The origins of the southern Scandinavian wolf Canis lupus population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice

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Rendez-vous

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The origins of the southern Scandinavian wolf *Canis lupus* population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice

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Ever since the present phase of wolf *Canis lupus* population growth began in southern Scandinavia in 1983 there has been controversy surrounding their origins. Genetical analyses have clarified that the wolves originate from the Finnish-Russian populations, but the debate continues about how they came to be in southern Scandinavia, with many wolf-opponents claiming they have been released in a clandestine action. By comparing the geography of Scandinavia to known wolf dispersal behaviour our analysis focuses on whether it is possible for wolves to have recolonised southern Scandinavia without human assistance. From 298 published dispersal distances for North American wolves, 10 were over 500 km, with the longest being 886 km in a straight line. When also including data on actual distance moved, several wolves have been recorded to travel more than 4,000 km, often within only a few months. However, the published data are biased towards short-distance movements. Any wolves travelling from the Finnish-Russian border to the site of the 1983 reproduction would have to have travelled > 1,000 km, with potential routes being overland, or over the ice covered Baltic Sea during winter. From their present distribution, wolves have shown a clear ability to cross areas of sea-ice of up to 70 km. Therefore, it is possible for wolves to have colonised south Scandinavia through natural dispersal, although it requires movements at the extreme edge of what has been documented. As wolves expand in both southern Scandinavia and Finland, the distance between the populations will decrease, although contact will require passing through 500 km of the conflict-full reindeer-herding areas or crossing of the Baltic Ice.

Key words: Baltic sea ice, Canis lupus, dispersal, recolonisation, wolf

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Following changing public attitudes and the introduction of favourable legislation many of the wolf *Canis lupus* populations in western Europe have expanded in the last 10-20 years (Boitani 2000). This expansion has seen the return of wolves to the Italian and French maritime Alps (Lucchini et al. 2002, Valière et al. 2003), the return of breeding wolves to Germany, the expansion of wolves south of the river Djuro in Spain, and the appearance of a few stray individuals in Switzerland and Austria (Boitani 2000). Scandinavia is no exception to this trend. Historically a combination of liberal hunting regulations and state bounties from the 19th century led to the virtual extermination of wolves in Scandinavia. A total of 12,645 bounties were paid for wolves killed during the periods 1827-1966 in Sweden and 1846-1971 in Norway. By the time that wolves were protected, i.e. 1966 in Sweden and 1971 in Norway, they were functionally extinct in both countries (Myrberget 1969, Persson & Sand 1998, Wabakken et al. 2001). The only documented reproduction in the period immediately after protection was in 1978 in northern Sweden (Wabakken et al. 2001). This pack was fragmented by legal and illegal killing, and subsequent rare observations were of mainly single wolves. By the end of the 1970s it was estimated that only a few solitary wolves were found on the entire peninsula (Wabakken et al. 1983, Wabakken et al. 2001). Then, in 1983 reproduction occurred in south-central Sweden, and subsequently there has been a rapid population increase throughout the border region south of 62°N (Wabakken et al. 2001, Wabakken et al. 2002). By winter 2001/02 there were an estimated 98-114 wolves distributed in 11 packs and 5-6 pairs in south Scandinavia (Wabakken et al. 2002).

Controversial origins

Ever since the start of the current (post-1983) phase of population increase there has been intense public debate about the origins of the wolves, and how they came to southern Scandinavia. The opinion most widely accepted by researchers is that the present population is descended from a few individuals (possibly as few as three) of Finnish-Russian origin that arrived in at least two waves during the 1980s and early 1990s. This view is clearly supported by intensive genetic analysis (Ellegren et al. 1996, Ellegren 1999, Sundqvist et al. 2001, Vilà et al. 2002). These studies do not support the idea that the wolves descend from some undetected survivors of a wild or captive population of native Scandinavian wolves. The question about the mechanism by which these Finnish-Russian wolves reappeared in southern Scandinavia remains controversial. Among a wide range of individuals and organisations that are opposed to wolf conservation it is widely claimed that the wolves have been illegally and secretly reintroduced by conservation groups or the Scandinavian governments (Skogen & Haaland 2001, Skogen et al. 2003). These claims are widespread in both countries (Unsgård & Vigerstøl 1998, Persson & Sand 1998, Norlén 2001, Toverud 2002) and have begun to take on the form of folklore (Klintberg 1994). Interestingly this form of conspiracy theory surrounding wolf recovery is widespread throughout Europe and North America (Boitani 1992, Svarstad & Skogen 2003, Skogen & Mauz 2002).

Large carnivores have been reintroduced in Europe during recent decades. Lynx *Lynx lynx* have been successfully reintroduced into Slovenia, Switzerland, France and the Czech Republic, with additional attempts in Germany and Italy, and ongoing efforts in Poland and Germany. Bears *Ursus arctos* have been reintroduced into Austria, Italy and France (Breitenmoser et al. 2001). So far there have been no recorded wolf reintroductions in Europe, although there have been very high profile projects in North America (Yellowstone and Arizona; Fritts et al. 2001, Brown & Parsons 2001), and a little known project in the Georgian section of the Caucasus Mountains (Badridze 1999). In light of these projects it is therefore theoretically possible for wolves to have been illegally reintroduced to southern Scandinavia, although it must be born in mind that many large carnivore reintroductions have failed, especially those that depend on captive born animals and/or those with small numbers of released individuals (Komers & Curman 2000, Breitenmoser et al. 2001). In addition, the proponents of this theory claim that such illegal reintroductions have continued to the present day. Here it is instructive to note that the same research, which has shown that Scandinavian wolves have their origins from the Finno-Russian population, also show unequivocally that this population has originated from only three individuals, with the last genetic input occurring in 1991 (Vilà et. al. 2002). While it is impossible to completely disprove the theory that wolves have been illegally reintroduced to south-

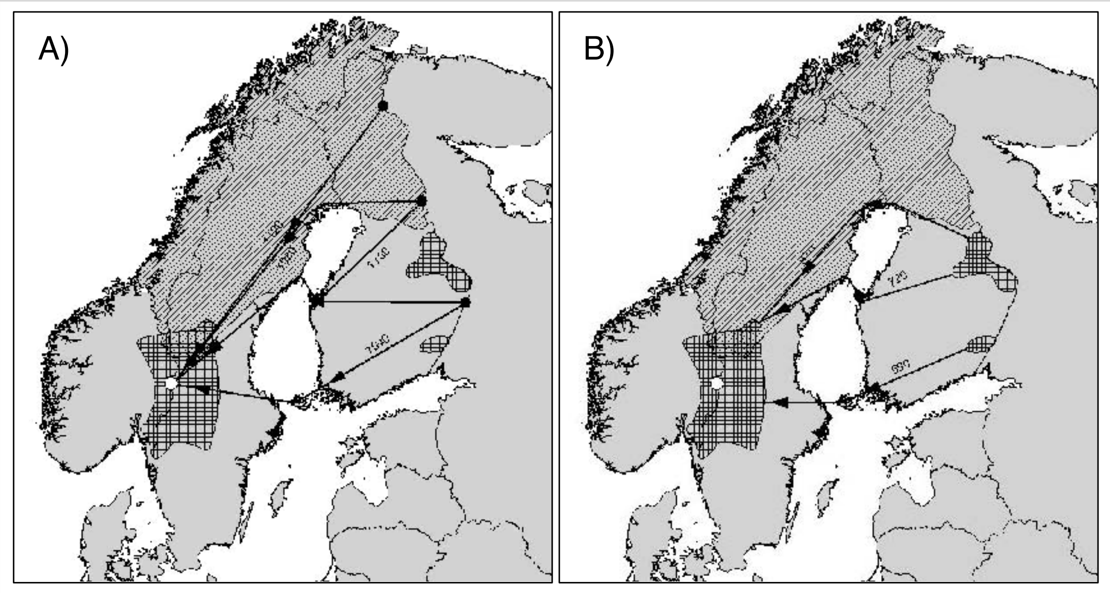

Figure 1. Potential wolf dispersal routes between Finland/Russia and southern Scandinavia. Reindeer herding districts are marked with diagonal hatching, present day wolf distribution with cross hatching and the site of the 1983 reproduction with an open circle. In A) the distances (in km) between the main areas where wolves crossed the Russian-Finnish border in the 1960-1980s (Pulliainen 1965, 1993) and the site of the first reproduction in the present expansion phase are given. In B) the distances (in km) between the edges of the present day wolf distribution areas in Finland and Scandinavia along different routes are given.

ern Scandinavia, there has so far been no scientific attempt to examine the alternative theory that wolves could have recolonised this region without the aid of humans. In the following sections we shall examine this possibility by relating the documented dispersal potential of wolves in relation to the local geography of Scandinavia.

Potential sources

Being an isolated peninsula, the only potential source for natural recolonisation of wolves is from neighbouring Finland or Russia to the east, something which is supported by the genetic evidence (Vilà et al. 2002, Flagstad et al. 2003). Wolves in Finland have had a similar history to those in Scandinavia. The population was almost exterminated in the period 1880-1900 (Ermala 2003) although constant immigration from Russia has led to the constant presence of at least some individuals in Finland along the eastern and northern borders (Pulliainen 1965, 1985, 1993). Wolves have occurred continuously throughout the Russian areas adjacent to Norway and Finland, with the highest densities in southern Karelia (Pulliainen 1985). During the period relevant for the recovery of Scandinavian wolves (the 1980s) there were few, if any, reproducing wolves in Finland, but the frequency of border crossings apparently in-

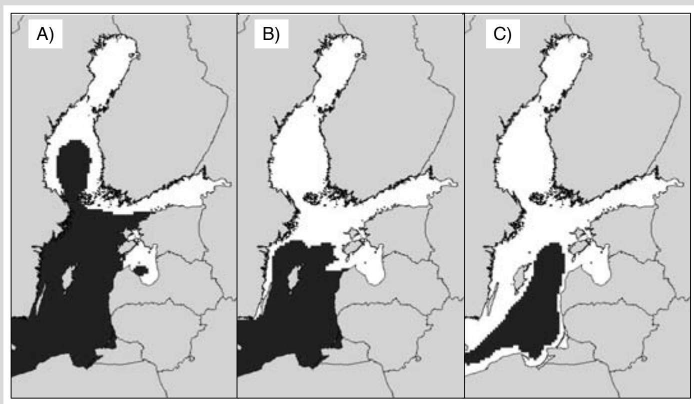

Figure 2. Schematic representation of the annual maximum ice extent on the Baltic Sea, showing A) mild, B) average and C) severe winters (based on 1720-1995 averages) as classified by Seinä & Palosuo (1996). Data on wolf distribution are from Wabakken et al. 2001, 2002.

Table 1. Frequency with which different areas of the Baltic Sea have been ice covered during winter in the period 1975/76 - 2002/03 (no data for 1995/96). Each year has been classified as having 1) continuous ice cover, 2) partial ice cover (i.e. covered, but with sections classified as rotten ice), or 3) not continuous or absent ice cover (open water remains). Data are based on the maximum ice extent for each winter and are from Kalliosaari & Seinä 1991, Kalliosaari 1982, Seinä & Kalliosaari 1991, Seinä et al. 1996 and the Finnish Ice Service at www2.fimr.fi.

Area	Total distance (km)	Longest stretch of open ice (km)	Continuous ice (% years)	Partial ice (% years)	Absent (% years)
Bothnian Bay	150	150	100	0	0
Quark	75	25	0	96	4
Bothnian Sea	230	230	34	11	56
Åland	150	40	34	22	44

creased in the 1980s (Pulliainen 1993). However, most individuals were rapidly located and killed (Pulliainen 1965, 1985, 1993, Wikan & Mysterud 1982). Therefore, during the period in question the nearest potential source for natural immigration was the border region between Russia and Finland where the crossing of wolves was well documented at the time.

A long walk, or a shortcut across the Baltic ice?

The main issue concerning the spontaneous versus assisted recovery debate is one of distance. The Baltic Sea represents a major obstacle for dispersing wolves. In summer any wolf would have to walk around the northern shore of the Gulf of Bothnia. This represents a distance of 1,080-1,120 km from Kola/northern Karelia to the site of the first reproduction in the present expansion phase (Fig. 1A). However, in winter a variable portion of the Baltic Sea is covered by ice (Fig. 2 and Table 1). In an average or severe year (36% of recent winters) the Baltic Sea freezes as far south as the Åland archipelago (60°N) where it is only 150 km between Finland and Sweden. The longest stretch of ice to cross without land is 40 km as the Åland islands are found in the middle of the straits. Wolves occupied the Åland islands until 1844, and stray individuals were seen again in 1875-1876 (Pulliainen 1965), implying that in historical times they have crossed the sea ice over half of the distance to Sweden. Even in mild winters the Baltic Sea freezes as far south as the Quark, i.e. the strait separating Umeå and Vaasa (63°N; 96% of recent winters). At this point it is only 75 km from mainland to mainland with the longest stretch of open ice being 25 km as the islands of Vallgrund and the Umeå archipelago span the straits. The periods from 1975/76 to 1987/88 were characterised by above average maximum ice extents (Koslowski & Loewe 1994, Jaani et al. 1999, Finnish Ice Service at www2.fimr.fi). If wolves were able to cross the ice it would imply that the larger populations in central Karelia would be at the same distance (ca 1,000-1,100 km) as the alternative potential source populations in the north. Interestingly when sarcoptic mange first spread to Sweden from Finland in 1975, the first cases were concentrated in north-central Sweden, close to the Quark straits (Morner 1992, Lindström & Mörner 1987), implying that red foxes *Vulpes vulpes* probably crossed the ice. The possibility of wolves travelling directly from Estonia to Sweden seems remote, as it would require a journey of 200-250 km over open ice, and the crossing of some busy shipping routes that are kept open by icebreakers.

From the present distribution of wolves it is apparent that they are able to cross substantial distances of sea ice, as they are found on most of the Canadian Arctic islands (involves ice crossing of at least 40-50 km at the shortest points) and have recolonised Greenland (30 km from Ellesmere Island in the last 30 years; Dawes et al. 1986). Historically, wolves were also found on Newfoundland (25 km from Labrador). More recently, wolves must have crossed at least 20-30 km of ice to get to Isle Royale in Lake Superior, Michigan, and the 70 km to Wrangel Island in Siberia (Peterson 1977, Hutt 2003). However, it is uncertain if the behaviour of these tundra-dwelling wolves (presumably accustomed to open habitat) can be transferred to forest-dwelling wolves in Fennoscandia. However, wolves are found throughout most of the islands in southeastern Alaska (Person et al. 1996) and British Columbia, including Vancouver Island (Scott & Shackleton 1982) which requires that wolves swim stretches of open water of several kilometres. In Alaska wolves have been demonstrated to swim at least 4 km (Person et al. 1996).

What do we know about wolf dispersal?

Unfortunately, there is as yet very little published data on wolf dispersal available from Europe. However, there are large amounts available from North American studies that have been conducted in Alaska, Minnesota, Wisconsin and Montana. In terms of habitat and landscape, these study conditions are comparable to Fennoscandia. In all field studies it is hard to document long-distance dispersal (Bennetts et al. 2001). This is especially true for carnivores that move over truly enormous distances (Waser et al. 2001). Radio-collars have allowed the collection of far less biased data, yet even with this technology coupled with aerial radio-tracking it can be difficult to follow animals that move beyond study area borders. Most of the longest movements are only detected when animals are shot, trapped or otherwise relocated by chance. Therefore, published dispersal distances are biased towards short-distance movements and must be regarded as conservative minimums of both the frequency and distances moved by long-distance dispersers.

From the published data (we located 298 published dispersal distances) it is apparent that wolves are truly incredible dispersers (Fig. 3). A high frequency of wolves of all ages disperse from their natal areas and travel considerable distances before settling (Peterson et al. 1984, Potvin 1987, Gese & Mech 1991, Ballard et al. 1987, 1997). The record is 886 km for a wolf from Minnesota (Fritts 1983). Another 21 records were over 300 km, and 10 of these were over 500 km. One population in northern Canada actually migrates seasonally 500 km after migratory caribou herds each year (Walton et al. 2001).

The straight line distance between capture location and recovery location is a minimum estimate of distance travelled, as movements are often complex. This is best

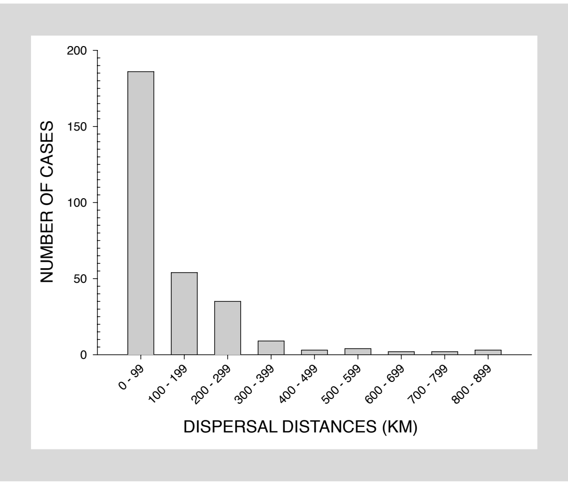

Figure 3. Frequency distribution of published wolf dispersal distances (N = 298) from North America. Data are from the following sources: Ballard et al. 1987, Ballard et al. 1997, Berg & Kuehn 1982, Boyd et al. 1995, Fritts & Mech 1981, Fritts 1983, Fuller 1989, Gese & Mech 1991, Licht & Fritts 1994, Mech et al. 1995, 1998, Merrill & Mech 2000, Messier 1985, Person et al. 1996, Peterson et al. 1984, Potvin 1987, Scott & Shackleton 1982, Stephenson & James 1982, Van Ballenberghe et al. 1975, Van Camp & Gluckie 1979, Wydeven et al. 1995. The data may contain many biases as many long-distance dispersers are never recovered. Therefore, the proportion of long-distance dispersers is probably severely underestimated.

illustrated by a wolf with a satellite collar that moved at least 4,251 km for a straight line distance of 494 km (Merrill & Mech 2000). In addition, wolves can cover these huge distances rapidly. Two wolves in the study by Merrill & Mech (2000) followed by satellite travelled 4,251 km in 180 days (23 km/day) and 1,054 km in 60 days (18 km/day) respectively. Other records based on recovery of marked animals indicate that one travelled 670 km in 81 days (8 km/day) and another travelled 886 km in 180 days (3 km/day; Van Camp & Gluckie 1979, Fritts 1983). Wolves of both sexes disperse, although a slight male bias has been demonstrated in a few studies (Ballard et al. 1987, 1997, Fuller 1989, Gese & Mech 1991, Wabakken et al. 2001). Among the documented long-distance dispersers (> 300 km) shown in Figure 3, males constitute 75% of all individuals. Wolves apparently disperse at all times of the year, with a main peak in spring and a smaller peak in the autumn in most populations.

A final perspective is from wolves that appear in areas far from any known reproductive population. Licht & Fritts (1994) report on 10 wolves shot or found dead in North and South Dakota up to 561 km from the nearest potential source. Wolves have also appeared in the states of Indiana, Missouri and Illinois in the United States, at distances of 400-700 km from the nearest breeding population (US Fish and Wildlife Service, unpubl. data). Similar data also exist from Scandinavia (Wabakken et al. 2001). These preliminary Scandinavian data indicate that dispersal distances are longer than expected from North America. For 15 individuals, the average distance was 313 km with a range of 80-880 km. Promberger et al. (1993) also present data from Germany where wolves were shot in the period 1945-1992 up to 600 km from the nearest reproductive populations in Poland and Slovakia. In many cases these wolves would have had to cross the iron curtain that existed at the time between the two German states.

Given these data it is apparent that wolves have been documented to disperse distances that could take them from the Finnish-Russian border to the area of reproduction in southern Scandinavia. While it is only a few individuals that have been documented to move this distance, it is likely that many other individuals have moved further without being detected.

Spontaneous or assisted recovery?

The distance that wolves would have to travel to get from the Russian border to southern Scandinavia is just within the range of documented wolf dispersal distances, indicating that it is biologically possible for them to have arrived naturally. Their ability to cross ice has also been frequently demonstrated from North America, Greenland, Europe and Siberia which implies that individuals could have availed themselves of the shorter route across the winter ice. The fact that wolves disperse in all seasons implies that individuals have the potential for crossing the frozen Baltic Sea during winter, or travelling long-distances during summer when they are likely to remain undetected. The hypothesis that the southern Scandinavian population was recolonised naturally from the east is both possible and reasonable. This view is further strengthened by genetic studies of historical material that have found individuals sampled in southern Scandinavia from 1862, 1950 and 1965 (before the speculation about clandestine releases) that have a high probability of being of Finnish-Russian origin (Flagstad et al. 2003). Thus, given the empirical evidence for long-distance dispersal for wolves, there is no need to invoke clandestine human assistance as the only plausible theory for the return of the wolf to the Scandinavian Peninsula.

Does it really matter?

At its most basic level, conservation is about maintaining genetic diversity of populations and species. In this context conserving wolves in southern Scandinavia makes little contribution to the overall conservation of the genetic diversity of the very large Russian wolf population of which Fennoscandian wolves constitute the extreme edge. However, recent thinking about biodiversity extends far beyond genes and now embraces ecosystem structure and ecological processes. Against this background, the return of wolves, and the other large carnivores, to the Scandinavian boreal forest can make a large contribution to restoring some of the ecosystem functionality. Finally, as it is becoming increasingly clear that the modern conservation movement is largely motivated by ethics and values (Collar 2003, Jepson & Canney 2003), the return of the wolf (irrespective of how they arrived) has enormous symbolic value for the majority of the population who favour their conservation. On the other hand, wolves have also served as a potent symbol for the majority of the population that opposes their return. However, as the controversy about the origins of wolves in Scandinavia may never be resolved, it seems far more productive to accept their presence and concentrate on developing management compromises that are as acceptable as possible to as many people as possible (Andersen et al. 2003).

Consequences for future management

The data presented here also have consequences for the future management of the southern Scandinavian wolf population. Concern has been raised about its long-term genetic viability considering the small number of founders (N = 3) and their relative isolation (Pedersen et al. 2003). The data from known dispersal distances (see Fig. 3) and genetics (Vilà et al. 2002, Flagstad et al. 2003) indicate that it is both possible for individuals to reach southern Scandinavia, and that it has occurred in the past. This indicates that the population is not completely isolated genetically. However, it seems clear that the distance from the source population is so great that immigration will always be a very rare event. The expansion of wolf populations in both eastern Finland and southern Scandinavia will slightly shorten the distance between the two populations (690-870 km; see Fig. 1B). However, the existence of semi-domestic reindeer husbandry areas throughout northern Sweden and northern Finland (reproductive wolf populations will probably not be tolerated in reindeer husbandry areas) implies that a continuous population, most likely, will never develop. There will therefore be a belt of at least 500 km of reindeer herding country between the two populations, although the distance via the Baltic ice route could be much shorter (< 200 km). However, under present predictions the duration and extent of Baltic ice cover is likely to decrease dramatically due to global warming (Haapala et al. 2001). The ice route over Åland will be the first to vanish, while the route over the Quark should persist for some more time.

Individual wolves are likely to continue to reach southern Scandinavia from the Fenno-Russian source population in the future. However, it is uncertain if the immigration rate will be adequate to fulfil the predicted need for 1-2 immigrants per generation to prevent loss of genetic diversity (Pedersen et al. 2003). If no immigration is possible, the population would need to be maintained at a higher level (ca 800 individuals) to avoid loss of diversity (Pedersen et al. 2003). Management would therefore have to maintain a larger population in southern Scandinavia than would otherwise be strictly necessary, and likewise should attempt to ensure the survival of wolves passing through the connecting regions despite potentially high conflicts with reindeer husbandry. On the other hand, allowing wolves to expand westwards in Finland, and eastwards in Scandinavia, will serve to shorten the distance. The direct translocation of individuals from Finland to Scandinavia also remains a technically feasible option, although it would require quarantine as rabies is present in the Russian wolf population of which Finland is a part. In lieu of this, an alternative is artificial insemination. However, in the present high conflict situation such invasive solutions are likely to be highly controversial.

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