DENSITY-DEPENDENT DISPERSAL DISTANCES OF SCANDINAVIAN WOLVES

A report from the Scandinavian Wolf Research Project (SKANDULV)

to the Swedish Environmental Protection Agency (SEPA)

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THE ASSIGNMENT

SKANDULV was asked by the Swedish EPA to answer two questions:

1. **Are natal dispersal distances by wolves in the Scandinavian wolf population affected by wolf density?**
   In Swedish: Påverkar tätheten av varg spridningsavståndet hos unga vargar?

2. **Have offspring from the translocated Finnish-Russian wolf pair in the Tiveden territory dispersed further than expected?**
   In Swedish: Har valparna från Tiveden reviret spridit sig längre än förväntat?

INTRODUCTION:

Wolves of both sexes most often disperse from their natal territory to seek out an own new territory for breeding. Still, in rare cases philopatry may occur, e.g. when the natal territory becomes vacant after the death or disappearance of one or both parents (Mech & Boitani 2003).

Little is known about the relationship between wolf population density and dispersal distances. Wolf density has been found to influence age of departure from the natal territory (month or season). This knowledge has so far mainly being based on data from radio collared wolves (Mech & Boitani 2003), but DNA-techniques may also offer a tool to investigate this pattern.

In this preliminary study we investigate if wolf dispersal distance is density dependent and if the offspring to the immigrant pair in the Tiveden pair dispersed longer distances than expected from other wolves in the population. None of the offspring born in the Tiveden

territory were radio-collared, so analyses of their and other wolves estimated dispersal distances in this report is based on confirmed mortalities of dispersers where the birth territory is known (i.e. natal dispersal) during the last five years, i.e. including the last two years of the Tiveden territory.

METHODS

Study animals and periods

To estimate the dispersal distance of wolves born in Scandinavia we used data on localities of retrieved dead wolves where the natal territory of the individual was known. The study period included all confirmed mortalities during the last 5 years, starting January 1st, 2011 and ending April 30th, 2015. All dead wolves used in this study were born within the 11-year period from 2004 through 2014, including the Tiveden-wolves, where pups were born in 2013 and 2014.

Sample size, id, sex and natal territory

During the study period a total of 275 wolf mortalities were confirmed and further analyzed in this study. Among these 275 dead wolves, we classified 173 as dispersers (died outside the natal territory), and 92 as non-dispersers (died within the natal territory. Ten wolves were by various reasons not possible to classify and were excluded from further analyses.

For each wolf, the identity, sex and territory of birth (i.e. natal territory) were identified by DNA- and pedigree analyses (Liberg et al. 2005, Åkesson and Svensson 2015), combined with the field-based, long-term wolf population monitoring in Scandinavia, e.g. the geographical distribution of reproduction and natal pack territories (Anon 2015).

Dispersers were classified as being either a) known from field work to be a member of a resident pair or pack within a new (non-natal) wolf territory, or b) where the distance between the center point of their the natal territory and the mortality site was > 33 km (confirmed maximum distance of a non-disperser < 33 km).

For the analysis of variables that may affect dispersal distance (question 1) we used all 173 wolf dispersers, all born during the period from 2004 to 2014. To evaluate if the dispersal distances of the five Tiveden offspring born in 2013 and 2014 were longer than expected (question 2), we compared them with a subsample of 32 wolves born during the same period (2013 or 2014).

Place and year of birth.

Although the natal territory of the each wolf was known for all wolves in the study, the exact place of birth within the actual territory was rarely known. As a proxy for the birth site we used the estimated center point of the 100% minimum convex polygon (MCP) presented in the official annual monitoring reports (Wabakken et al. 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, Anon 2015), the following winter after the actual year of birth. The spatial location of these territory polygons were based on data from several methods including

radio collars, snow tracking of individuals, and DNA-analyses of non-invasive sampling during snow tracking.

In cases when the exact year of birth was not known the last possible year was chosen for the analyses because the majority of Scandinavian wolves do disperse as 10-13 months old and yearlings has the highest mortality rate (Sand et al. 2014).

Dispersal distance and wolf population density

For each of the 173 wolves, the dispersal distance was estimated as the straight line between the place of birth and the mortality site.

Annual wolf population densities were estimated per 1000 km^2 as 90% of the average total population sizes divided by 100% minimum convex polygons (MCP) of the corresponding annual total Scandinavian wolf breeding range. On an annual basis, 10% of the wolves were assumed to be outside the breeding range. This assumption was based on two data sets of sub-population structure. 1) On average, the proportion of wolves found outside pair and pack territories have been estimated to be 20% of the Scandinavian wolf population. These wolves were found to be a mixture of resident, single territorial wolves waiting for a partner, and dispersers still on the move (Wabakken et al. 2013), and 2) 57 % of wolves still dispersing or recently settled (N=173) died outside the Scandinavian wolf breeding area (data from this report).

All analyses were performed in ArcGIS (ESRI 2011. ArcGIS Desktop: Release 10.3. Redlands, CA: Environmental Systems Research Institute, also used as a tool in all other spatial analyses.

Statistical analysis

The relationship between dispersal distances (DISTANCE) and population density of wolves were tested by using GLM-analyses in which sex (SEX) and wolf density (DENSITY) were included as fixed factors. For potential effects of wolf population density (DENSITY) on dispersal distances we corrected for sex and tested the model: DISTANCE = DENSITY + SEX + DISTANCE*SEX. All tests were performed in R version 3.2.0 (R Core Team 2015)..

RESULTS

Sex-dependent dispersal distances

Among the 173 dispersed wolves, dispersal distances of wolves were significantly different between sexes (Figure. 1; $F_{1,171} = 9.36$, $P = 0.003$, and Figure 2) and male dispersers covered a larger area than females (Figure 2). The average dispersal distance for males was 225 km (95% CI = 199-251 km) and 154 km for females (95% CI = 115-192 km). For males and females, these averages represented dispersal distances equivalent to six and four average wolf territory diameters, respectively (territory diameters estimated from Mattisson et al. 2013).

Density-dependent dispersal distances

Within the Scandinavian wolf breeding range, wolf density increased almost 3-fold during the study period (Figure 3). Natal dispersal distances were positively correlated with wolf population density ($F_{1,171}$ = 9.36, P = 0.003), and the effect of sex was additive ($F_{1,170}$ = 9.67, P = 0.002). However, the interaction sex*wolf density was not significant ($F_{1,169}$ = 0.08, P = 0.773).

Dispersal from the Tiveden territory

During 2014-2015 (until April 30), five offspring dispersed from their natal territory Tiveden (Figure 4) and were compared to the distances of all other confirmed dispersers (N=32) born in Scandinavian wolf territories during the same period (Figure 5).

Among the 37 dispersers born during 2013-2014, dispersal distances of the five wolves born in the Tiveden territory were significantly longer than the dispersal distances of the other 32 wolves born during the same period (Figure 1, 4 and 5; $F_{1,30}$ = 5.93, P = 0.021). The average dispersal distance for the five Tiveden-wolves was 405 km (95% CI = 264-547 km), whereas for the other 32 wolves it was 222 km (95% CI = 161-282 km).

DISCUSSION

The difference in dispersal distances found between sexes, where males on average disperse further than females, is in accordance with earlier wolf dispersal studies in Scandinavia (Wabakken et al. 2001). The preliminary analyses of dispersal presented in this report indicate the presence of density dependent dispesral distace among wolves Scandinavina. However, although these results are highly interesting and novel we stress the need of a more in depth analyses to be better able to understand the mechanisms at work. For example, the spatial distribution of wolf territories within in the breeding range, variable methods for estimating population density, and the amount of suitable habitat should be considered.

Tiveden wolves were found to disperse further than other Scandinavian wolves born in the same period. However, we caution any firm conclusions from this result, mainly because of the small sample size used in combination with stochastic variation (type 1 error). Also important may be the observation that much of the surrounding area of this territory was unoccupied by other wolf territories, suggesting a potential for the Tiveden offspring to establish a territory nearby its natal territory, if a partner of the opposite sex had been present.

In an earlier study, we revealed that Scandinavian born wolves dispersed on average further than confirmed from any other wolf population (Wabakken et al. 2001). For both the comparison of the Scandinavian dispersal data with other populations and the comparison between the Tiveden and other Scandinavian wolves, a hereditary component from long-range Finnish-Russian immigrant founders could be a key explanatory factor. SKANDULV is currently working on this research question.

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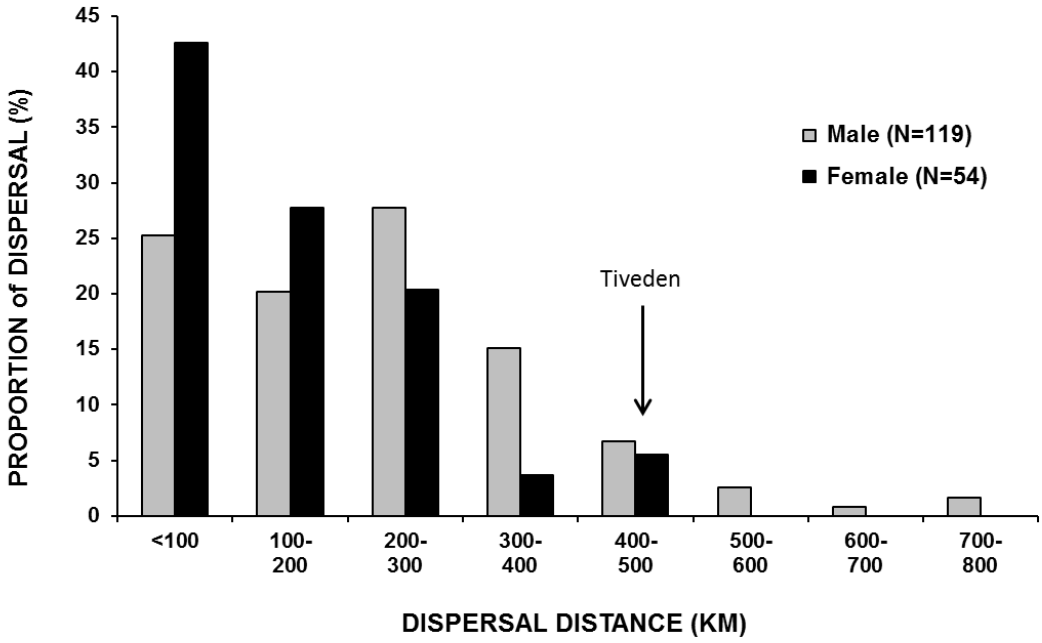

Figure 1. Proportion of natal dispersal distances by 173 Scandinavian born wolves confirmed dead, 2011-2015 (per April, 30th). Bars are presented as proportions of the total number dispersed for each distance class, where gray bars are distances for males and black bars are for females. Also shown is the average dispersal distance of five Tiveden offspring, marked with an arrow.

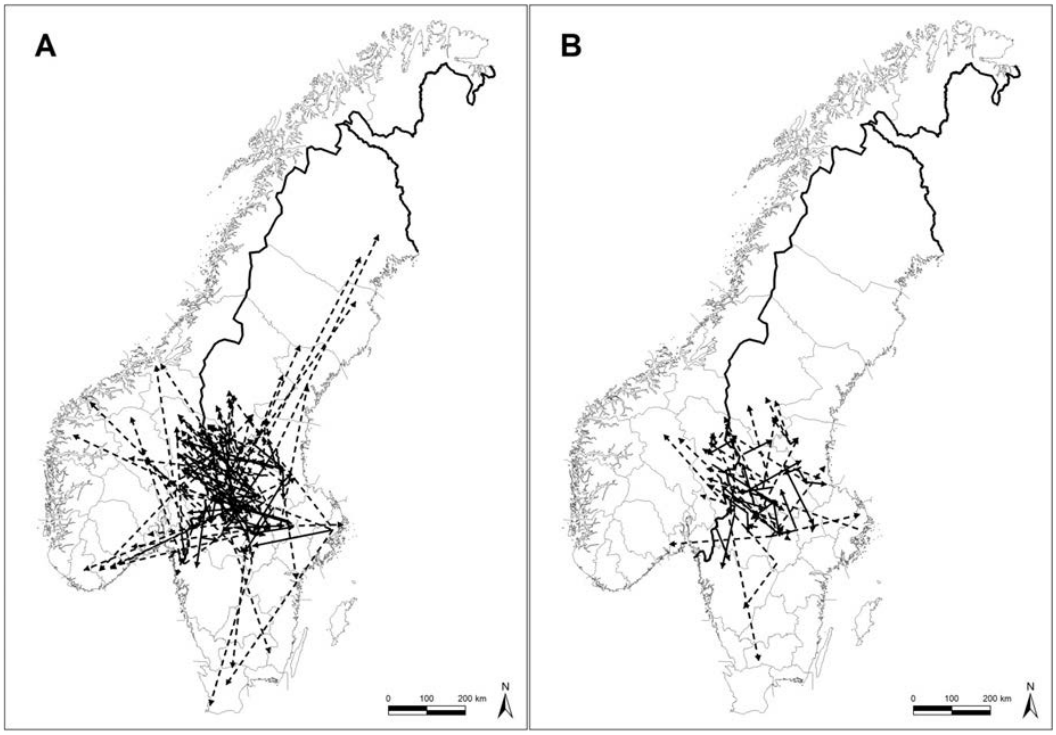

Figure 2. Dispersal distances of males (A) and females (B), measured from center point in the natal territory to place of death during the years 2011-2015.

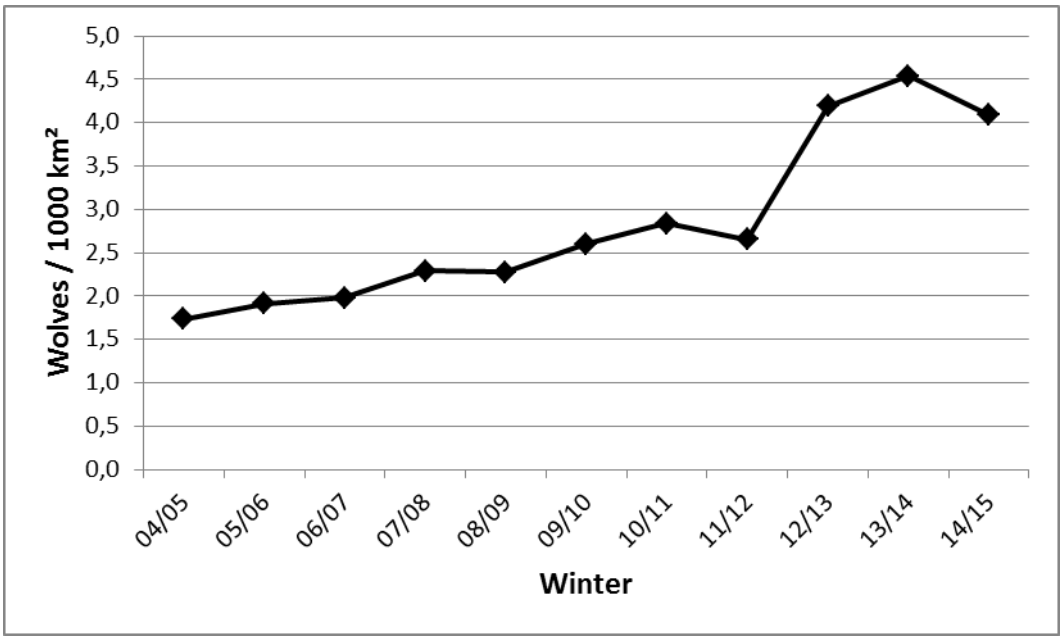

Figure 3. Annual wolf density within the Scandinavian wolf breeding range during the study period, 2004-2015.

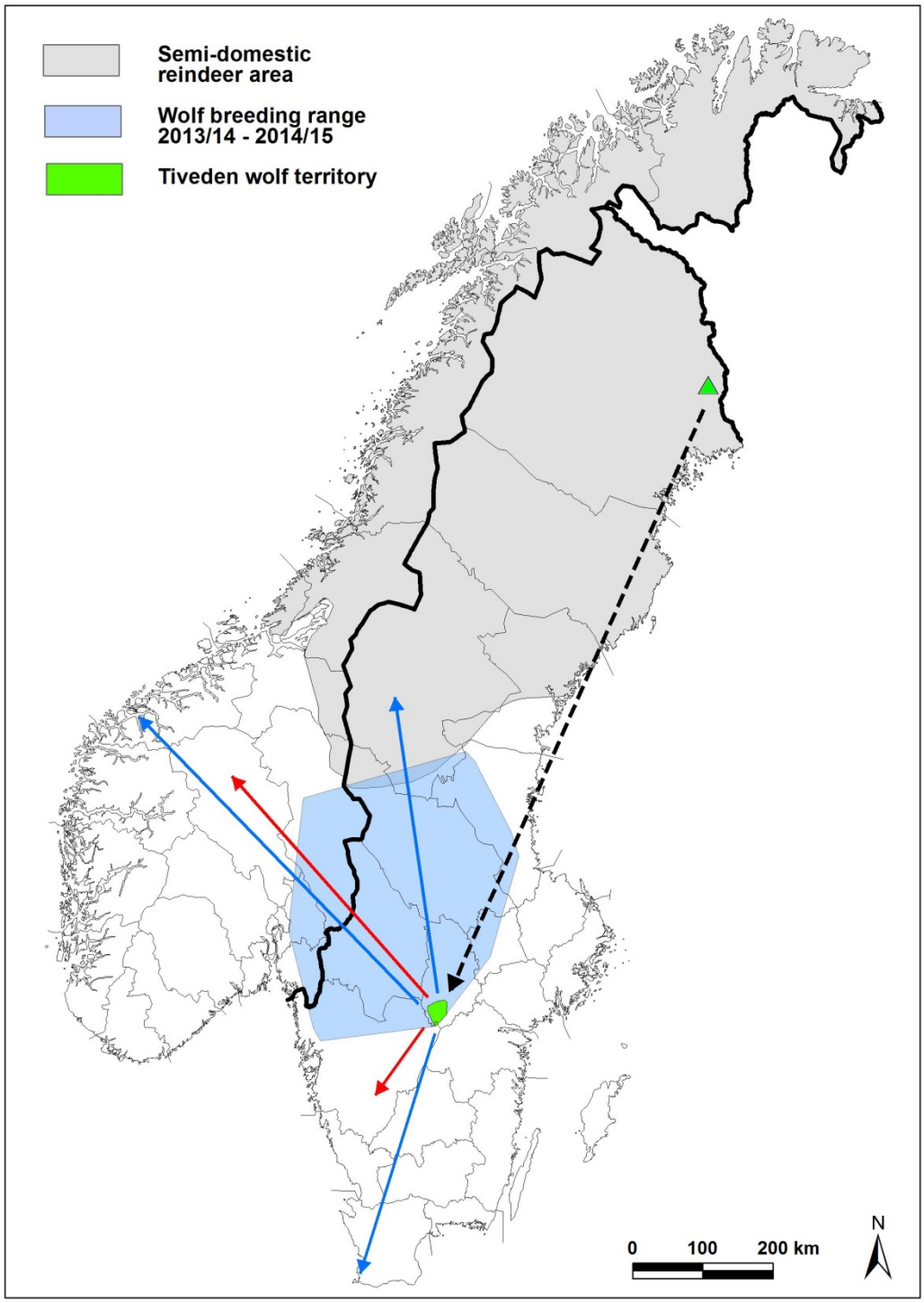

Figure 4. Translocation (dotted line) of a pair of Finnish-Russian immigrant wolves established in northern Sweden during summer-fall 2012 and moved by the management authorities to the southern edge of the Scandinavian wolf breeding range. The pair became resident and established in the Tiveden territory (green polygon) in February 2013. Natal dispersal distances of offspring born in the Tiveden territory and confirmed dead between the years 2014 and 2015 are shown for males (blue arrows) and females (red arrows). The cumulative Scandinavian wolf breeding range of the two years (2013/14-2014/15) when the Tiveden pair reproduced (blue shaded) and the distribution of the semi-domestic reindeer grazing area (grey) are also shown.

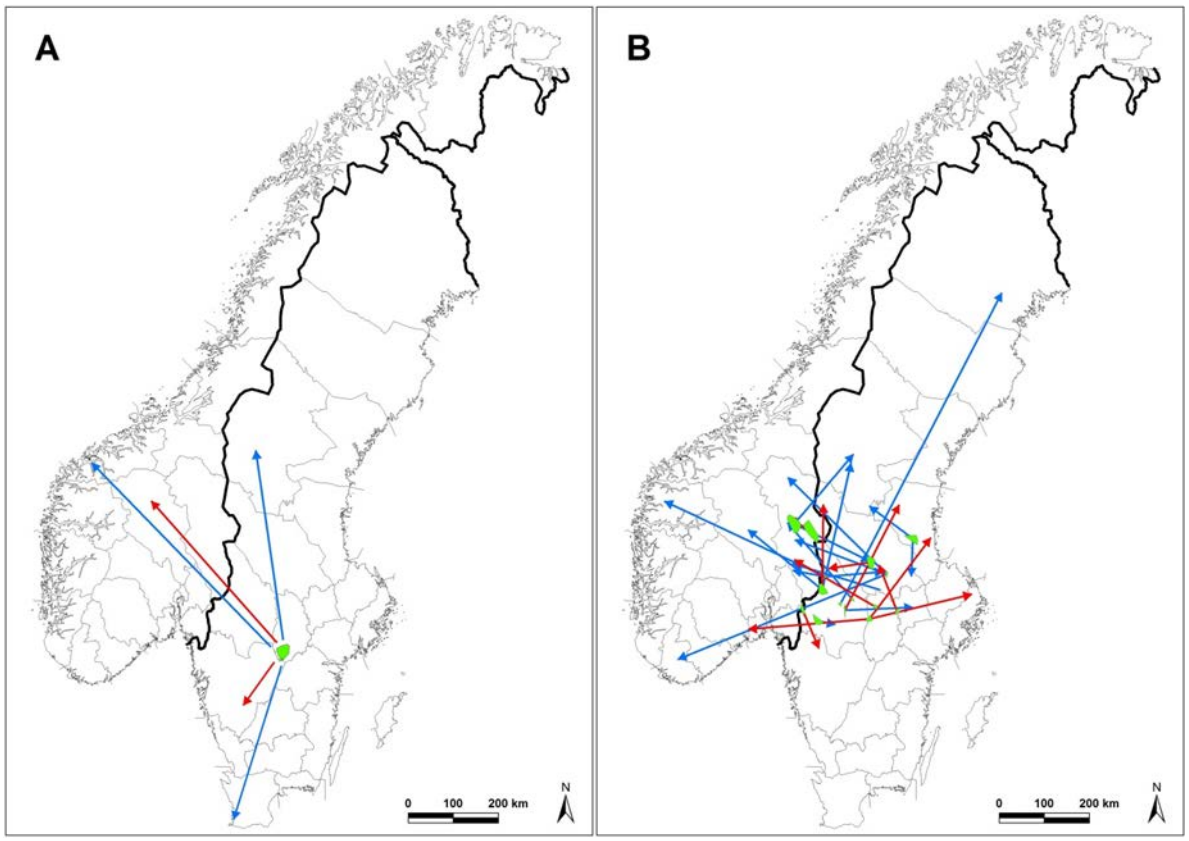

Figure 5. Distances of natal dispersal for wolves born in Scandinavia 2013 and 2014, and later confirmed dead between 2014 and 2015 (until April 30). Dispersals by males (blue arrows) and female (red arrows) are shown from the Tiveden territory (A) and the other territories (B), respectively. Natal territories are illustrated as 100% MCPs (green).