



Long-distance dispersal in red foxes *Vulpes vulpes* revealed by GPS tracking

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Abstract

Dispersal is a fundamental process that facilitates population and range expansion by providing a mechanism for colonization and metapopulation linkages. Yet quantifying the dispersal process, particularly long-distance dispersal events, has been inherently difficult due to technological and observational limitations. Additionally, dispersal distance calculated as the straight-line distance between initiation and settlement fails to account for the actual movement path of the animal during dispersal. Here, we highlight six long-distance dispersal events, representing some of the longest dispersal distances recorded for red foxes. Cumulative dispersal movements ranged from 132 to 1036 km and occurred within both sexes (1 female, 5 males). With one exception, dispersal events ranged from 7 to 22 days and tended to be directed north-northwest. Importantly, cumulative movements were up to five times longer than straight-line distances, with two foxes traveling an additional 114 and 256 km before returning to, and settling in, areas previously encountered during dispersal. This suggests a role of habitat assessment and homing behavior during dispersal and indicates that the capacity and potential for dispersal are not limiting factors to either sex in a red fox population. Dispersal capacity should thus be considered regarding transboundary management and disease control of red fox populations.

Keywords Canid · Dispersal · Long-range movements · Meso-carnivore · Scandinavia · Transboundary management · Range expansion · Disease transmission · Red fox · Norway · Sweden · Global positioning system (GPS)

Introduction

Dispersal is a fundamental process in ecology providing the mechanism behind population and range expansion (Sutherland et al. 2000; Lambin et al. 2001). Yet quantifying the dispersal process, particularly long-distance dispersal movements, has been inherently difficult due to technological and observational limitations (Nathan et al. 2003; Nathan 2005; Whitmee and Orme 2013). This also contributes to difficulties defining what represents a long-distance dispersal movement for different species. Long-distance dispersal has been alternately defined as an absolute dispersal distance, or,

as those individuals that disperse substantially further than the rest of the population (Nathan 2005). Here, we follow the latter, defining long-distance dispersal as individuals that represent outliers on the spectrum of dispersal distances recorded for a particular species.

Far-ranging individuals and the role that they play in range expansion, colonization, and metapopulation linkages are of great interest to researchers (Shigesada and Kawasaki 2002; Wabakken et al. 2007; Ciucci et al. 2009). Long-distance dispersal events by canids have been previously recognized (wolves *Canis lupus* (Wabakken et al. 2007); coyotes *Canis latrans* (Harrison 1992; Kolbe and Squires 2004); red foxes *Vulpes vulpes* (Allen and Sargeant 1993; Colson et al. 2017)). However, data are scarce and such events are believed to be notable but uncommon (Sutherland et al. 2000; Nathan et al. 2003). Thus, quantifying such movements has largely remained elusive.

Much of the previous knowledge regarding dispersal has relied on capture-mark-recapture studies or very high frequency (VHF) radio tracking technology, where dispersal is often quantified as the straight-line distance between initiation and settlement. However, this fails to account for the actual

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movement path of the animal during dispersal (Storm et al. 1976; Harris and Trehwella 1988; Allen and Sargeant 1993; Gosselink et al. 2010). Further, dispersal data may be of coarse temporal resolution or may fail to record animals dispersing long distances, potentially beyond study area or country boundaries. This oversimplification of dispersal can have implications regarding the extent of dispersal events and the understanding of the dispersal process (Nathan et al. 2003; Whitmee and Orme 2013).

The red fox, a highly adaptable and flexible generalist mesopredator, has successfully colonized most of the northern hemisphere, leading to one of the largest geographic ranges of any terrestrial mammal (Larivière and Pasitschniak-Arts 1996). The behavioral plasticity of red foxes and their ability to respond to landscape productivity changes and human subsidies has allowed them to expand into increasingly northern latitudes, which has direct implications for these ecosystems (Colson et al. 2017; Elmhagen et al. 2015, 2017). Dispersal is a prerequisite for range expansion (Clobert et al. 2001) but our understanding of how long-distance dispersal events may contribute to range expansion remains largely unknown. With advances in GPS and satellite tracking technology, it is now possible to capture dispersal events in their entirety, with high spatial and temporal resolution (Nathan 2005; Cagnacci et al. 2010). This greatly facilitates a more comprehensive quantification of individual dispersal patterns and distances traveled than previously attainable.

Here, we examine six individual long-distance dispersal events by red foxes from three different populations in Norway and Sweden using GPS telemetry. With these data, we aim to improve understanding of the characteristics of long-distance dispersal events of red foxes. Specifically, we quantify both straight-line and cumulative distances traveled, as well as the timing, duration, and directionality of these long-distance dispersal events. Further, we explore whether long-distance movements occur as a multistage process or as single events and discuss their potential implications for northern range expansions and disease transmission.

Methods

Between 2011 and 2017, we captured 101 red foxes within four different study areas in Sweden and Norway, as part of a long-term research project (see Walton et al. 2017 for details). The four study areas represent a gradient of landscape productivity and human land use. The southernmost study area, Kolmården (58° N), Sweden, consists of boreonemoral forests, agricultural lands, and scattered human settlements, while northern boreal forests and alpine tundra of low diversity and productivity characterize the northernmost study area in Hedmark County (62° N), Norway. Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominate the forests in all areas, but birch

(*Betula pubescens* and *B. verrucosa*) and other deciduous tree species are increasingly present to the south.

All captured foxes > 5 kg were fitted with GPS radio collars (Tellus Ultralight, 210g, Televilt, Inc. Lindesberg, Sweden). We further sexed, measured, weighed, and aged all captured foxes. Age was defined as sub-adult (< 1 year) or adult (> 1 year) based on the amount of tooth wear and tooth coloration. Additionally, we assumed a birth date of April 1 for young of the year (Harris and Trehwella 1988) to approximate age in months at time of dispersal. For additional description of study areas and capture methodology see Walton et al. (2017).

GPS collars varied in position schedules, with collars deployed before October 2015 programmed to take three positions per day with a drop-off after 270 days (9 months), and collars deployed after October 2015 programmed to take six positions per day with a drop-off after 180 days (6 months). We additionally had several foxes captured after 2015 with position data collected at 10-min intervals for up to 3-week periods within their standard six positions per day programming.

We determined foxes engaging in dispersal using net squared displacement (NSD) (Börger and Fryxell 2012; Gurarie et al. 2017), and visual inspection of movement data in QGIS 2.18.0 (Quantum GIS Development Team 2017). Individuals that dispersed straight-line distances greater than 60 km represented outliers on the spectrum of dispersal distances recorded, and we, thus, defined these individuals ($n = 6$) as long-distance dispersers following Nathan (2005). To allow comparison of dispersal distances among these foxes, we standardized position interval to three positions per day (the lowest maximum number of positions per day recorded). In total, 6629 GPS positions were available for further analysis. The GPS fix success rate was 98.1% with a mean horizontal dilution of precision (HDOP) of 1.06 ± 0.8 SD (range = 0–25.5). Lower HDOP values are considered to be more precise (D'Eon and Delparte 2005) and 99.7% of positions available had a HDOP < 5.0. We did not have associated HDOP satellite data for one fox, captured in 2012 ($n = 515$ records).

We identified the initiation and end points of dispersal events as the last location in the home range (prior to dispersal), to the first post dispersal location associated with settlement. Three of the six foxes were likely captured while already dispersing, as they had no pre-dispersal area use. In these cases, we classified the dispersal initiation point as the capture location. The end point of dispersal was determined by an individual remaining in the area for more than 8 weeks after dispersal, indicating settlement. However, one fox was killed by a vehicle while dispersing, and here, we classified the mortality site as the end point of dispersal. We then extracted the GPS locations associated with each dispersal movement and determined dates of initiation and end points, dispersal duration, and directionality, using R 3.4.0 (R Core

Team 2017). We calculated dispersal duration as the number of days between initiation and end points. Directionality was calculated as the geographic bearing of the straight-line between start and end positions. We used a Rayleigh test in the R package circular (Agostinelli and Lund 2017) to test if there was orientation towards a particular direction during dispersal. Dispersal distance was calculated as both the straight-line distance from initiation point to end point and as the cumulative distance of the dispersal path. We calculated cumulative distance traveled as the sum of the Euclidian distances traveled between successive 8-h positions (i.e., the movement path) of positions between the start and end points. We further calculated the ratio between cumulative dispersal distance and straight-line distance for each individual.

Results

Thirty of the 101 red foxes collared in this study dispersed during monitoring. Of these, six foxes traveled straight-line distances greater than 60 km during their dispersal period. These long-distance dispersers included both sexes (female = 1, male = 5), with sub-adult males (67%) predominantly making these movements. However, one adult male (17%) and one sub-adult female (17%) also engaged in these movements (Table 1). Straight-line dispersal distances averaged $60\% \pm 30\%$ SD (range 20–88%) of cumulative long-distance dispersal movements. The cumulative dispersal distances ranged from 132 to 1036 km and were on average 2.3 ± 1.7 SD times longer than the straight-line distances. The two longest cumulative distances were by a sub-adult female (1036 km) and a sub-adult male (423 km) (Fig. 1). Two dispersal events were

multistaged, with temporary periods of settlement during dispersal. For these foxes, the exploratory movements during their temporary settlement periods were not included in their cumulative dispersal distances (i.e., only those periods when the animal was dispersing were included in the distance calculations). The temporary settlement period for the sub-adult male, Trond, was 8 days. However, the female, Gunnel, had three temporary settlement periods lasting 4, 17, and 19 days respectively. These two foxes later returned to settle in areas they had previously explored, via different movement paths, after traveling an additional 114 and 256 km, respectively. The remaining four dispersal events were single-stage movements of short duration, ranging from 7 to 22 days (Table 1). These single-stage dispersal events occurred quickly, on average 12.5 ± 6.7 SD days, and were directed movements with cumulative distances averaging only 1.3 ± 0.1 SD times longer than the straight-line distances. With one exception, long-distance dispersal tended to occur in a north-northwest direction, with a mean geographical bearing of 329° (range 304° – 3°), though this trend was not statistically significant (Rayleigh's $r = 0.6475$, p value 0.0758). Only one fox, from the northernmost study area, dispersed south (186°).

Discussion

We recorded extraordinary, long-distance dispersal events for red foxes, exceeding expected distances based on body size (Sutherland et al. 2000) and similarly calculated published records for red foxes (Storm et al. 1976; Allen and Sargeant 1993; Gosselink et al. 2010). We found that males, and in particular, sub-adult males, were more prone to engage in

Table 1 Summary of dispersal distances for six red foxes in Norway and Sweden

FoxID	Sex	Age at dispersal (months)	Study area	Days monitored	Dispersal start (date)	Dispersal end (date)	Dispersal duration (days)	Cumulative distance (km)	Straight-line distance (km)	Dispersal bearing (degrees)
Gunde ¹	M	10.5	Hedemora	111	13 Feb	22 Feb	9	160	140	304°
Gunnel ¹	F	11	Kolmården	180	3 Mar	11 Jun	100 ³	1036	255	338°
Stefansson ^{1,2}	M	11.5	Hedemora	25	12 Mar	2 Apr	22	423	294	3°
Trond	M	13	Hedmark	50	2 May	31 May	21 ⁴	328	67	305°
Tufsing	M	8	Hedmark	210	30 Nov	6 Dec	7	133	108	186°
Wilhelm	M	23.5	Kolmården	188	10 Mar	22 Mar	12	274	216	334°

Sampling interval is standardized to three positions per day for all foxes (i.e., 8-h intervals). Included are the total dispersal movement distance (Cumulative distance) and straight-line dispersal distance from initiation point to end point. Directionality of dispersal is based on the geographic bearing of the straight-line distance. The dispersal duration includes date of initiation to date of settlement with dispersal duration calculated in days. Two foxes had multistage dispersal (Gunnel and Trond). For these foxes, temporary settlement movements are excluded from cumulative distance but included in dispersal duration. Sex, age at the onset of dispersal, and the total number of days each individual was monitored are also included

¹ Foxes were likely already dispersing upon capture

² Fox was killed by vehicle during dispersal

³ Duration includes 26 days spent navigating dispersal barrier around lake and three temporary settlement periods of four, 17 and 19 days, totaling 66 days during dispersal

⁴ Duration includes one temporary settlement period of 9 days during dispersal

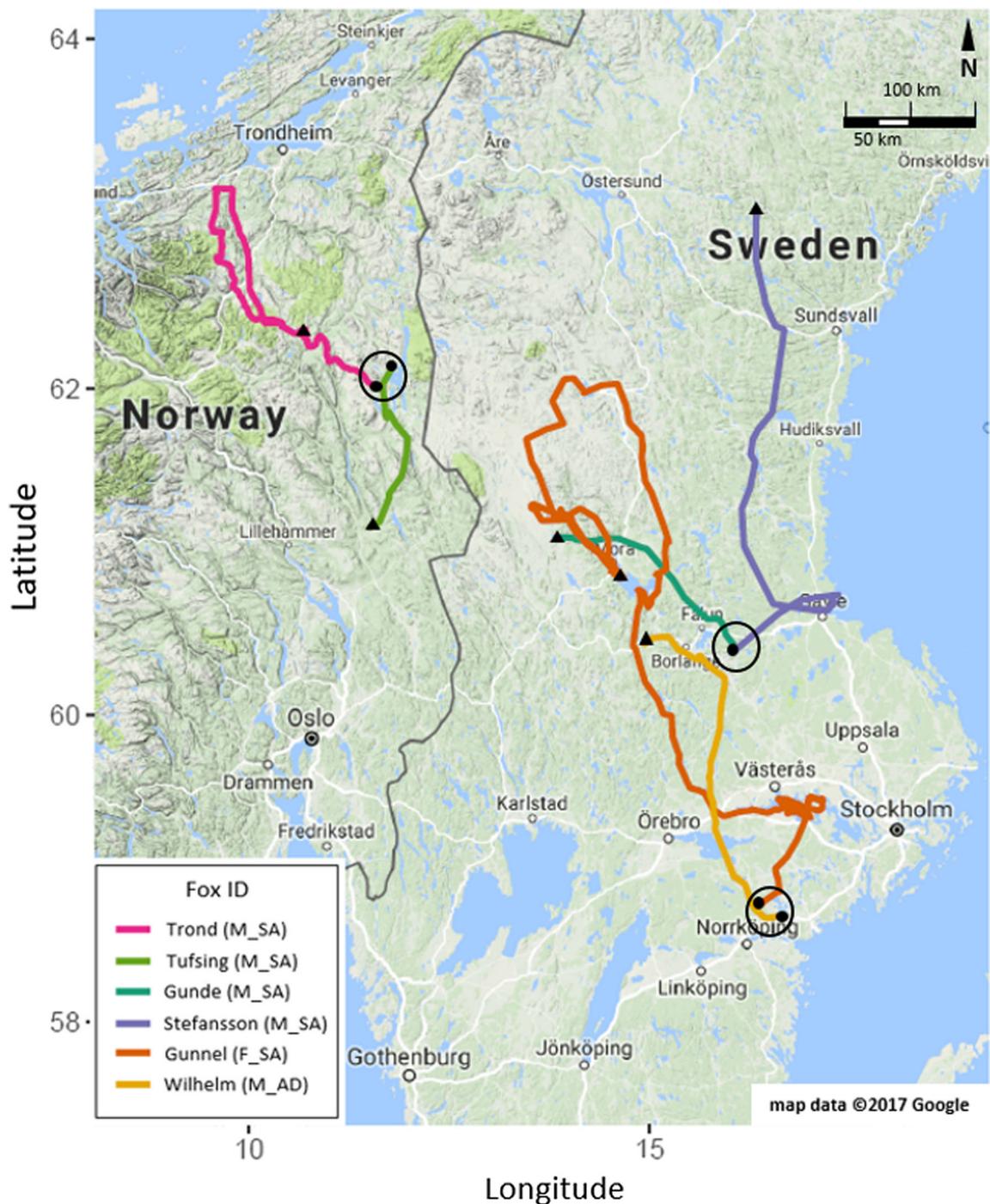


Fig. 1 Long-distance dispersal movements of six GPS-collared red foxes in Sweden and Norway. Solid black circles and triangles indicate initiation (start) and settlement (end) points of dispersal movements, respectively. The three study areas where foxes were initially captured

are outlined by black circles corresponding to Hedmark, Hedemora, and Kolmården, from North to South. The sex and age (sub-adult = SA, adult = AD) of each individual are given in parentheses in the legend

long-distance dispersal, which follows male-biased dispersal in red foxes, and mammals in general (Storm et al. 1976; Allen and Sargeant 1993; Gosselink et al. 2010). However, similar to the findings by Allen and Sargeant (1993), the longest cumulative dispersal distance (1036 km) was by a sub-adult female red fox. Genetic data also supports that, while not

common, female foxes also contribute to long-distance colonization and population expansion via long-distance dispersal movements (Colson et al. 2017). This indicates that the dispersal capacity and potential for dispersal are not limiting factors to either sex in a red fox population (Allen and Sargeant 1993; Norén et al. 2015).

We further show that long-distance dispersal and settlement occurs very quickly. On average, foxes dispersed distances greater than 100 km within 2 weeks, illustrating the potential for rapid colonization of new habitats. A comparison of straight-line distance to the cumulative movement distance for single-stage dispersal events also show that cumulative movement distances were on average only 1.3 times longer than straight-line distances. This lends support to dispersal movements being faster and straighter than other types of movements, and follows that found in earlier studies of the species as well (Storm et al. 1976; Kamler et al. 2004; Soulsbury et al. 2011).

Interestingly, with one exception, dispersal events were oriented in a north-northwest direction. A northern dispersal trend has been recognized in other red fox populations found in the northern hemisphere as well (Phillips et al. 1972; Storm et al. 1976; Allen and Sargeant 1993; Gosselink et al. 2010). Northern landscapes of lower productivity likely have lower population densities of red foxes, suggesting that dispersal and settlement may be limited by crowding and competition for available space (Lambin et al. 2001). Additionally, it is also possible that a warming climate, in synergy with agricultural expansion, forestry practices, and anthropogenic subsidies, is increasingly providing suitable habitat north of a red fox's climate-imposed distribution limit, thereby facilitating red fox range expansion into increasingly northern regions (Elmhagen et al. 2015, 2017). A northwestward dispersal direction, in combination with the distances red foxes are capable of traversing, is thus likely contributing to the rapid northern range expansion by red foxes in the northern hemisphere (Allen and Sargeant 1993; Colson et al. 2017; Elmhagen et al. 2017).

Importantly, the total distance traveled during the dispersal events can also be much longer than the distance between initiation and settlement. For example, two foxes (1 male, 1 female) had multistage dispersal events rather than single, directed movements, temporarily settling and exploring areas before continuing dispersal. Both foxes returned to settle in areas they had previously explored. However, neither of them returned via the previously used route but circumnavigated through novel terrain to the area they had previously visited. For these foxes, their cumulative dispersal distances were up to five times longer than their respective straight-line distances. Interestingly, Storm et al. (1976) recognized a similar pattern, with multistage dispersal and circular return movements to previously explored areas, in red foxes in the Midwestern USA. This suggests a degree of en route habitat assessment and homing behavior during the dispersal process.

During long-distance dispersal movements, red foxes likely traverse a variety of suitable habitat, both occupied and unoccupied. The presence of other foxes may indicate suitable settlement areas to dispersing foxes, as fox presence itself may act as an indicator of suitable habitat (Lloyd 1980). Conversely,

the presence of other foxes may also prevent establishment, as foxes may avoid occupied areas and therefore continue to move, seeking vacant areas for settlement (Lambin et al. 2001), which is concordant with establishment in mammals and birds often being limited by crowding (Wolff 1997).

The proportion of animals that disperse and their dispersal movements may be highly variable among fox populations. Our results showed that only a small proportion of individuals dispersed long distances (6 of 101 foxes collared) and these were predominantly sub-adult males, which is in concordance with previous studies (Storm et al. 1976; Trehwella et al. 1988; Allen and Sargeant 1993; Sutherland et al. 2000; Gosselink et al. 2010). Further, our study showed that there appear to be some general commonalities detected for long-distance dispersal movements regarding onset, duration, and geographical orientation. With advances in GPS technology and quantitative tools for analysis of animal movement data, it may be possible to obtain a more precise picture of dispersal and the decision-making processes underlying these movements. With these techniques, we can also begin to address important questions involving population dynamics, range expansion, and disease spread (Phillips et al. 1972; Morales et al. 2010).

Although long-distance dispersal is infrequent, our study demonstrates the red fox's ability to traverse between populations, across landscapes, and potentially across international boundaries. Circumpolar data show that red foxes are advancing into increasingly productive tundra (Colson et al. 2017; Elmhagen et al. 2017). As a highly adaptable species, red foxes with strong dispersal abilities likely dominate this expansion front and drive these northern range expansions (Norén et al. 2015). As such, long-distance events are important for the spread of the species (Kot et al. 1996) and have implications for disease transmission (Letková et al. 2006; Vervaeke et al. 2006) and the surrounding ecosystems (Elmhagen et al. 2017). Long-distance dispersal capacity should thus be considered regarding transboundary management, range expansion, and disease control of red fox populations.

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