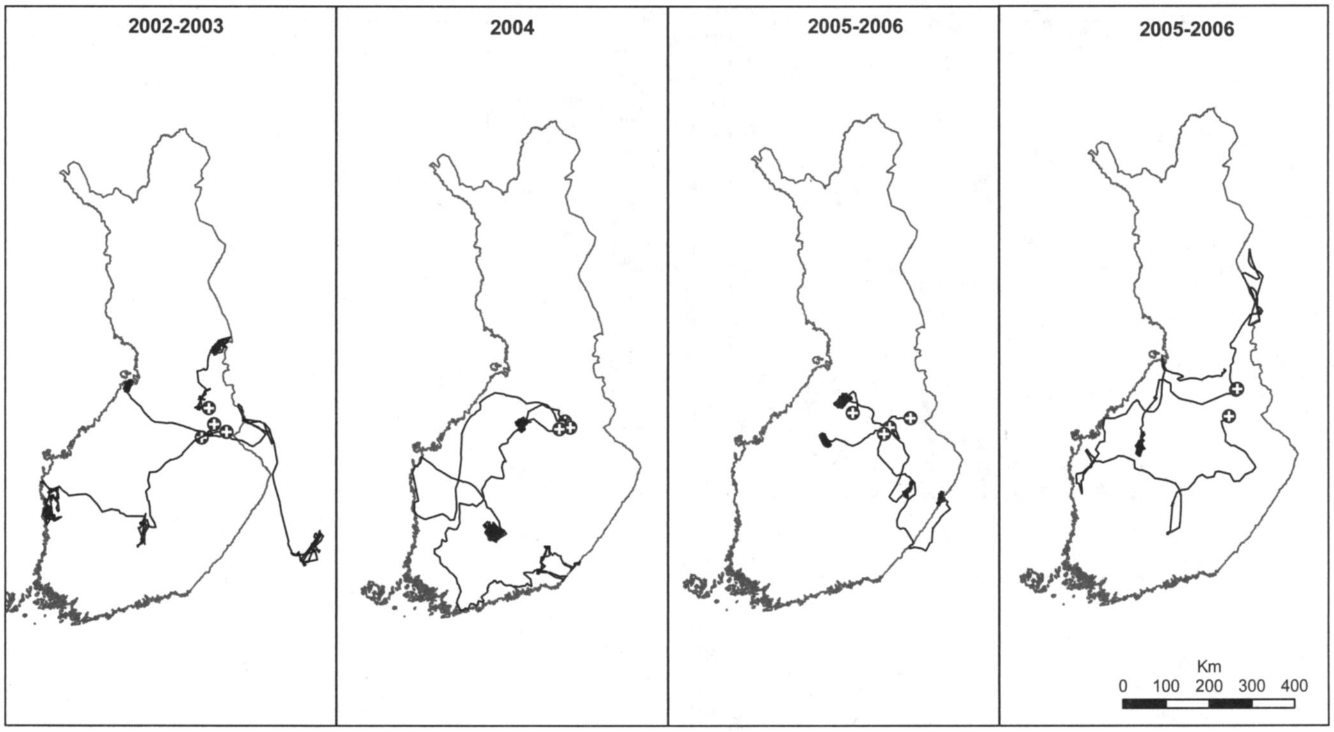

Figure 3. Dispersal routes by Global Positioning System–collared wolves, Finland, 15 April 2002–2 February 2006. + indicates the location of home territory.

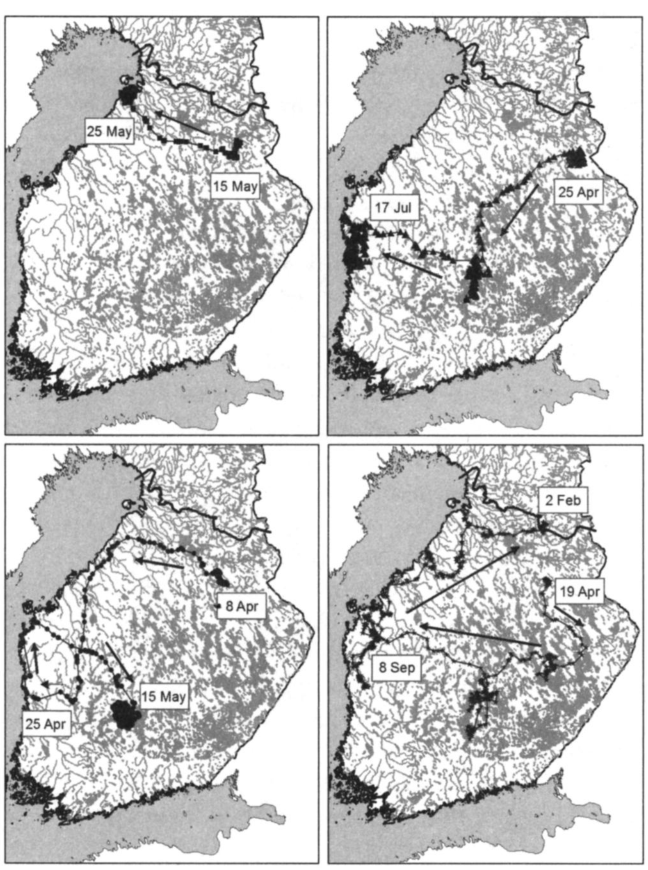

Figure 4. Dispersal routes and time of departure from home territory, time of arrival to Bothnian Bay, time settling down in the new territory or the day of the last location (lower right) by 4 Global Positioning System–collared wolves that moved to Bothnian Bay, Finland, 2003–2006. Ice melted during April and thawing occurred by mid-January.

spring peak of dispersal exists in several other wolf populations (Fritts and Mech 1981, Ballard et al. 1987, Fuller 1989), but seasonality may vary even between geographically close wolf populations (Gese and Mech 1981, Fuller 1989).

The breeding wolf population in Finland has been gradually expanding and the first litters have recently been born in western Finland after an absence of >100 years (Kojola et al. 2006). The geographic distance to the Scandinavian population is shorter from western territories than from the core area in the east, which will increase the chances of dispersal from Finland. On the other hand, the population increase in western Finland may shorten time spent in dispersal because at present wolves probably find a mate sooner than in recent history, when only very few wolves were roaming in western Finland (c.f. Pulliainen 1980).

MANAGEMENT IMPLICATIONS

The goal of increasing the number of breeding packs in southwestern Finland will result in a higher number of wolves traveling in the western part of the Finnish reindeer management area (Ministry of Agriculture and Forestry 2005). Mortality of wolves in northern Scandinavia is likely to remain high, in spite of full compensation paid by governments. Tolerance is low because of extra labor caused by wolves breaking up herds. Thus the connection between Finnish and Scandinavian populations will remain limited. Translocation is a potential option to increase viability of the Scandinavian wolf population. Reintroduction, from a biological standpoint is a proven technique for restoration (Fritts et al. 1997). Yet there is need to have only a few wolves enter the Scandinavian population every generation to maintain genetic diversity (Vila et al. 2003).

ACKNOWLEDGMENTS

We wish to express our sincere thanks to L. Korhonen, R. Ovaskainen, S. Ronkainen, and M. Suominen, for their invaluable work in capturing wolves, and J. Schregel for useful comments on the manuscript.

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