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Movement across scales: red fox spatial ecology

PhD in Applied Ecology and Biotechnology
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“Understanding animals from the animals’ perspectives will be a messy, irregular, complex process and the results will be difficult to map. We must embrace this messiness; it simply represents the real behaviors of animals in complex and variable environments.”

- Powell and Mitchell, 2012 *Journal of Mammalogy*

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Abstract

Movement across scales: red fox spatial ecology

The impact of human activities is altering natural habitats, reducing the ability of some animals to move, while facilitating other, generalist species, such as the red fox *Vulpes vulpes*. Our understanding of red foxes in rural and human modified landscapes is constrained by a lack of knowledge about how foxes use these landscapes. In this thesis I investigated the spatiotemporal movement patterns of red foxes along a landscape gradient of human influence using individual based GPS telemetry data from red foxes collected in Norway and Sweden between 2011- 2019. Herein, I identified much larger home ranges than previously recorded for red foxes and a high degree of individual variation, partially explained through environmental factors along a landscape gradient. At lower elevations, where productivity and the amount of available agricultural land increased, red foxes had home ranges approximately four times smaller than the home ranges of foxes in the northern boreal vegetation areas. I also identified cognitive mapping as a feature of red fox space use, linked to recursive movements within home ranges and contributing to bounded space use. On average, 43% of a red fox's positions were found in defined clusters that covered a proportional area of only 1% of their home range. I highlighted the red fox's ability to traverse between populations, across landscapes, and potentially across international boundaries, by identifying six long-distance dispersal events, representing some of the longest dispersal distances recorded for red foxes. However, I also showed that fine scale familial structuring in red foxes occurred by social mechanisms not linked to their movement ability or dispersal capacity. I found significant differences in pairwise geographic distances between highly related same sex pairs with the average distance between related males, 37.8 km, being six times farther than that of related females, averaging 6.3 km. This highlights how social dynamics (e.g. kin clustering and female philopatry) play a role in the spatial organization of red foxes. Finally, I showed that recognizing red fox behaviors is dependent on not only identifying their associated movement patterns, but also understanding the temporal and spatial scales at which their movements occur. Identifying the unique and variable behaviors of a highly flexible species such as the red fox is difficult and shows the ecological plasticity of the species. Together, this information represents new observations that greatly expand our knowledge of red fox space use and dispersal in rural landscapes and opens the door for future research into the broader ecosystem consequences of such movements. Overall, this thesis increases our understanding of red fox movement behaviors and their interactions with social and environmental factors at multiple spatial scales, with implications for future research, management and demographic and disease modeling.

Keywords: animal movement, GPS, behavior, home range, dispersal, philopatry, excursions, cognitive mapping, landscape productivity, individual variability, social structure, range expansion, *Vulpes vulpes,* Scandinavia

Sammendrag

Rødrevens forflytningsmønster på forskjellige romlige skalaer

Menneskelig påvirkning på naturlige habitater kan medføre reduserte bevegelsesmuligheter for noen dyrearter, eller fasilitere typiske generalister som rødrev *Vulpes vulpes*. Vår forståelse av rødrev i landskaper dominert av menneskelige aktiviteter er begrenset av manglende kunnskap om hvordan revene beveger seg i disse områdene. I denne avhandlingen undersøkte jeg temporale og romlige mønstre i forflytningene til rødrever langs en gradient av menneskelig påvirkning ved bruk av GPS-telemetridata innhentet i Norge og Sverige fra 2011 til 2019. Rødrevenes leveområder var langt større enn observert i tidligere studier, og med en markant individuell variasjon som delvis kunne relateres til miljøfaktorer langs en landskapsgradient. I lavereliggende sørlige områder med relativt høy primærproduksjon og mye landbruk var revenes leveområder fire ganger mindre enn i høyereliggende nordlige barskogområder. I gjennomsnitt var 43% av revenes posisjoner innenfor klustere som dekket bare 1% av leveområdene. Dette indikerte at rødrevenes kognitive kartlegging innebar repetitive bevegelser som bidro til avgrensing av leveområdene. Noen rever viste også en betydelig evne til å forflytte seg lange avstander under spredning, mellom populasjoner og landskaper, og potensielt over nasjonale grenser. Allikevel viste revene en genetisk struktur på liten romlig skala som var knyttet til sosiale mekanismer heller enn forflytningsevne og spredningskapasitet. Parvise distanser mellom nært beslektede hunndyr (gjennomsnitt = 6.3 km) var signifikant kortere enn avstandene mellom beslektede hanner (37.8 km). Dette understreker at sosiale forhold (som slektskap) spiller en viktig rolle i rødrevenes romlige organisasjon. Mine resultater viser at forståelsen av rødrevens forflytninger forutsetter god innsikt i hvilken temporal og romlig skala bevegelsene foregår. Å klassifisere unike og variable atferdstrekk hos en svært fleksibel art som rødrev er veldig vanskelig, og dette understreker artens økologiske plastisitet. Alt i alt har denne avhandlingen gitt ny innsikt i hvordan rødrevens forflytningsmønster er påvirket av sosial struktur og miljøfaktorer på forskjellige romlige skalaer. Dette har betydning for framtidig forskning og forvaltning, samt for modellering av revenes demografi og sykdomsspredning. Informasjonen gir økt innsikt i rødrevens områdebruk og spredning i rurale områder, og åpner for nye muligheter for forskning på denne artens påvirkning på økosystemer.

Nøkkelord: dyrebevegelse, GPS, atferd, leveområde, spredning, utflukter, kognitiv kartlegging, landskapsproduktivitet, individuell variabilitet, sosial struktur, utvidelse, *Vulpes vulpes*, Skandinavia

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Abbreviations

AIC – Aikake's Information Criteria

VHF – Very High Frequency

GLM – Generalized Linear Model

GPS – Global Positioning System

GSM – Global System for Mobile communication

HR – Home Range

LDD – Long Distance Dispersal

NSD – Net Squared Displacement

rNSD – Relative Net Squared Displacement

SNP – Single Nucleotide Polymorphism

UTM – Universal Transverse Mercator

List of Papers

This thesis is based on the following original publications and manuscripts, referred to by roman numerals in the text.

Paper I

Walton, Z., Samelius, G., Odden, M., & Willebrand, T. 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. PLoS ONE 12(4): e0175291. https://doi.org/10.1371/journal.pone.0175291

Paper II

McKeown, B., Walton Z., Willebrand, T. 2020. Does recursive use of resource locations shape a home range? Exploring the red fox's cognitive map. Wildlife Biology 2020(1). https://doi.org/10.2981/wlb.00602

Paper III

Walton, Z., Samelius, G., Odden, M., & Willebrand, T. 2018. Long-distance dispersal in red foxes *Vulpes vulpes* revealed by GPS tracking. European Journal of Wildlife Research, 64(6). https://doi.org/10.1007/s10344-018-1223-9

Paper IV

Hagenlund, M., Walton, Z., Østbye, K., Samelius, G., Odden, M., Norman, A., Willebrand, T., Spong, G. 2019. Fine scale genetic and spatial structure of a red fox population reveals kin clusters and sex-biased dispersal patterns – *Manuscript*

Paper V

Walton, Z., Devineau, O., Mattisson, J., Odden, M., Samelius, G., Willebrand, T. 2019. Foxes don't fit in boxes: variability in movement patterns of the red fox – *Manuscript*

Papers I, II and III are reprinted with permission from the publishers.

Introduction

An animal's ability to move is a fundamental aspect of its ecology and reflects how an individual perceives and reacts to its environment (Nathan et al. 2008). Different animal movement behaviors, such as residency and dispersal, may expose individuals to conditions that can differentially affect their survival and reproduction (Bergman et al. 2001, Bowler and Benton 2005). Not all animals within a population may respond or behave in the same way, and these individual differences can lead to variation in habitat selection and space use patterns at multiple scales. These differences are important, as the behavioral plasticity of individuals to respond to changing environmental and social conditions through movement may be crucial to their survival and reproduction, influencing their population dynamics (Berger 2004, Debeffe et al. 2014, Cote et al. 2017, Lai et al. 2017, Couriot et al. 2018).

The red fox *Vulpes vulpes,* is a species remarkable in both its geographic range and its adaptable behavior. The ability of red foxes to positively respond to land use change and human subsidies has led to successful colonization across most of the northern hemisphere and contributed to one of the largest geographic distributions of any wild, terrestrial mammal (Larivière and Pasitschniak-Arts 1996). This behavior has also facilitated red fox exploitation of habitats ranging from arctic to temperate and rural to highly urbanized landscapes, more successfully than many other species (Contesse et al. 2004, Prugh et al. 2009, Rotem et al. 2011, Šálek et al. 2015). This has contributed to both population increases and northern range expansions (Prugh et al. 2009, Elmhagen et al. 2017, Gallant et al. 2019). Indeed, red foxes are now viewed as 'invasive' or overabundant in much of their range (Hradsky et al. 2017).

In Scandinavia, there is concern that the red fox is becoming a driving species affecting the food webs of arctic systems, boreal forests, agricultural landscapes and even more urban areas (Marcström 1968, Goszczyński 2002, Kujawa and Łęcki 2008, Elmhagen et al. 2010, Mo et al. 2018). As human land use is likely to further intensify in synergy with climate warming (Elmhagen et al. 2015), red foxes are expected to increasingly exploit these areas, causing negative impacts in these systems, for example through increased competition or predation pressure on threatened, endangered or popular game species, or through facilitating the spread of zoonotic diseases, such as *Echinococcus multilocularis* (Lindström et al. 1994, Tannerfeldt et al. 2002, Elmhagen et al. 2015, Oksanen et al. 2016, Gallant et al. 2019). However, our understanding of red foxes in rural and human modified landscapes is constrained by our lack of knowledge about how foxes use these landscapes on a daily, monthly or seasonal basis. Knowledge regarding red fox ecology and their impacts in such systems is therefore of growing interest in conservation and management (Ritchie and Johnson 2009). Thus, it is increasingly relevant to have a better understanding of the ecology of red foxes in both natural and modified landscape settings within Scandinavia.

In order for management actions to be effective, they require sound ecological knowledge of the target species. Monitoring individuals from multiple areas across their distribution can improve our understanding of red fox spatial ecology across large geographic areas. Additionally, identifying the spatiotemporal scale at which movements take place is also important as demographic and behavioral process can operate at a range of scales to generate different ecological patterns (Anderson et al 2010). Despite the red fox being a ubiquitous canid across the northern hemisphere, their cunning and elusive nature has complicated movement data collection, particularly in rural populations. This has constrained our understanding of red fox spatial ecology. Electronic tracking (VHF, GPS) has perhaps been one of the most important technological advancements in our understanding of animal movements and their ecology (Nathan et al. 2008, Wilmers et al. 2015). Today, GPS telemetry allows for collection of high resolution data across large spatial and temporal ranges for smaller and smaller species, resulting in the ability to gather of magnitudes more detailed, fine-scale data than previously possible with conventional VHF transmitters. Access to data collected over large spatial and temporal ranges allows us to examine questions at different spatial scales using the same datasets (Benhamou 2014) and ultimately provides better understanding of behavioral patterns, individual movements, home range sizes and predictions of resource use than previously available for foxes.

To understand the spatial dynamics of red fox populations it is necessary to study the individual variation in their space use and dispersal characteristics. Furthermore, limited research has been conducted comparing spatiotemporal variation between mesocarnivore populations with different habitat characteristics and across latitudinal gradients (Gompper and Gittleman 1991, Šálek et al. 2015). By examining the spatiotemporal movement patterns of red foxes along a landscape gradient of human influence, and the variation that may be exhibited within those movements, we can begin to understand different space use and behavioral patterns that may be relevant for management (Allen et al. 2016). This will aid in improving species knowledge as well as contribute to better predictive models of disease spread, range expansion, social interactions and resource exploitation. This also opens the door to understanding the drivers of these movement decisions, the transitions between movements (e.g. dispersal rates), and fine scale movement behaviors underlying broad scale movement patterns (Nathan et al. 2008, Demšar et al. 2015).

This thesis broadly represents a step towards a better understanding of the spatial ecology of the red fox in boreal ecosystems, with implications for future research, management and demographic and disease modeling. I provide expanded insights into movement behaviors of red foxes, using individual based data acquired through GPS tracking of 134 red foxes spanning eight years within four study areas. As one of the first GPS telemetry studies of red foxes, this high resolution data provides opportunities to study the spatial dynamics of the red fox in a manner that was not previously possible. I investigate the spatial ecology of the red fox at different spatial scales, exploring factors contributing to variation in home range size along a landscape gradient, use of resource locations within a home range, the influence of social structure on red fox spatial structure and long distance dispersal events by red foxes. I also explore the variation and complexities of categorizing the different movement patterns that red foxes exhibit.

Objectives

I focus in detail on resident and dispersal behaviors of red foxes at differing spatial scales to answer the following general questions:

Does home range size of red foxes vary along a landscape gradient or by sex? What factors contribute to variability in home range size of resident red foxes? (Paper I)

Home range size is one of the most commonly reported ecological attributes of free-ranging mammals, which can vary greatly across taxa, populations and individuals (Harestad and Bunnel 1979, Maher and Lott 2000, Mcloughlin et al. 2000). Home range size can be influenced by a complex array of ecological and social factors (Nilsen et al. 2005, Mattisson et al. 2013, Duncan et al. 2015, Šálek et al. 2015). Previous studies indicate that red foxes display great variability in home range size (reviews in Voigt and Macdonald 1984 and Cavallini 1996). Yet, there has been little focus on the space use of the red fox from boreal Scandinavian ecosystems, and surprisingly little consensus as to why home range sizes of red foxes can vary so extensively. Further, few studies have examined how the size of red fox home ranges may be influenced by landscape changes along a gradient (but see Šálek et al. 2015). Paper I targets these knowledge gaps.

Do red foxes show recursive movements to resource locations within their home range? Does reuse of resource locations shape a home range? (Paper II)

An animal's spatial memory of landscape features and resources within a home range and their evaluated attributes represents its cognitive map. To assess if a home range is shaped by recursive movements between memorized resource locations i.e. through cognitive mapping (Mitchell and Powell 2004) we identified the resources and landscape features that likely influenced movement decisions by ground-truthing the site-specific attributes of revisited locations. In this way, we identified key habitats, including landscape features and foraging areas, to better understand the resources and sites identified as important within each individual's home range. We also examined whether recursive movement patterns influenced the spatial configuration of a home range by constraining space use, allowing us to better understand the mechanistic processes underlying home range formation.

Does long distance dispersal occur in red foxes? (Paper III)

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). Quantifying the dispersal process, particularly long-distance dispersal events, has been inherently difficult due to technological and observational limitations. With advances in GPS tracking technology, it is now possible to capture dispersal events with high spatial and temporal resolution (Nathan 2005, Cagnacci et al. 2010). Paper IV provides new insight regarding long distance dispersal movements of the red fox.

Does the genetic structure of the red fox vary at different spatial scales? (Paper IV)

Combining genetic information with spatial movement data allows us to determine an individual's relatedness to other members of the population to better understand how social structure can contribute to red fox spatial structure and to dispersal and other movement behaviors seen at larger scales. It also aids in understanding how dispersal translates to gene flow (Prugnolle and De Meeus 2002). In Paper IV, we investigated the spatial and genetic structuring of red foxes within south-central Sweden at two different scales. First, we looked at regional scale genetic structuring among red foxes. We then evaluated the spatial and genetic structure of highly related male, female and mixed sex pairs to explore patterns of philopatry and dispersal at a more localized scale.

Does a behaviorally flexible species such as the red fox fit to commonly recognized movement patterns of resident, disperser and nomad movement behaviors? (Paper V)

Characterizing movement behaviors of red foxes is an important step in understanding their ecology (Bastille-Rousseau et al. 2015, Wheat et al. 2017) and interpreting these behaviors is dependent not only on identifying their associated movement patterns, but also the temporal and spatial scales at which their movements occur (Bunnefeld et al. 2011). In Paper V, we assessed the movement behaviors that characterize a behaviorally flexible and generalist species, the red fox. We also examined the spatial scale at which resident, disperser and nomadic movement behaviors occurred.

Methods

Study areas

The studies took place in four different areas within Sweden and Norway between 2011 and 2019. These areas represent a landscape gradient of decreasing environmental productivity and human land use (58°–62° N; Fig 1). The main study area, around Kolmården, Sweden (58°40′N-16°22′E), is a mosaic of agriculture lands, boreonemoral forests and human settlements, representing a more productive and anthropogenically modified landscape. The northernmost fox trapping area, in Hedmark County, Norway (61°53′N 12°2′E), lies around 600-800m a.s.l. and is a transitional border zone between northern boreal forest of low productivity and alpine tundra. Hedemora (60°16′N-15°59′E) and Grimsö (59°40'N-15°25'E) are both located in south-central Sweden and consist of a transitional border zone between boreonemoral forests in the south and boreal forests in the north. Kolmården (58°40'N-16°22'E) is a mosaic of productive agriculture areas, boreonemoral forests and human settlements, thus representing a productive and more anthropogenically modified landscape. In general, the southernmost landscapes are more fragmented, consisting of boreonemoral forests, agricultural lands, and scattered human settlements. 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

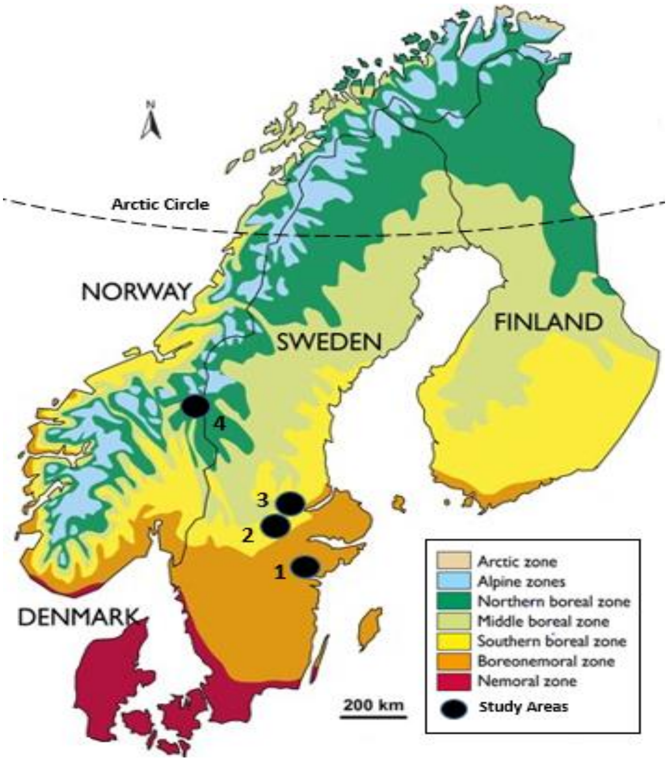

Figure 1. The four study areas in Sweden and Norway along a landscape gradient of environmental productivity, human land use, and latitude. From south to north the study areas are: (1) Kolmården, (2) Grimsö, (3) Hedemora, and (4) Hedmark. Vegetation zone classifications were adapted from Moen and Lilletun (1998) and Rydin et al. (1999) for Norway and Sweden, respectively.

increasingly present to the south. Geographically, Hedmark is approximately 300-350km northwest of Hedemora and Grimsö, and 500km northwest of Kolmården, Sweden (Fig. 1). Kolmården is separated from Hedemora by approximately 200km, whereas Grimsö is ~130km north of Kolmården (Hedemora is located ~70km north of Grimsö). Further detailed description of the study areas can be found in Paper II.

Capture & handling of red foxes

Ethical Statement

Red fox capture and handling protocols differed in Norway and Sweden, however all capture and handling procedures followed the ethical guidelines required by the Swedish Animal Ethics Committee (permit numbers DNR 70-12, DNR 58-15) and the Norwegian Experimental Animal Ethics Committee (permit numbers 2009/122825, 2012/20038,2014/207803). In addition, permits to capture wild animals were provided by the Norwegian Directorate for Nature Management and the Swedish Environmental Protection Board (NV-03459-11).

Red fox capture

Between 2011 and 2019, we captured and equipped 134 red foxes with GPS/GSM telemetry collars (Tellus Ultralight, 210g, Televilt, Inc. Lindesberg, Sweden). All foxes were initially captured using baited wooden box traps. Foxes captured in Sweden were then immobilized using 2mg/kg ketamine which was later reversed with 0.4mg/kg atipamizole (Kreeger and Arnemo 2012). In Norway, adjustable straps were used to restrain captured foxes, which were then processed quickly and safely without chemical immobilization. Captured foxes were sexed, measured, weighed, and aged. Age was defined as pup (<6 months), sub-adult (<1 year) or adult (>1 year) based on an approximate birth date of April 15th (Englund 1970) and the amount of tooth wear and tooth coloration. Only foxes meeting necessary weight requirements (>5kg) were fitted with radio collars. Six foxes were re-collared during the study period.

Data collection

All papers in this thesis are based on individual GPS collar technology used to track the movements of 134 red foxes captured in Sweden and Norway between 2011 and 2019. Papers I, II and V include red foxes from both Norway and Sweden while Papers III and IV focus on red foxes from Sweden only. In addition, for Paper IV we supplemented the GPS data with individual genotypes of red foxes from our southernmost study area, Kolmården.

GPS data

Collars deployed before October 2015 were programmed to take three positions per day with a drop-off after nine months, and collars deployed after October 2015 were programmed to take six positions per day with a drop-off after six months. For Papers I, II and V positioning was standardized to eight hour intervals across all foxes. For paper III, four hour positioning was used.

Genetic data

We collected genetic material (hair, tissue or blood) from all live captured red foxes and opportunistically collected red fox scat and tissue samples from deceased, unmarked red foxes found during field monitoring of GPS collared foxes. DNA extraction and genotyping were performed at the Swedish University of Agricultural Sciences (SLU) in Umeå, Sweden. DNA was extracted from sampled tissue, blood, feces and hair after a review of eight different methods/kits by the lab. Individuals were then genotyped using a 96 marker Single Nucleotide Polymorphism (SNP) assay specifically developed for Scandinavian red foxes (H. Königsson and M. Hagenlund unpublished methodology).

Data analyses

We used the program R (R Development Core Team 2019) throughout the thesis. However, ArcGIS 10.1 (ESRI 2011; Paper II) and QGIS 2.18 (QGIS Development Team 2011; Paper III and Paper IV) were used for spatial analysis of habitat and elevation characteristics within each red fox's home range. Home range estimates for papers I and II were calculated using the R package adehabitat (Calenge 2006). Additional analyses of the red fox genotype data were accomplished using the software programs Genepop 4.2 (Raymond and Rousset 1995, Rousset 2008), Structure (Pritchard et al. 2000), Structure Harvester (Earl and von Holdt 2012) and the R packages Adegenet (Jombart 2008) and Related (Wang 2011, Pew et al. 2015). Specific methodologies and analyses are described for each paper below.

Variation in home range size (Paper I)

We used GPS data collected between 2011-2015 from 52 stationary red foxes (with at least 84 days of monitoring) across four study areas representing a gradient of landscape productivity and human landscape alteration in Norway and Sweden. We derived home range estimates using Local Convex Hulls, a nonparametric kernel method using a fixed number of nearest neighboring points calculated as the square root of the number of positions for each animal (LoCoH-k) (Getz and Wilmers 2004, Getz et al. 2007), as well as minimum convex hulls (MCPs) for comparison with previous studies. We then examined how red fox home range size varied in relation to elevation, vegetation zone, proportion of agricultural land and human settlement within a home range, and sex and age through AIC model selection of linear models. We obtained land cover and elevation from digitized topographic maps of Sweden (Swedish Land Cover (SMD) National Land Survey of Sweden) and Norway (Norwegian Mapping Authority). We calculated the proportion of agricultural land and human settlement within each home range. Similarly, we calculated the mean elevation for home ranges and the latitude for the centroid of each home range. Finally, we used vegetation maps adapted from Moen and Lillethun (1999) and Rydin et al. (1999) for Norway and Sweden, respectively, to categorize red fox home ranges according to the vegetation zone in which the home range was located; as either the boreonemoral zone (BN), the southern boreal zone (SB), or the northern boreal zone (NB) (Fig 1).

Recursive movements within a home range (Paper II)

We investigated within home range movements for recursive behavior, suggesting a cognitive map, using 14 GPS collared foxes programmed to take positions at four-hour intervals. All red foxes had a minimum of 30 days of stable home range use within one of two seasonal periods: winter (1st Dec. - 28th Feb.) or summer (1st May - 31st Aug.). These periods were chosen to both investigate seasonal differences and to largely avoid temporal periods coinciding with the birth period of red foxes, which can influence the number of successful GPS positions due to underground denning behavior. We estimated 100% MCPs to represent the spatial extent available to each fox during their study period. Clustering of GPS positions was used to identify recursive site use and movement patterns, using the R package ‘dbscan’ (Hahsler et al. 2017). Dbscan is a density based clustering algorithm, using both a user defined radius around each position and a minimum of positions to define a cluster. We counted the total number of independent visits to each cluster to measure recursive use of cluster locations. Independent visits were defined as a position in a cluster following a preceding position that was not. To investigate whether the dispersion of recursively used resources was directly linked to the total area traversed by the foxes, we compared the area of the median center points of all clusters to the home range size of the fox. It was then possible to test for correlation between the dispersion of cluster centers, and the total area traversed by the foxes.

Each individual cluster was visited in the field. By ground-truthing the site-specific attributes of cluster locations, we identified key habitats, including landscape features and foraging areas, to better understand the resources and sites identified as important within each individual’s home range. Here, we attributed cluster causes to five broad categories: ‘food’, ‘shelter’, ‘vantage point’, and ‘route’ or ‘unidentified’. ‘Food’ was subdivided into ‘Hunting’, where there was clear sign of live prey such as burrows, or game and wildfowl feeding stations; or ‘Scavenging’ where we found food waste or other carrion. ‘Shelter’ was subdivided into ‘Bed’ where we found evidence of surface resting sites with signs of fox presence (e.g. hairs), or 'Den' where we found subterranean excavations. Where clusters were located on or around natural highpoints, or outcrops in the local topography, we identified these as 'Vantage Points'. Positions along paths, roads, clear game trails or necessary routes through gaps and holes in fences were identified as 'Routes'. Locations where we were unable to identify a probable use remained as 'Unclassified'. We recorded the primary habitat within a twenty-meter radius of the cluster center according to five broadly classified habitat types. We also recorded an estimate of horizontal sightability, ruggedness, and distance to human settlement. A classification tree method was used to identify the variables that best classified cluster use as either food, route, shelter or vantage using the package R.Part (Therneau et al. 2017). Explanatory variables included diel phase, season, sex, habitat-type, distance to human settlement, sightability, ruggedness and canopy openness.

Long distance dispersal movements (Paper III)

Here, individuals were defined as a long distance dispersers by having dispersed a straight-line distance greater than 60km, thus representing outliers on the spectrum of red fox dispersal distances (Nathan 2005). We examined the proportion of individuals representing long-distance dispersers in Norway and Sweden and the dispersal characteristics of these long distance dispersers using GPS telemetry. 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). We determined the initiation and end points of each dispersal event using change points of net squared displacement (NSD) (Börger and Fryxell 2012, Gurarie et al. 2016), and visual inspection of movement data in QGIS 2.18.0 (QGIS Development Team 2011). 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 eight weeks after dispersal, indicating settlement. One fox was killed by a vehicle while dispersing, and here, we classified the mortality site as the end point of dispersal. Dispersal duration was calculated 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 and 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. In this way, we could provide a descriptive summary of long distance red fox movements.

Social structure and spatial organization patterns (Paper IV)

To explore the genetic structure of red foxes we ran Genepop 4.2 (Raymond and Rousset 1995, Rousset 2008) on adult and subadult foxes. In Genepop, we calculated basic marker statistics, such as expected heterozygosity (He), observed heterozygosity (Ho) and deviations from Hardy Weinberg equilibrium (HWE). We then ran a spatial principal component analyses (sPCA) in the R package Adegenet (Jombart 2008) to visualize genetic differentiation geographically, both regionally and locally. The sPCA was run on the full dataset, as well as for subsets of male and female individuals from the southernmost trapping area around Kolmården, Sweden, to explore how distribution of genetic variation varied with sex locally. The K Nearest Neighbor algorithm was used with two neighbors for all runs (Jombart and Collins 2015). For comparison, we also ran Structure software (Pritchard et al. 2000) to explore genetic structure using an admixture model and correlated allele frequencies with 100 000 burn-in steps and 100 000 Markov chain Monte Carlo (MCMC) iterations and 10 replicates for each of the runs for K populations = 1-10. Here again, all individuals and the subsets of local females and males from the Kolmården area, as described above were run. The most likely number of clusters (based on LnP(K) and ΔK) was determined using Structure Harvester (Earl and von Holdt 2012) and cluster membership was assigned using a cutoff q-value of 0.80.

To determine kinship among individuals, we determined the relatedness coefficient (r) using the R package Related Related (Wang 2011, Pew et al. 2015) between all individual pairs going back two generations. The r-value is estimated from similarities in the number of shared identical alleles, in relation to the population level allele frequencies. A first-degree pair is expected to show an r-value of approximately 0.5. Such relationships include the individual's parents, full siblings, and offspring. A second degree relative will show an r-value of approximately 0.25, which includes the individual's grandparents, grandchildren, aunts, uncles, nephews, nieces or half-siblings. To determine if kin were spatially clustered at the local scale, we evaluated the pairwise mean geographic distances among all pairs of first degree relatives ($r \geq 0.40$) for the different sex combinations: female-female, opposite sex, and male-male, using Welch two sample t-tests. For analysis of spatial structure and calculating pairwise relatedness distances, we used the last position of each GPS collared animal. Using the last position rather than the original trapping location allowed for animal movements over time, such as dispersal, to occur. For scat or tissue, we used the coordinates taken directly at the site of field collection using a hand held GPS unit. For analyses at the regional and local levels we included only adult and subadult foxes. We also examined how pairwise distances varied according to differing degrees of relatedness. For this, we categorized all red fox individuals according to their relatedness values where values of 0-0.10 and 0.10-0.20 indicated unrelated or distantly related individuals, 0.21-0.40 intermediate or second-degree relatives and ≥ 0.40 to be first-degree relatives.

Classification of movement behaviors (Paper V)

We classified the movement patterns of all foxes monitored more than 30 days, standardized to 8 hour intervals across all individuals (n= 112 individuals) using calculations of net squared displacement (NSD). The movement metric NSD represents the squared Euclidean distance from an individual's first position to each subsequent position. When plotted over time, patterns of NSD are informative for characterizing broad scale animal movement patterns (Bunnefeld et al. 2011, Börger and Fryxell 2012), such as residency, transience, migration, mixed migration or dispersal (Bastille-Rousseau et al. 2015, Gurarie et al. 2016, Singh et al. 2016, Spitz et al. 2017; Fig. 2) both within and across taxa (Cagnacci et al. 2016, Abrahms et al. 2017).

We initially classified individuals by plotting a time series of NSD to identify patterns and change points in each trajectory indicative of different animal movement behaviors. We used these NSD patterns, in conjunction with visual inspection of each animal's movement trajectory to identify resident, dispersing and nomadic movements. We then quantitatively fit each individual's time series of NSD values to a priori statistical models representing idealized conceptualizations of three movement behaviors: resident = asymptotic, disperser = sigmoid, or nomad = linear using

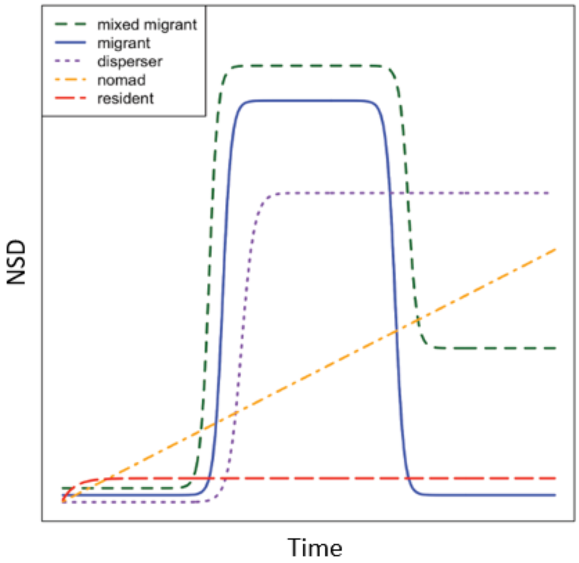

Figure 2. Conceptual illustration of net squared displacement (NSD) based model families representing the five a priori movement classifications: mixed migrant, migrant, disperser, nomad and resident. For red foxes, we focused on disperser, nomad and resident behaviors. Figure reprinted with permission from Spitz et al. (2017).

the R package migrateR (Spitz et al. 2017). MigrateR uses maximum likelihood estimation to determine which of the patterns fit the data best. We input a species-specific restriction into the model, specifying a minimum duration of secondary range occupancy of five days as criteria for quantifying dispersal behavior in order to reduce the influence of exploratory excursions. We determined the best supported NSD and rNSD models and retained both sets of model classifications for comparison with the visual classifications. The visual and model based classifications were then assessed for consistency in movement behaviors. For individuals that showed consistent classification across methods, we considered their range of values as representing more stereotypical movement patterns (Cagnacci et al. 2016). In contrast, inconsistencies between classifications, likely due to individual variation within these patterns, were explored in further detail. We also examined classifications to assess the biological relevance of the different classifications according to sex and age classes of red foxes. We further examined the net displacement (ND) values (e.g. variances, means and maximums) to understand the scale at which red fox movements were taking place.

Results and Discussion

Does home range size of red foxes vary along a landscape gradient or by sex? What factors contribute to variability in home range size of resident red foxes? (Paper I)

We found considerable individual variation in red fox home range sizes, ranging between 0.95km^2 to 44km^2 (LoCoH 90%). These home range sizes were much larger than previously reported for red foxes (Voigt and Macdonald 1984, Cavallini 1996). GPS collars likely detected red fox movements over greater spatial scales and frequency or duration than previous spatial studies using VHF technology, thereby enlarging previous estimates of red fox home range size (Johansson et al. 2016). Elevation, proportion of agricultural land and sex accounted for 50% of the variation in home range size found in the foxes, though differences attributed to sex were negligible. Elevation had the strongest effect, with home range sizes predicted to increase by 0.03km^2 for every 100m of increased elevation ($\beta 1 = 0.003 \pm 0.001$ SE). Along a landscape gradient, latitude and elevation play a role in determining environmental productivity and related prey availability (Jedrzejewski and Jedrzejewska 1996, Herfindal et al. 2005, Saïd et al. 2009). Increasing elevation or latitude can constrain landscape productivity (e.g. through food availability, length of vegetation growth period, duration and thickness of snow cover) and increase energy consumption for animals living in northern ecosystems (e.g. thermoregulation, movement and foraging in snow) (Boitani and Powell 2012). This likely contributed to the larger home ranges of red foxes in less productive, higher latitude or elevation environments (Table 1). For example, only one red fox home range in the northern study area was smaller than 10 km^2

(90% LoCoH-k, n = 8), while only three red fox home ranges located in the three southern study areas were larger than 10 km^2 (90% LoCoH-k, n = 44). Larger home ranges at higher latitudes and elevations have also been found for wolves in Scandinavia (Mattisson et al. 2013), and this pattern has been found in ungulates as well (Morellet et al. 2013).

At lower elevations, where productivity and the amount of available agricultural land increased, red foxes had home ranges approximately four times smaller than the home ranges of foxes in the northern boreal vegetation areas (Table 1). Fragmented agricultural landscapes often allow for higher prey densities compared to northern areas dominated by boreal forest (Panzacchi et al. 2010) and increased habitat heterogeneity can allow for resource needs to be met within smaller areas (Lucherini and Lovari 1996). Studies of other mid-sized canids have also shown smaller home ranges near human settlements compared to natural areas due to increased resource availability (Coman et al. 1991, Lucherini and Lovari 1996, Rotem et al. 2011).

Overall, our study clearly demonstrates the connection between environmental factors and red fox space use. The results in Paper I indicate resident foxes use much larger areas than previously found (averaging 7.1 km^2 LoCoH-k 90%) and demonstrate the ability of GPS collars to enhance our knowledge of red fox movements across landscapes. Additionally, the pronounced home range size variability illustrates the individual variation and flexibility of red foxes' space use, a trait that may enhance their ability to respond to both climate and human mediated landscape changes, and facilitate red fox population increases and northern range expansions (Elmhagen et al. 2015).

Table 1. Mean home range size estimates (LoCoH-k 90%) of red foxes according to the different vegetation zones they occurred in, listed from south to north.

Vegetation Zone	Home Range Size (km^2)	Proportion Agriculture Land (%)	Elevation (m)
Boreonemoral			
All Foxes (n=30)	**4.7 ± 4.7**	**28% ± 21%**	**54 ± 22**
Male (n=21)	5.4 ± 5.8	26% ± 21%	54 ± 24
Female (n=9)	3.0 ± 1.4	33% ± 22%	54 ± 19
Southern Boreal			
All Foxes (n=14)	**5.2 ± 8.6**	**25% ± 21%**	**106 ± 40**
Male (n=9)	6.5 ± 10.6	26% ± 22%	118 ± 42
Female (n=5)	2.7 ± 2.0	22% ± 22%	84 ± 29
Northern Boreal			
All foxes (n=8)	**19.5 ± 11.8**	**2% ± 2%**	**605 ± 164**
Male (n=3)	14.7 ± 5.9	1% ± 1%	454 ± 195
Female (n=5)	22.5 ± 14.0	3% ± 2%	695 ± 25

Do red foxes show recursive movements to resource locations within their home range? Does reuse of resource locations shape a home range? (Paper II)

Red foxes showed extensive clustering of recorded positions within their home ranges. In total, 126 individual clusters were identified. Of the total number of positions forming clusters, 71% were identified as unique or recursive visits, and not subsequent consecutive positions. Purely recursive clusters (n = 34) consisted of a median of 7.5 positions (range = 6–34). Only one cluster was formed by a single consecutive visit and clusters containing a mix of recursive and consecutive positions represented the largest proportion, 72.2% (n = 91) of clusters. These clusters contained a median of seven unique visits (range = 3–52) and a median of three (range = 1–53) consecutive positions.

On average, 43% of a red fox's total recorded positions were clustered because of recursive use. These clusters represented a small proportion (1.1%) of the total area available (100% MCP; Table 2; Fig. 3). The relatively small area of clusters suggests that foxes use and revisit highly localized resource locations within their home ranges compared to the total area of their potential range. This non-homogenous space use is in line with previous observations that home ranges are often made up of distinct locations that are occupied more intensively than other locations (MacDonald 1983). This provides evidence that red foxes use space disproportionately through recursive movement patterns implicit of cognitive mapping.

The dispersion of clusters was not correlated with the total area traversed by the individual foxes, however. Exploratory movement beyond regularly visited locations was also evident, although this varied between individual foxes. Whilst navigating between one resource location to another, foxes make exploratory forays to patrol and mark their wider surroundings (Gosling and Roberts 2001), perhaps seeking new foraging or mating opportunities, thus updating their cognitive map. We expect a cognitive map to be dynamic as new sites are added and others decay over time, in response to changes in environmental heterogeneity, resource availability, and social dynamics. Food resources are likely to be temporally or seasonally dynamic, and carrion and human subsidies may be unpredictable (Eide et al. 2004) or temporally pulsed (Gomo et al. 2017).

Table 2. The average proportion of red fox GPS positions defined as clusters, and the proportional area of clusters within a red fox home range (100% MCPs). For comparison, foxes have been divided into the season of their study period (summer, n=6; winter, n=9), as well as all foxes combined (n=15).

	Prop. of positions in clusters			Prop. of 100% MCP covered by clusters		
Season	Mean	SD	Range	Mean	SD	Range
Summer	39.8%	14.2	(22.8 - 60.8)	1.3%	0.9	(0.5 - 2.7)
Winter	44.6%	14.9	(21.9 - 64.4)	1.4%	1.4	(0.1 - 4.1)
Combined	42.7%	14.3	(21.9 - 64.4)	1.1%	1.2	(0.1 - 4.1)

Movement in these dynamic environments allows updates of a memorized landscape (i.e. a cognitive map) to current environmental conditions and resource availability. Such updates may include the status of other species or neighboring conspecifics in the area (Temeles 1994, Wikenros et al. 2017) or the availability of resources beyond the home range, allowing individuals to retain their territories or home ranges despite resource shortages inside these areas (hyenas, Hofer and East 1995; red fox, Tsukada 1997; beavers, Mayer et al. 2017). The extent of these movements was found to be highly individual, and a cognitive map may also feature locations that are seldom visited or avoided completely (Powell and Mitchell 2012). Our representation of a cognitive map is therefore limited. However, we suggest that by identifying resource locations that are used recursively, it is possible to move a step closer in revealing an animal's cognitive map, or indeed, the movement behavior underlying home range formation and space use.

Field visits identified reused sites as beds, dens, and clumped food sources (Table 3). Construction of classification trees (Paper III), revealed that clusters around buildings and in agricultural or wetland habitats, were most likely related to food sources, suggesting how human activity and landscape alteration may subsidize red foxes (Gompper and Vanak 2008, Newsome et al. 2014). It additionally suggests the red fox's preference for water voles (*Arvicola amphibius*), that are abundant in wetlands, as a natural food source in this region. Diurnal clusters in most habitats or in the most rugged terrain, were attributed to shelter, or to distinct highpoints and outcrops, presumably used as vantage points for surveillance or escape (Wam et al. 2012).

Table 3: a) The percentage of clustered red fox GPS positions vs. non-clustered GPS positions in the different habitats. b) The percentage of clustered and non-clustered positions attributed to specific causes in the field. N = 126 for both clustered and non-clustered positions.

a)	Settlement	Agriculture	Parkland	Scrubland	Forest	Wetland
Cluster	1.6%	15.1%	8.7%	14.3%	55.6%	4.8%
Non cluster	1.6%	26.2%	3.2%	10.3%	56.3%	2.4%

b)	Den	Bed	Scavenging	Hunting	Vantage	Route	Unclassified
Cluster	11.9%	25.4%	8.7%	22.2%	16.7%	7.9%	7.1%
Non cluster	0.0%	3.2%	2.4%	11.1%	14.3%	23.8%	45.2%

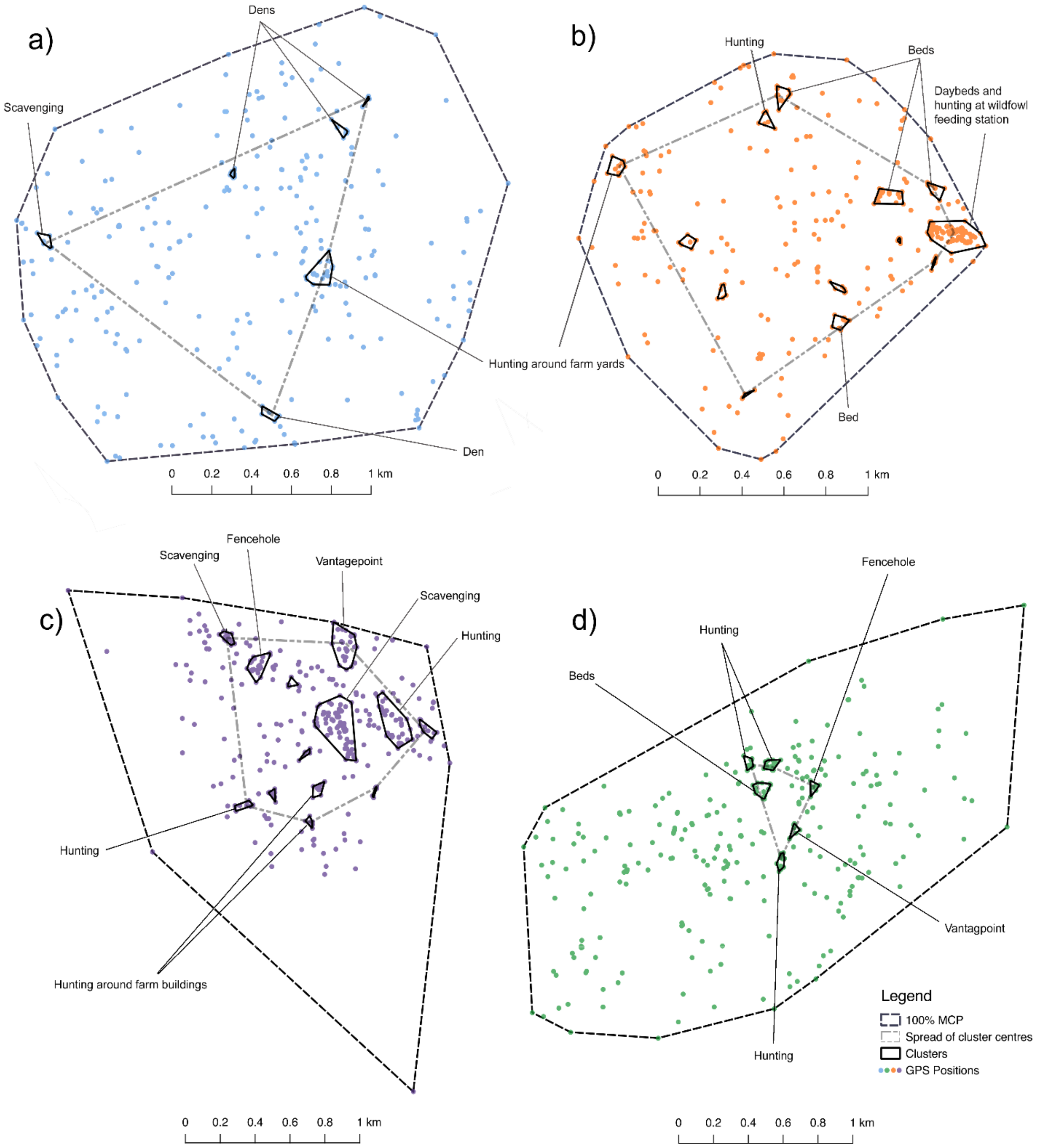

Figure 3. Illustration of the spatial dispersion and proportional area of clustered GPS positions within the 100% MCPs of two female and two male foxes: a) F3 over 89 days in the winter, (b) F7 over 66 days in the summer, (c) M5 over 75 days in the winter and (d) M3 over 52 days in the summer.

Does long distance dispersal occur in red foxes? (Paper III)

Thirty of the 101 red foxes collared in this study dispersed during monitoring. Of these, six foxes were recognized as long distance dispersers, travelling straight-line distances greater than 60 km, thereby representing outliers on the spectrum of red fox dispersal distances (Fig. 4), following the definition of Nathan (2005). These long-distance dispersal events exceeded similarly calculated published records for red foxes (Storm et al. 1976, Allen and Sargeant 1993, Gosselink et al. 2010) and included both sexes (female = 1, male = 5). The cumulative dispersal distances moved ranged from 132 to 1036 km and were on average 2.3 ± 1.7 SD times longer than the straight-line distances. Sub-adult males predominantly made these movements, 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 (Fig. 5). Genetic data also supports that, while not common, female foxes contribute to long-distance colonization and range expansion via long-distance dispersal movements (Colson et al. 2017).

We further show that long-distance dispersal and settlement occurs very quickly. Four long distance dispersal events were single-stage movements of short duration, ranging from seven to 22 days**.** On average, foxes dispersed distances greater than 100 km within 2 weeks, illustrating the potential for rapid colonization of new landscapes. Additionally, two dispersal events were multi-staged, with temporary periods of settlement during dispersal. 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.

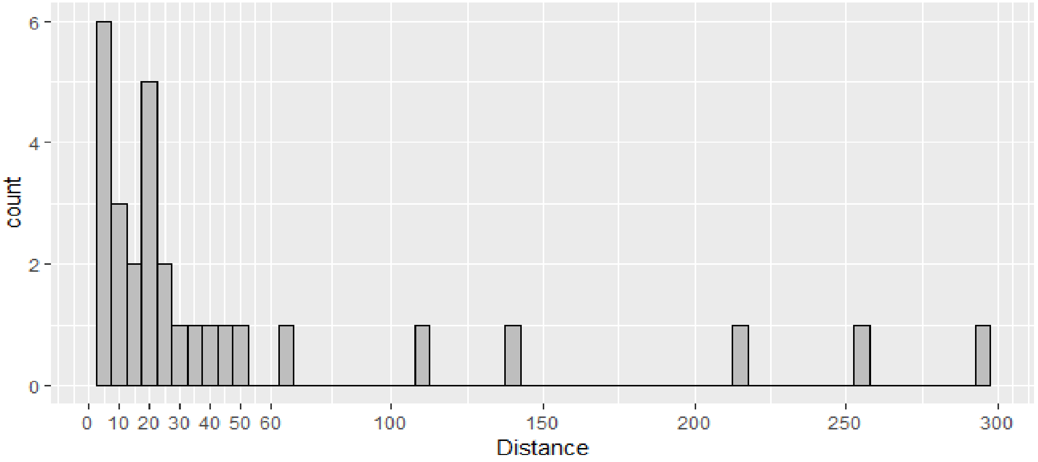

Figure 4. Distribution of red fox dispersal distances. Red foxes were considered long distance dispersers if their dispersal distances represented outliers or the tail of the distribution of dispersal distances, seen here as a natural cutoff at 60km.

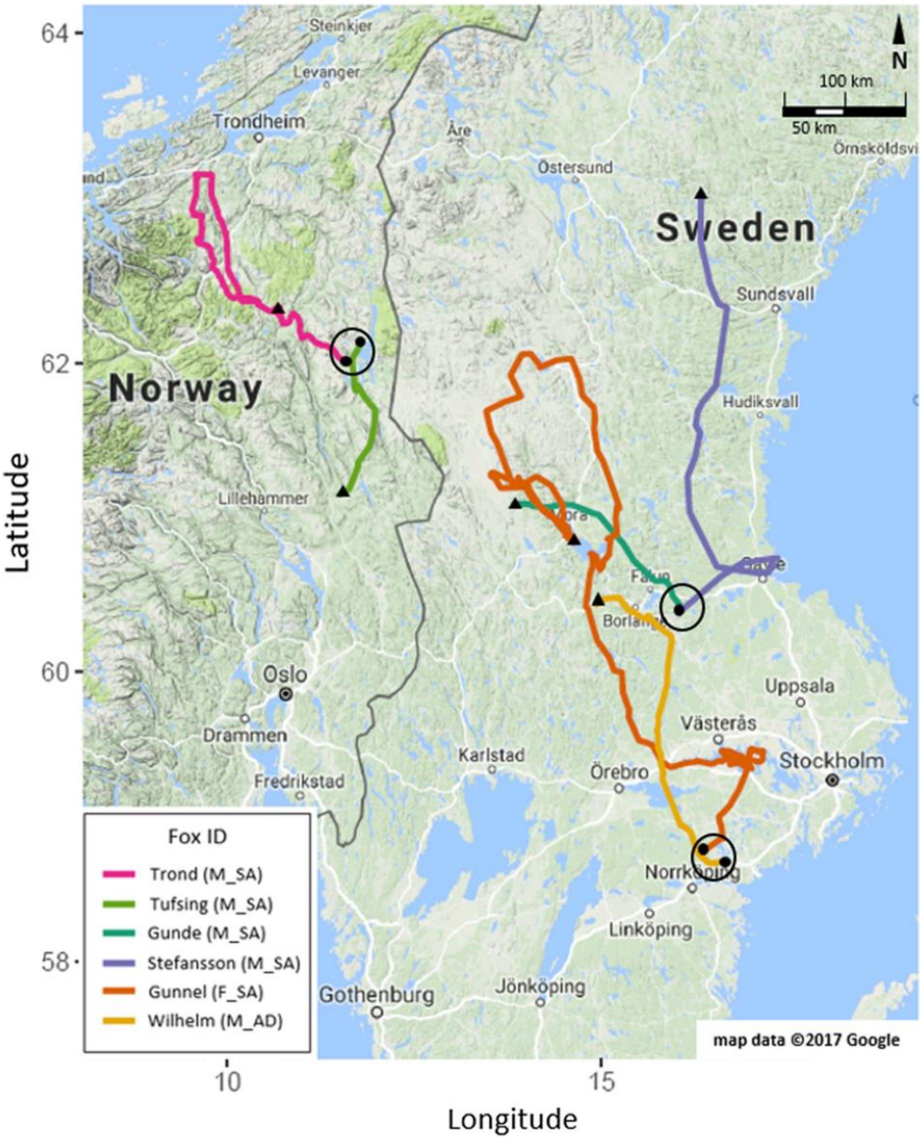

Figure 5. Long-distance dispersal movements of six GPS-collared red foxes in Sweden and Norway. Solid black circles and triangles indicate initiation (start) and settlement (end) points of dispersal movements, respectively. The three study areas where foxes were initially captured are outlined by black 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.

Overall, Paper III indicates red foxes of both sexes are capable of moving long distances. Thus, despite patterns of male biased dispersal (Papers III, IV and V), the dispersal capacity and potential for dispersal do not appear limited to either sex in a red fox population (Allen and Sargeant 1993, Norén et al. 2015). Interestingly, with one exception, long distance dispersal events were oriented 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 = 0.65, p = 0.08), it would be interesting to see if this trend holds when examining additional dispersal data from red foxes. A northern dispersal trend was noted in other red fox populations in the northern hemisphere as well (Storm et al. 1976, Allen and Sargeant 1993, Gosselink et al. 2010).

Northern landscapes of low productivity likely have lower population densities of red foxes, suggesting that dispersal and settlement in more productive southern landscapes may be limited by crowding and competition for available space (Lambin 2001). However, we have a limited understanding of what factors contribute to a red fox's decision to settle. What represents a good habitat to a red fox? Is it an area with few other foxes, providing less competition, or does the presence of other foxes signal an area with good habitat attributes and resources, in both food and breeding opportunities? Further research in this area might prove beneficial for predicting how (and where) populations might expand.

Paper III demonstrates the red fox's ability to traverse between populations, across landscapes, and potentially across international boundaries, contributing to connectivity and gene flow. Circumpolar data show that red foxes are advancing into increasingly productive tundra (Colson et al. 2017, Elmhagen et al. 2017, Gallant et al. 2019). As a highly adaptable species, red foxes with strong dispersal abilities or exploratory behaviors may dominate this expansion front and drive these northern range expansions (Norén et al. 2015). As such, long-distance dispersal 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 altered community dynamics in northern ecosystems (Elmhagen et al. 2017).

How does the spatial and genetic structure of the red fox vary at different spatial scales? (Paper IV)

In this study, we investigated the spatial and genetic structuring of red foxes within south-central Sweden at two different spatial scales, regional and local. Here, we found evidence that red foxes exhibit high levels of gene flow, finding limited genetic differentiation amongst sampled foxes at the regional level. This low level of genetic differentiation found between red foxes at the regional level follow expectations that red foxes are a mobile species and dispersal causes gene flow across large spatial scales (Peakall et al. 2003). Similarly, other canid species exhibiting dispersal over long distances also show limited phylogeographic structuring (e.g. grey wolf (*Canis lupus*), coyote (*Canis latrans*) and arctic fox (*Vulpes lagopus*) (Lehman and Wayne 1991, Vilà et al. 1999, Lai et al. 2017). This also indicates that the long distance dispersal events documented in Paper III can contribute to gene flow over large spatial scales.

Locally, we identified significant differences in the spacing behavior between all pair types of red foxes, with female pairs and male pairs being most different ($t = 3.3661$, $df = 43.132$, p-value = 0.00161; Fig. 6). The average distance between first-degree relatives was approximately 38km for male pairs, which was over six times larger than the distance between similarly related female pairs (6km; Table 5). This supports our prediction that highly related females are located closer to each other and thereby show a degree of kin clustering by occurring in closer proximity to related females compared to related opposite sexed or male-male red fox pairs. This spatial patterning is indicative of philopatric behavior in females combined with male biased dispersal. In polygynous mating systems such as those in red foxes, philopatric behavior is thought to benefit females more than males through access to breeding sites (e.g. underground den systems), cooperative social interactions, knowledge of resource areas, or through inheritance of the home range (von Schantz 1981, MacDonald 1983, Baker et al. 1998). Inbreeding avoidance (Pusey and Wolf 1996), on the other hand, may contribute to a male biased dispersal patterns, as dispersal is an effective mechanism against inbreeding (Johnson and Gaines 1990) and may be a prerequisite for reproduction or to find a breeding vacancy (Greenwood 1980). Thus, the genetic sub-structuring seen at the local scale is most likely driven by behavioral traits such as male biased dispersal and female philopatry altering gene flow between groups, subsequently shaping local spatial genetic patterns. These genetically identified patterns fit well with dispersal patterns found in other red fox studies (Storm et al. 1976, Allen and Sargeant 1993) and that sex and social system are correlates of carnivore spacing behavior (Clobert et al. 2001).

Understanding local spatial patterns of relatedness can offer important insights into how social structure can contribute to red fox spatial structure and to dispersal and other movement behaviors seen at larger scales. Here, our results indicate that while low genetic diversity is seen at larger scales, different patterns of genetic structure can be seen at finer scales. Many species in the order Carnivora show great flexibility in their social systems (MacDonald 1983) which can influence population genetic structuring at a very fine scale. Distinguishing between population structure and the underlying fine-scale social and kinship patterns that affect population genetic structure can ultimately lead to a more thorough understanding of the spatial, social and

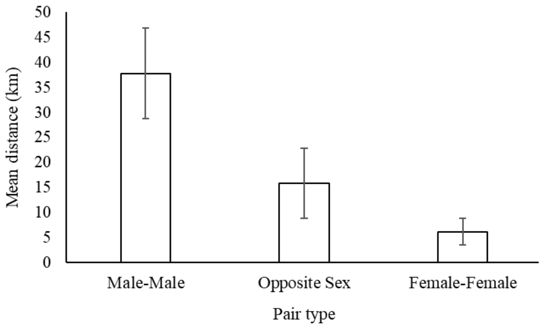

Figure 6. Local scale average pairwise geographic distances ±2SE between highly related (r ≥0.40) pairs of red foxes: male-female (opposite sex), female pairs (female-female) and male pairs (male-male).

Table 5. Mean pairwise geographic distances between highly related adult and subadult red fox pairs (n=124; r≥0.40) within a local area in south-central Sweden. Red foxes under six months of age (pups) and those of undetermined sex were excluded from analysis.

Pair Type	N	Distance (km)	SD
Male-Male	38	37.79	55.54
Opposite Sex	64	15.85	28.49
Female-Female	22	6.17	12.45

population dynamics of a species. Yet, these are still among some of the least understood attributes of both individual animals and populations (Sutherland et al. 2000, Nathan 2001, Kokko and López-Sepulcre 2006). Indeed, Kamler et al. (2019) indicated that exploratory movements by black-backed jackals (*Canis mesomelas)*, are affected by social status as well as the seasonal availability of preferred prey, and the reproductive cycle of jackals. In addition, these social mechanisms likely do not work independently and genetic clustering and female biased philopatry may differ across populations where different demographic components are at play (Kamler et al. 2013).

Does a behaviorally flexible species such as the red fox fit to recognized movement patterns of resident, disperser and nomad movement behaviors? (Paper V)

In Paper V, we assessed the movement behaviors that characterize a behaviorally flexible and generalist species, the red fox. Resident, dispersing and nomadic movements were all recognized as movement behaviors of the red fox. However, only 53% of the 112 red fox trajectories analyzed showed agreement across the three methods (Visual, Quantative NSD or rNSD) and no agreement was found within the nomad category (Fig. 7; Table 6). Visually, 69% of foxes were identified as residents, 27% as dispersers and 4% as nomads. In comparison, both NSD models classified 43-44% of the foxes as resident, 50% as dispersers and 6-7% as nomads. This high level of inconsistency in classifications suggests that red foxes move in a manner or at a scale that is not 'typical' of idealized resident or dispersing behaviors (Cagnacci et al. 2016, Ducros et al. 2019). However, this variability in red fox movement patterns is not surprising, given their variation in home range size, social behavior, diet, and other life history attributes and behaviors (von Schantz 1981, Cavallini 1996, Walton et al. 2017, Dorning and Harris 2019). It is reasonable to expect such variability to occur in their movement behaviors, as seen here.

When examining the spatial scale at which movements took place, we found that red fox movement behaviors could occur at vastly different scales and that similar movement patterns could represent different behaviors depending on the spatial scale. Mean NSD and rNSD values included much lower values in the disperser category than did visual classifications, resulting in more individuals placed into the disperser category. Higher NSD values were also visually placed in nomadic categories compared to model driven approaches.

Collectively, the visual classifications were more in line with ecological patterns that are known for red foxes; subadult male biased dispersal patterns (Storm et al. 1976, MacDonald 1983), a high degree of residency and stability among adult individuals and in particular adult females and only

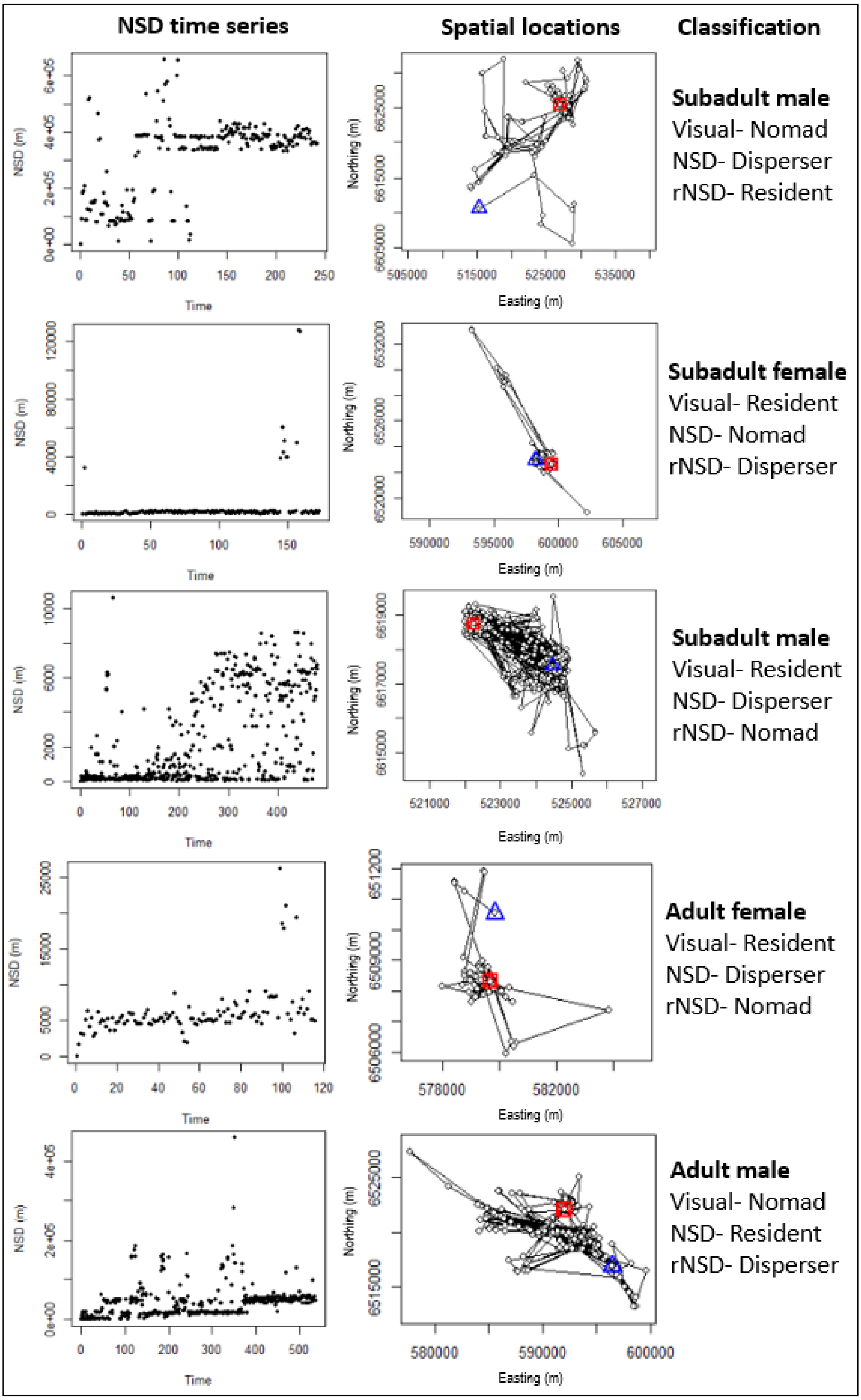

Figure 7. The NSD time series and movement trajectory patterns for the five red fox individuals that showed no agreement across all three methods. The age and sex of each fox is given in bold along with the movement classification according to the different methods (Visual, NSD or rNSD). Note the spatial scale, in square meters, of the NSD time series plots. The blue triangle represents the start position and the red square the last position in each animal's movement trajectory.

a small proportion of nomadic individuals identified, which were predominantly male (von Schantz 1981). The visual inspection of movement patterns allowed for the subjectivity to fit outlying behaviors where more rigid quantification methods do not. Therefore, visual pattern analysis should not be ignored as an important tool for complex data and for matching behaviors to the appropriate scale (Andrienko and Andrienko 2013, Demšar et al. 2015). However, it is important to recognize that there are no 'true' reference values with which to compare our model or visual results, ie. there is no 'correct' classification. Each movement classification is open to interpretation depending on the method used and the spatial scale. Overall, the high level of inconsistency between visual and model based classifications highlights both the difficulties in quantifying complex animal movements and the variability within red fox movement patterns, lending support to the conclusion of Cagnacci et al. (2016) that movement patterns should be considered as a gradient of behaviors rather than as fixed patterns.

Table 6. Summary of the average maximum (Max), mean and standard deviation (SD) of net displacement (ND) values in kilometers for classifications which agree and do not agree across methods. Comparison of each method is to the visual classifications. Among resident individuals that agree and do not agree, displacement values are largely similar, indicating spatial scale is used for visual classifying residents while displacement pattern might play a larger role in other classifications.

Method	Classification	Count	Max ND (km)	Mean ND (km)	± SD
Agree	disperser	26	7.30	1.20	1.72
Agree	resident	33	0.42	0.06	0.07
Do not agree	disperser	4	0.68	0.50	0.17
Do not agree	nomad	5	0.54	0.31	0.14
Do not agree	resident	44	0.37	0.07	0.07

Conclusions

This thesis increases our understanding of red fox movement behaviors and their interactions with social and environmental factors at multiple spatial scales (Hebblewhite and Haydon 2010, Bauer and Hoye 2014). In summary, we identified much larger home ranges than previously recorded for red foxes. However, the high degree of individual variation found in home range size shows the ecological plasticity of the species and follows results from previous red fox studies (Voigt and Macdonald 1984, Cavallini 1996). We partially explained this variation through environmental factors along a landscape gradient. We also identified cognitive mapping as a feature of red fox space use, linked to recursive movements within home ranges and contributing to bounded space use. Through identifying long distance dispersal events, we identified the red fox's ability to traverse between populations, across landscapes, and potentially across international boundaries, contributing to population connectivity and gene flow. Fine scale familial structuring occurred locally in red foxes by social mechanisms not linked to their movement ability or dispersal capacity and further highlights how social dynamics (eg. relatedness) play a role in the spatial organization of red foxes. Classifying the unique and variable behaviors of a highly flexible species such as the red fox is difficult. Recognizing red fox behaviors is dependent on not only identifying their associated movement patterns, but also understanding the temporal and spatial scales at which their movements occur. Together, this information is important for understanding red fox spatial ecology (Bunnefeld et al. 2011; Bastille-Rousseau et al. 2015, Wheat et al. 2017). Finally, individual variability appears to be a key feature of red fox spatial ecology, and this behavioral plasticity and individuality within animal movements is of unique ecological value and warrants further research. However, our understanding of the behavioral flexibility of animal movements is still in its infancy, and extending our knowledge will likely require development of new metrics accounting for 'behavioral plasticity' in movement models (Nathan et al. 2008, Cagnacci et al. 2016).

Although exploratory excursions are not considered a conceptual movement behavior in itself, such exploratory movements featured in almost all papers herein. Given their prominence as a behavior of red foxes, I hypothesize that such excursions enhance an individual's fitness, thereby being an important ecological behavior of red foxes. I suggest that exploratory excursions should thus be regarded as an adaptive behavior of red foxes. The exploratory behavior of red foxes that leads to movements beyond commonly utilized resource areas (i.e. the home range) my help to explain the dynamic nature of home ranges, variability of red fox movements, and potentially their success as a species.

Scale is increasing acknowledged as an important aspect in the field of ecology (Fryxell et al. 2008, van Moorter et al. 2013, Benhamou 2014). The spatial scales of animal movements will vary among species, within species, but also between individuals through time. Similarly, demographic and behavioral processes can operate at a range of scales to generate different ecological patterns (Anderson et al. 2010, Van Dijk et al. 2015). By monitoring individuals from multiple areas across their distribution, we have improved the understanding of red fox spatial ecology across a large geographic range (Fraser et al. 2018) and distinguished between population structure and the underlying fine-scale social and kinship patterns that affect population genetic structure and red fox spatial organization (Anderson et al. 2010). It is therefore important to apply the appropriate spatiotemporal scale to both movement and genetic studies.

Additionally, integrating animal movement data with other data sources provides opportunities to expand the scope of our research questions. For instance, combining home range estimates with noninvasive approaches such as individual genetic identification through hair or scat sampling and/or remote camera trapping may enable comparative or complementary population density estimates. Further integration of GPS data and genetic data can open up new possibilities for investigating how dispersal distances derived from GPS data compare to genetic estimates of dispersal distances, or how dispersal translates to gene flow, thereby connecting estimates of dispersal to effective dispersal (Prugnolle and De Meeus 2002). Genetic identification of individuals showing spatiotemporal overlap can also provide insight into the social structure of red foxes (i.e. by indicating territoriality or a high degree space use sharing amongst unrelated individuals). This information will likely prove useful to management and research alike. Such information can ultimately lead to a more thorough understanding of the spatial, social and population dynamics of a species and is necessary for understanding red fox ecology. Thus, we see the power of high resolution genetic markers, such as SNPs, proving valuable for future genetic studies, providing new avenues for non-invasive sampling, population estimates and species monitoring, and further studies combining genetic information with movement data.

Future Research and Perspectives for Management

The impact of human activities is altering natural habitats, and while this is reducing the ability of some animals to move (Tucker et al. 2018), it is facilitating others, such as generalist species like the red fox (Elmhagen et al. 2015, Gallant et al. 2019). To understand the impacts of these processes on different organisms it is important to acquire baseline data on the species. The demographic responses of a species depends on its' ability to secure resources and mates. Improving our understanding of how changing land use, the risk of predation (including lethal control), and food availability alters the spatial structure of mesopredator populations has important implications for species' population dynamics and local densities (Herfindal et al. 2005, Mattisson et al. 2013). However, while this thesis helps expand our knowledge of red fox spatial ecology in boreal landscapes, we still lack basic data on red fox ecology, such as broader dispersal behavior, daily movement distances and activity patterns, and social drivers of population dynamics and population density estimates. Such ecological information will be key for informing spatial models to understand the role movement behaviors can play in range expansions, disease transmission, population dynamics and defining an appropriate scale for population management. The lack of basic ecological data such as estimates of population density, habitat and space use requirements, and foraging and dispersal behavior remains an obstacle to status assessments and our ability to make informed management decisions (Fraser et al. 2018).

Food resources are likely to have a direct effect on animal movement patterns across the landscape. Agricultural expansion, forestry practices, and anthropogenic subsidies, will increasingly providing suitable habitat north of a red fox's climate-imposed distribution limit, thereby facilitating red fox range expansions into northern regions (Elmhagen et al. 2015, 2017). Hunting pressure and human attitudes towards red foxes can further impact the spatial and population dynamics of this species (Jetz et al. 2004, Duncan et al. 2015). How anthropogenic provisioning influences the space use of red foxes is of benefit to focus on for future studies. Further, a better understanding of how lethal control of populations affects movement patterns, spatial organization and population dynamics is also needed (Maletzke et al. 2014).

As the red fox is a species with one of the largest geographic ranges of any wild terrestrial mammal, I believe that our research, while targeted to Scandinavia, is also relevant to a global audience. This thesis represents new observations that greatly expand our knowledge of red fox space use and dispersal in rural landscapes and opens the door for future research into the broader ecosystem consequences of such movements. Specifically, by understanding the scale at which movements take place and how this changes along a landscape gradient, we can recommend targeted research and management at scales that will be of the greatest value for informing conservation or management (Allen and Singh 2016).

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Paper I

RESEARCH ARTICLE

Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration

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Abstract

Home range size is a fundamental concept for understanding animal dispersion and ecological needs, and it is one of the most commonly reported ecological attributes of free-ranging mammals. Previous studies indicate that red foxes *Vulpes vulpes* display great variability in home range size. Yet, there has been little consensus regarding the reasons why home range sizes of red foxes vary so extensively. In this study, we examine possible causes of variation in red fox home range sizes using data from 52 GPS collared red foxes from four study areas representing a gradient of landscape productivity and human landscape alteration in Norway and Sweden. Using 90% Local Convex Hull home range estimates, we examined how red fox home range size varied in relation to latitude, elevation, vegetation zone, proportion of agricultural land and human settlement within a home range, and sex and age. We found considerable variation in red fox home range sizes, ranging between 0.95 km^2 to 44 km^2 (LoCoH 90%) and 2.4 km^2 to 358 km^2 (MCP 100%). Elevation, proportion of agricultural land and sex accounted for 50% of the variation in home range size found amongst foxes, with elevation having the strongest effect. Red foxes residing in more productive landscapes (those in more southern vegetation zones), had home ranges approximately four times smaller than the home ranges of foxes in the northern boreal vegetation zone. Our results indicate that home range size was influenced by a productivity gradient at both the landscape (latitude) and the local (elevation) scale. The influence of the proportion of agriculture land on home range size of foxes illustrates how human landscape alteration can affect the space use and distribution of red foxes. Further, the variation in home range size found in this study demonstrates the plasticity of red foxes to respond to changing human landscape alteration as well as changes in landscape productivity, which may be contributing to red fox population increases and northern range expansions.

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Introduction

The location and size of the area that an animal uses to secure resources and mates (i.e. its' home range [1]) is fundamental to understanding animal dispersion and ecological needs. Home range size and location is also an important characteristic which structures species interactions, trophic processes and communities [2]. As such, home range size is one of the most commonly reported ecological attributes of free-ranging mammals [3].

Home range size can vary greatly across taxa, populations and individuals [4–7], and it is influenced by a complex array of ecological and social factors. Among carnivores, home range sizes have been found to vary by several orders of magnitude both within and among species [5, 8, 9]. Some of this variation has been attributed to differences in body mass [3, 10], population density [8, 11], prey availability [12, 13], environmental productivity and seasonality [14, 15], and intrinsic factors such as sex [16], reproductive status [17], and territoriality and social structure [18, 19].

However, there has been much debate as to the relative importance of these factors in shaping home range size, and often, such mechanisms are examined separately despite their synergistic effects on home range size [16, 20]. Thus, the factors influencing variation in home range size are still not well understood, especially across different scales [4, 21–23].

The red fox *Vulpes vulpes* is a species that demonstrates great flexibility in distribution, foraging behaviour and social structure [24–26]. Red foxes are highly adaptable habitat generalists with a distribution encompassing the entire northern hemisphere from arctic to temperate climes, and landscapes ranging from natural to exceedingly urban [27, 28]. Similarly, red foxes demonstrate a wide foraging niche as an opportunistic generalist predator. Further, they exhibit changing degrees of territorial behavior [25, 29] and display a complexity in their social structure ranging from pair bonding to family groups with helpers [26, 30].

Previous studies indicate that red foxes display high variability in home range size (see reviews in [26, 30]). Yet, there has been surprisingly little consensus as to the reasons why home range sizes of red foxes vary so extensively. Further, few studies have examined how the size of red fox home ranges may be influenced by changes along a landscape gradient (but see [8]). Landscape changes resulting from human alteration (e.g. agriculture, urbanization) and environmental productivity (increasing seasonality) have the ability to alter resource distribution as well as the availability and predictability of resources [8, 31, 32]. Furthermore, reductions in the availability of necessary resources can influence population density [15] and territoriality [4], which may alter social regulation and spacing patterns, thus leading to variation in home range size [4, 5]. Intersexual differences in response to spatial and temporal changes in resource distribution across landscapes can affect both individual and population demography [20, 33] and life history characteristics for a given species [34]. Thus, it is increasingly important to have a better understanding of sources of variation in red fox home range size along a productivity gradient.

Additionally, much of our previous knowledge regarding red fox spatial ecology has relied on VHF technology, with the choice of home range estimation technique and sampling scheme further influencing reported home range sizes [35, 36]. Advances in technology and analytical methods now allow for a more representative sample of an animal's space use [36].

The objective of this study was to examine possible causes of variation in home range sizes of red foxes using data from 52 GPS collared foxes from four study areas representing a gradient of environmental productivity and human landscape alteration. Specifically, we examined variation in home range size in relation to extrinsic factors (latitude, elevation, vegetation zone, proportion of agricultural land and proportion of human settlement within a home range) and intrinsic factors (sex and age) of red foxes.

We predicted variation in home range sizes of red foxes along both a landscape (latitude) and localized (elevation) gradient, with home ranges being smallest in the south and increasing in size to the north and towards higher elevations, as increasing latitude and elevation have been shown to constrain environmental productivity and increase seasonality which alters resource availability [14, 33, 37]. Further, in more productive agricultural landscapes and areas of human settlement, resource needs can often be met within a smaller area [38, 39], thus, home range sizes were predicted to decrease with increasing proportion of agriculture land and human settlement.

Methods

Study areas

We conducted this study within four different areas in Sweden and Norway representing a gradient of decreasing landscape productivity and human land use from Kolmården, Sweden, in the south to Hedmark County, Norway, in the north (58˚–62˚ N; Fig 1). In general, the southernmost landscapes are more fragmented, consisting of boreonemoral forests, agricultural lands, and scattered human settlements, while the northern landscapes are characterized by boreal forests and alpine tundra of low diversity and productivity. 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 present increasingly to the south.

Kolmården (58˚40′N-16˚22′E) lies at an average altitude of 24 meters above sea level (a.s. l.), and the southern portion of the study area is coastal. This area is a mosaic of productive agriculture areas, boreonemoral forests and human settlements, thus representing a productive and more anthropogenically modified landscape. Daily mean temperatures range from 20˚C in summer to –5˚C in winter. Snow covers the ground irregularly from December to March.

Grimsö (59˚40'N-15˚25'E) and **Hedemora (60˚16′N-15˚59′E)** are both located in south-central Sweden and consist of a transitional border zone between boreonemoral forests in the south and boreal forests in the north. Grimsö is a 140km^2 wildlife research area dominated by mixed coniferous forest (74%) and bogs (18%) with farmland comprising approximately 3% [43, 44]. Hedemora is located along the river Dalälven and contains settlements and productive agricultural areas along the river valley. Within both areas, the landscape is generally flat with altitude rising from 75m a.s.l. in the south to 180m a.s.l. in the north. Daily mean temperatures average 15˚C in summer to –5˚C in winter. The ground is generally snow covered from late December up to March.

Hedmark County, Norway (61˚53′N 12˚2′E) is a transitional border zone between northern boreal forest of low productivity and alpine tundra. The study area lies in the eastern part of Hedmark county, Norway, which extends from the Swedish border in the east to the Glomma River in the west. Most of the area lies 600m-800m a.s.l. Less than 1% of the area is cultivated or residential land, one third is productive forest, and the remainder consists of tundra, mountains, lakes, and rivers. Daily mean temperatures range from 10˚C in summer to –25˚C in winter, and the ground is generally snow covered from November to May.

Fox capture

Between 2012 and 2016, we captured and equipped 80 red foxes with GPS radio collars (Tellus Ultralight, 210g, Televilt, Inc. Lindesberg, Sweden). Animal capture and handling protocols differed in Norway and Sweden, however all capture and handling procedures were approved by and followed the ethical guidelines required by the Swedish Animal Ethics Committee (permit numbers DNR 70–12, DNR 58–15) and the Norwegian Experimental Animal Ethics Committee (permit numbers 2009/122825, 2012/20038, 2014/207803). In addition, permits to

Fig 1. Study areas in Sweden and Norway classified by vegetation zone. The four study areas in Sweden and Norway along a landscape gradient from south to north classified within three vegetation zones: (1) Kolmården, (2) Grimsö, (3) Hedemora, and (4) Hedmark. Vegetation zone classifications were adapted from Moen and Lilletun [40] and Rydin et al. [41] for Norway and Sweden, respectively. Map is reprinted with permission from Hagen et al. [42].

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capture wild animals were provided by the Norwegian Directorate for Nature Management and the Swedish Environmental Protection Board (NV-03459-11). All foxes were initially captured using baited wooden box traps. Foxes captured in Sweden were either immobilized using a mixture of 2 mg/kg ketamine and 0.08mg/kg medetomedine, where the medetomedine was later reversed with 0.4mg/kg atipamizole, or with 10 mg/kg tiletamine-zolazepam, for which there is no reversal [45]. In Norway, a noose pole was used to restrain captured foxes, which were then processed quickly and safely without chemical immobilization. Both capture methods were continuously refined to minimize handling time, animal stress and the risk of injury to the animals. Captured foxes were sexed, measured, weighed, and aged. Age was defined as sub-adult (< 1 year) or adult (> 1 year) based on the amount of tooth wear and tooth coloration. Only foxes meeting necessary weight requirements (>5kg) were fitted with radio collars. Total processing time of fox removal from the trap to fox release at capture site was approximately 25–35 minutes for Sweden and 10–15 minutes for Norway. Most foxes (88%) were captured between October and March. Collars deployed before October 2015 were programmed to take 3 positions per day with a drop-off after 270 days (9 months), and collars deployed after October 2015 were programmed to take 6 positions per day with a drop-off after 180 days (6 months). Four study animals were re-collared during the study period.

Estimation of home range size

We determined the minimum monitoring duration of red foxes needed for home ranges to reach a stable asymptote based on area-observation curves [46]. This was done by using a subset of foxes monitored for >6 months (n = 15) to calculate when 100% Minimum Convex Polygon (MCP) estimates, using 30 day increments, started to reach an asymptote (Fig 2). Based on the area-observation curves, we restricted our analyses to foxes monitored ≥ 90 days (i.e. 3 months) that represented 82% of home range sizes for foxes monitored for 6 months. We did, however, include two females that were monitored for 84 and 87 days. Overall, mean monitoring duration of included foxes was 170 days ± 78 SD. We further limited our analyses to stationary foxes where we used a combination of visual inspection of the spatial data and net squared displacement (NSD) following Bunnefeld et al. [47] and Bastille-Rousseau et al [48] to identify different movement strategies corresponding to stationary, transient or dispersing foxes. In total, 52 foxes (M = 33, F = 19) met the requirements for inclusion in home range analysis.

We derived home ranges using two different non parametric methods: MCP, for comparison with previous red fox studies, and Local Convex Hull, a nonparametric kernel method using a fixed number of nearest neighboring points (LoCoH-k) [49, 50]. We chose to use

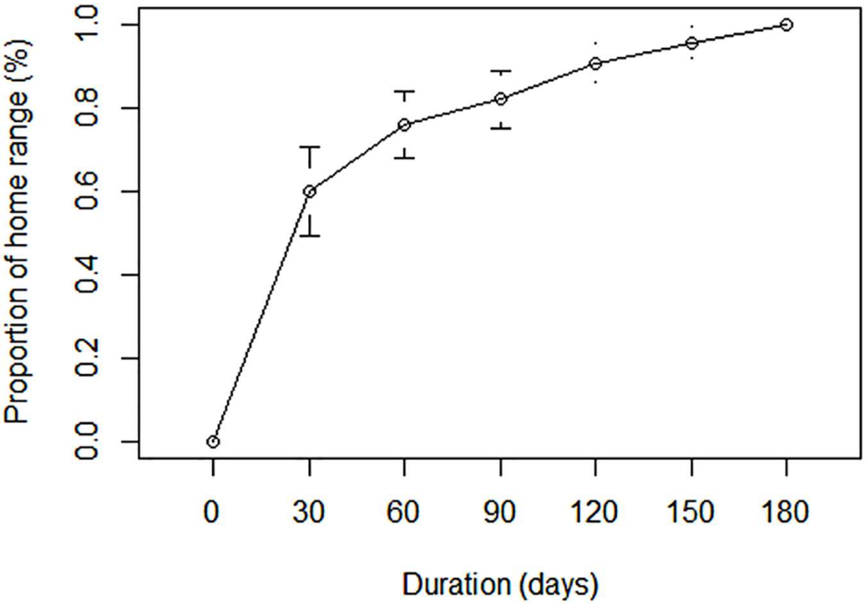

Fig 2. Area-observation curve showing variation in home range size in relation to sampling duration based on 100% MCP estimates of red foxes *Vulpes vulpes*. A duration of 90 days represented 82% of the home range size for red foxes followed for 6 months.

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LoCoH because it is more suitable for animals with home range borders that follow hard-edged features such as roads or rivers [50–52]. LoCoH estimates also exclude areas not likely to be utilized by an animal that may be included in MCP analysis [50]. For LoCoH-k estimates, individual k-values were calculated as the square root of the number of positions for each animal [49]. Using R 3.2.4 [53], we derived MCP and LoCoH-k home range estimates at 90%, 95% and 100% levels using the R package adehabitat [54].

Home range composition

We obtained land cover and elevation from digitized topographic maps of Sweden (Swedish Land Cover, SMD, National Land Survey of Sweden) and Norway (Norwegian Mapping Authority). Using ArcGIS 10.1 [55], we converted the Swedish Land Cover map from raster data to vector layer by using the raster to polygon function. We then calculated the proportion of agricultural land and human settlement within each LoCoH-k 90% home range using the intersect function where surface areas were recalculated by using the calculate geometry function. Agriculture lands were defined as arable lands and pastures, and human settlements were localities of clustered inhabitants, buildings and associated infrastructure, forming small to large communities. Small amounts of arable lands within areas of human settlement, such as backyards, gardens, golf courses and parks were considered human settlements. Similarly, we calculated the mean elevation for home ranges by using (1) the zonal statistics as table function for home ranges in Sweden and (2) the intersect function of the elevation curves for home ranges in Norway, where the length of the elevation curves were recalculated using the calculate geometry function. We calculated the latitude for the centroid of each home range by using the polygon to point function. Finally, we used vegetation maps adapted from Moen and Lillethun [40] and Rydin et al. [41] for Norway and Sweden, respectively, to classify red fox home ranges according to the vegetation zone in which the home range was located. All fox home ranges were either located in the boreonemoral zone (BN), the southern boreal zone (SB), or the northern boreal zone (NB).

Statistical analysis

We compared differences in mean home range sizes between all reciprocal levels of MCP and LoCoH-k estimates, and tested for statistical significance using a paired (Student's) one-way t-test. For analysis of variation in home range size, we selected the more conservative 90% LoCoH home ranges estimates, (removing 10% of the outermost locations [56], as this level excluded extraterritorial movements which greatly expanded home range sizes at the 100% level (S1 Table, [49]). Further, Nilsen et al [57] cautioned against the use of MCP estimates for examining intraspecific sources of variation among home ranges. Therefore, by excluding occasional exploratory movements, the 90% LoCoH-k home range estimates probably produced more accurate depictions of the areas utilized by the animal than less conservative estimators [50]. We examined how home range size varied in relation to latitude and mean elevation, the proportion of agricultural land and the proportion of human settlement within a home range, and sex and age of foxes using these 90% LoCoH estimates and linear models in the program R (S2 Table [53]). Home range size was log transformed to achieve a more normal distribution of the data. We used a correlation matrix to evaluate collinearity among the fixed variables with a limit of ($r \geq 0.6$). Latitude was highly correlated with elevation (Pearson's $r = 0.89$). Elevation performed better than latitude when comparing full models ($\Delta AICc = 8.915$), thus we retained elevation for further modeling. We derived 31 candidate models from the independent variables above, excluding latitude, and ranked the models based on the Akaike's Information Criterion with small sample adjustment (AIC_C) [58] using the R package

MuMin [59]. We selected the model with the lowest AIC_C value as the best model though we considered models within two AIC_C units to be of similar quality [58]. Model assumptions were checked and final models were validated by examining the residuals.

Results

Home range size estimates

Red fox home ranges showed considerable variation in size between the different home range estimators and among individuals (S1 Table). MCP estimates were significantly larger than the corresponding LoCoH-k home ranges at all levels (paired *t*-test, 90% $t_{51} = 3.13$, p = 0.003, 95% $t_{51} = 2.96$, p = 0.005, 100% $t_{51} = 3.35$, p = 0.002). The GPS data emphasized the occurrence of excursions and exploratory movement patterns, which resulted in outlying positions greatly increasing home range sizes, depending on the estimator used. LoCoH-k estimates decrease substantially when outlying fixes were removed, compared to MCP estimates, resulting in overall more conservative home range size estimates. Specifically, using 90% of the core relocations resulted in the average MCP home range size almost triple the size compared to LoCoH-k estimates (13km^2 difference; Table 1).

Red fox home ranges in this study showed considerable individual variation in size as well, ranging between 0.95 km^2 to 44 km^2 (LoCoH 90%) and 2.4 km^2 to 358 km^2 (MCP 100%). Home ranges averaged 7.1 km^2 ± 1.3 SE (90% LoCoH-k) or 52 km^2 ± 10 SE (100% MCP) which varied depending on estimator and level (Table 1). In general, the home ranges of red foxes in more productive vegetation zones (i.e. those in the boreonemoral and the southern boreal vegetation zones) were approximately four times smaller than home ranges of foxes in the northern boreal zone (90% LoCoH-k), and this trend held independent of estimator or proportion of relocations included in the estimates (Table 2). Only three red fox home ranges located in the three southern study areas were larger than 10 km^2 (90% LoCoH-k, n = 44) while only one home range in the northern study area was smaller than 10 km^2 (90% LoCoH-k, range = 8.3–44 km^2, n = 8).

Home range variation along a gradient

The red fox home ranges in this study contained on average 23% agricultural land (± 0.21SD, range 0%-76%) and 3% human settlement (± 0.08SD, range 0%-50%), which varied along a landscape gradient (Table 2). Notably, only 11 of 52 foxes had home ranges containing >1% human settlement while more than a third of the foxes (n = 22 of 52) had less than 10%

Table 1. Mean home range sizes of red foxes.

	Mean Home Range Size (km^2)					
	Mean ± SE Range		**Mean ± SE Range**		**Mean ± SE Range**	
LoCoH-k	**90%**		**95%**		**100%**	
All Foxes (n = 52)	7.1 ± 1.3	(1.0–44)	11 ± 1.9	(1.3–63)	32 ± 5.4	(1.9–185)
Females (n = 19)	8.0 ± 2.6	(1.0–44)	11 ± 3.5	(1.3–57)	27 ± 10	(1.9–185)
Males (n = 33)	6.6 ± 1.3	(1.0–35)	11 ± 2.3	(1.9–63)	35 ± 6.2	(4.7–114)
MCP	**90%**		**95%**		**100%**	
All Foxes (n = 52)	20 ± 5.2	(1.5–193)	26 ± 6.7	(1.9–273)	52 ± 10	(2.4–358)
Females (n = 19)	16 ± 5.1	(1.7–77)	20 ± 6.7	(1.9–111)	33 ± 12	(2.4–206)
Males (n = 33)	23 ± 7.6	(1.5–193)	30 ± 9.8	(2.6–273)	63 ± 15	(6.0–358)

Mean home range sizes of red foxes *Vulpes vulpes* based on 90%, 95% and 100% Local Convex Hull (LoCoH-k) and Minimum Convex Polygon (MCP) estimates. Estimates are for all study areas combined. Standard error (SE) and range of minimum to maximum home range sizes are also provided.

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Table 2. Mean home range size estimates (LoCoH-k 90%) of red foxes according to the different vegetation zones they occurred in, listed from south to north.

Vegetation Zone	Home range size (km^2)	Human Settlement	Agriculture Land	Mean Elevation (m)
Boreonemoral				
All Foxes (n = 30)	**4.7 ± 4.7**	**1% ± 4%**	**28% ± 21%**	**54 ± 22**
Male (n = 21)	5.4 ± 5.8	2% ± 4%	26% ± 21%	54 ± 24
Female (n = 9)	3.0 ± 1.4	0% ± 0%	33% ± 22%	54 ± 19
Southern Boreal				
All Foxes (n = 14)	**5.2 ± 8.6**	**7% ± 15%**	**25% ± 21%**	**106 ± 40**
Male (n = 9)	6.5 ± 10.6	4% ± 9%	26% ± 22%	118 ± 42
Female (n = 5)	2.7 ± 2.0	11% ± 22%	22% ± 22%	84 ± 29
Northern Boreal				
All foxes (n = 8)	**19.5 ± 11.8**	**0% ± 0%**	**2% ± 2%**	**605 ± 164**
Male (n = 3)	14.7 ± 5.9	0% ± 0%	1% ± 1%	454 ± 195
Female (n = 5)	22.5 ± 14.0	0% ± 0%	3% ± 2%	695 ± 25

Mean LoCoH-k 90% home range size estimates of red foxes according to the different vegetation zones they occurred in. Also shown are the differences in mean proportion of human settlement and agriculture within home ranges (%) and mean elevation (m) for each vegetation zone. Vegetation zones are listed from south to north, with sample sizes (n) and standard deviations (SD) also provided.

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agriculture land within their home ranges. Eighty-five percent of the red fox home ranges were situated below 200m elevation, with the remaining 15% (n = 8 foxes) only occurring in the northern boreal vegetation zone at elevations above 200m (range 264m-729m).

Variation in home range size

The best ranked model of home range size variation included mean elevation, proportion of agriculture land and sex, and accounted for 50% of the variation in home range size amongst foxes ($R^2 = 0.50$) and 52% of cumulative model weight (Table 3). Mean elevation had the strongest effect on home range size with home ranges increasing by 0.3 km^2 when elevation increased by 100 m ($\beta_1 = 0.003 \pm 0.001$ SE, Fig 3A). A 10% increase in the proportion of agriculture land within a home range resulted in a decrease of 0.14 km^2 in home range size ($\beta_2 = -1.37 \pm 0.51$ SE, Fig 3B). The inclusion of sex improved the final model by 0.3 ΔAICc over the second ranked model, but there was little difference in home range size between sexes ($\beta_3 = 0.34 \pm 0.21$ SE, Fig 3).

Table 3. Model selection for variables affecting variation in home range size of red foxes.

Model	df	logLik	AICc	ΔAICc	AICω
Elevation + Agriculture + Sex	5	-52.28	115.87	0	0.28
Elevation + Agriculture	4	-53.67	116.20	0.33	0.24
Elevation + Agriculture + Human settlement	5	-53.30	117.91	2.05	0.10
Elevation + Agriculture + Human settlement + Sex	6	-52.03	117.93	2.06	0.10
Elevation + Agriculture + Human settlement + Sex + Age	6	-52.05	117.96	2.09	0.09
Elevation + Agriculture + Age	5	-53.52	118.34	2.47	0.08
(*Null*)	*2*	*-71.86*	*147.96*	*32.09*	*0.00*

Model selection for variables affecting variation in home range size of red foxes using LoCoH-k 90% home range estimates with the covariates: sex, age, proportion agriculture land within home range (agriculture), proportion human settlement within home range (human settlement) and mean elevation (elevation). Presented models had a delta AICc value <4, except the null model (in italics) which is provided for comparision. Model selection was based on ΔAICc values and model weights (ω) with models $\leq$ 2 ΔAICc considered equivalent.

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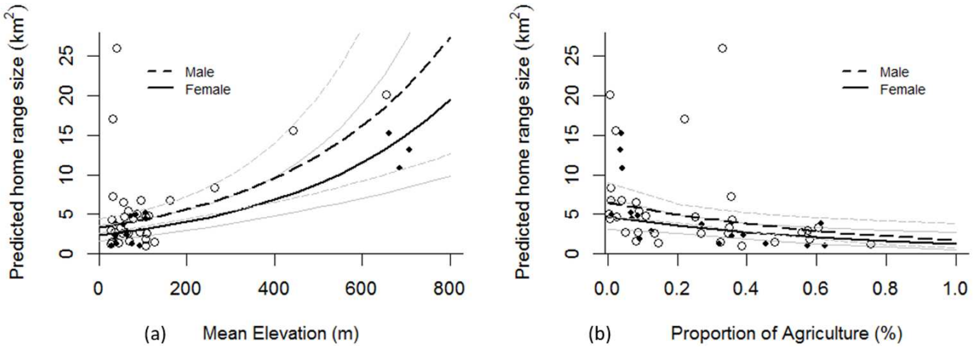

Fig 3. Predicted changes in red fox (*Vulpes vulpes*) home range size in relation to increasing elevation and proportion of agriculture land. Predicted changes in home range size (LoCoH-k 90%) of female and male red foxes in relation to increasing elevation (a) and proportion of agriculture (b). Female home range values are indicated by the solid black dots and male home ranges are open circles. Regression lines (dashed black for males and solid black for females) are from backtransformed model estimates with the 95% C.I.s of predicted values shown (solid or dashed gray lines, for females and males, respectively).

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Discussion

The red fox home range sizes in our study were much larger than those previously reported for red foxes [26, 30]. Remarkably, our average 100% MCP home range size estimate for all foxes (52 km^2) was three times larger than estimates from comparable studies of red foxes, in similar boreal and tundra landscapes [60–62]. Our use of GPS technology may have detected excursions and outlying positions to a greater degree than previous studies using VHF technology, which may have limited previous estimates of home range size. LoCoH-k estimates decreased substantially when outlying fixes were removed, compared to MCP estimates, and our average 90% LoCoH estimates were of similar size to 100% MCP estimates from the comparable studies above.

Furthermore, the GPS collars used in this study are not limited to our ability to follow and relocate animals. They therefore have the ability to increase our knowledge of movements and behaviors across landscapes and far distances. Our use of GPS technology not only highlights larger sized home ranges than previously known, but also the exploratory movement patterns of red foxes, indicating that excursions may be more common among red foxes than previously thought. Several foxes within our study showed a pattern of utilizing multiple, separate core areas within large home ranges. Further, six foxes, not included in this study, used two distinct home ranges and regularly traveled between them. Meia and Weber [63] cautioned the use of nomadic foxes in averaging home range estimates due to the significant home range size differences between resident and nomadic foxes. However, this study shows movement patterns that indicate resident foxes use much larger areas than previously presumed. 'Nomadic' foxes may actually be resident foxes traveling between core areas of resources within very large home ranges. These spatial patterns demonstrate the ability of GPS collars to enhance our knowledge of red fox movements and behaviors across landscapes, and highlight the flexibility of red foxes in their space use. This further challenges the traditional home range concept for a highly adaptable, generalist predator such as the red fox and warrants further attention.

Red fox home ranges at higher elevations and in the northern boreal vegetation zone were approximately four times larger than those of foxes at lower elevations and in the two southern vegetation zones, indicating that home range size was influenced by a productivity gradient at both the landscape (latitude) and the local (elevation) scales. Larger home ranges at higher latitudes and elevations have also been found for wolves in Scandinavia [7], and this pattern has been found in ungulates as well [64].

Elevation showed the strongest effect on home range size. This is possibly because the changes in environmental productivity along a latitude gradient were not as evident as the environmental variation (snow cover and seasonality) experienced at a local scale with increasing elevation. Further, increasing seasonality has been found to decrease population density [15]. It may be that foxes with large home ranges in the high elevation, northern study area are not constrained in their space use by social regulating factors, mediated through population density or territoriality [65], which could further restrict space use patterns of foxes in the more southern and productive study areas.

At lower elevations, where the amount of available agricultural land increased, red foxes with a higher proportion of agriculture land maintained smaller home ranges. Fragmented agricultural landscapes often allow for higher prey densities compared to northern areas dominated by boreal forest [39] and increased habitat heterogeneity can allow for resource needs to be met within smaller areas [66]. Studies of other mid-sized canids have shown smaller home ranges near human settlements compared to natural areas due to increased resource availability [6, 67, 68].

Red foxes did not demonstrate clear intersexual differences in home range size. However, the inclusion of sex in the final model indicates intersexual differences within elevation gradients and proportion of agricultural land in home ranges. We do not know breeding status of female foxes, thus it is possible the impact of sex may have been related to seasonal differences related to breeding status [17] or an artifact of sample size as fewer female foxes were monitored. Similarly, there was a sex mismatch between home range estimators, where the maximum home range sizes using LoCoH-k estimates (90% and 100%) belonged to female foxes, and the upper values of MCP estimates at the same levels belonged to male foxes. This indicates that home range size was affected by sexual differences in movement patterns, or possible underlying behavioral differences, which could in turn lead to over/under-representation of home range size depending on the method of estimation.

The overall flexibility of the red fox in its space use, social structure and resource utilization makes disentangling the sources of intraspecific variation in home range size complex. Further, both population density [69] and territoriality [4] are key intrinsic factors that can decrease home range sizes. These may be altered by human influences and lethal control of populations [70]. Hunting pressure and human attitudes towards red foxes can further impact the relationship between resource availability and home range size [9]. Nevertheless, our study clearly demonstrates the importance of environmental productivity and seasonality to red fox space use. The pronounced variation in home range size illustrates the plasticity of red foxes' space use, and this trait may enhance their ability to respond to both climate and human mediated landscape changes and facilitate red fox population increases and northern range expansions [71, 72]. While this study provides insight into possible mechanisms underlying variation in red fox home range size, the influence of a such a generalist species, and its' potential for population expansion warrants further attention [73, 74].

Supporting information

S1 Table. Summary of home range sizes of all red foxes included in this study. Summary of home range sizes of all red foxes (*Vulpes vulpes*) included in this study. All foxes were resident individuals that were monitored $\geq$ 3 months, with the exception of two females monitored for 84 and 87 days (fox number 16 and 41). The LoCoH-k 90% estimates highlighted in grey represent the home range sizes used in data analysis and modeling.
(DOCX)

S2 Table. Fox data and metadata.
(XLSX)

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Does recursive use of resource locations shape a home range? Exploring the red fox's cognitive map

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A home range represents the outcome of the interplay between an environment, an animal's understanding of that environment, and its subsequent movement decisions. Yet, recent studies suggest that recursive movement strategies have been overlooked in the shaping of animal home range patterns. Using fourteen GPS collared red foxes, we investigated within home range movements for recursive movement behaviour, suggesting a cognitive map, and explored how these shape animal space-use patterns. We found that red foxes showed significant clustering in recorded positions, indicative of recursive site use. An average of 43% of positions were found in defined clusters that covered a proportional area of only 1% of their recorded range. Ground-truthing revealed that clusters were attributed to recursive visits, and extended residence time at clumped food sources, bed or den sites, routes and vantage points in the landscape. Our results provide evidence that, while red foxes maintained exploratory movement, recursive site use played a significant role in optimising movements between distinct core areas. We conclude that these patterns support the concept of cognitive mapping enabling recursive resource use, which can lead to emergence of bounded space use, rather than a continuous drifting across the landscape. We propose that by identifying resource locations that are used recursively; it is possible to move a step closer in revealing an animal's cognitive map, or indeed, the movement behaviour underlying home range formation.

Keywords: animal movement, clustering, GPS, ground truthing, memory, space use, *Vulpes vulpes*

The size and configuration of an animal's home range is fundamental to understand a species' dispersion and spatio-ecological requirements. A variety of methods have evolved to estimate the operational dimensions of a home range following recent advances in telemetry technology, particularly that of global positioning system (GPS) tagging. There is criticism however that 'the technological cart' may have been 'ahead of the conceptual horse', and there is a lack of studies that connect animal behaviour, movement and home range characteristics (Powell and Mitchell 2012). Animal movements are decisions in response to an animal's internal state, its sensory inputs and previous experience. The resulting home range thus represents the outcome of the interplay between an environment, and the animal's understanding of that environment, i.e. its cognitive map (Fabrigoule and Maurel 1982, Powell 2000, Powell and Mitchell 2012).

Memory aids in landscape navigation and may include the informed choice of safe shelter locations, den sites or proven foraging sites (Berger-Tal and Bar-David 2015, Seidel and Boyce 2015). Remembering and returning to these locations will accrue fitness benefits (Fagan et al. 2013). An animal's spatial memory of landscape features and their evaluated attributes represent its cognitive map. Mechanistic movement models which incorporate memory-like components, such as recursive movement patterns, successfully demonstrate the emergence of bounded space-use characteristics that are indicative of a home range (Van Moorter et al. 2009, Gautestad 2011). If a home range is shaped by recursive movements between memorised resource locations (Mitchell and Powell 2004) then identifying the resources or landscape features that most influence movement decisions will aide in understanding the mechanistic processes underlying home range formation.

A common procedure to analyse the intensity of animal space use within a home range is to compute a utilization distribution (Getz et al. 2007). Utilization distributions do however, risk bias from temporal autocorrelation, particularly if active or passive behaviour is not distinguished, or associated site residence time is not taken into account (Benhamou and Riotte-Lambert 2012). Sites with relatively long residence times, such as resting and bed sites, may appear of higher utility than sites that are frequently visited, but for shorter durations. It follows that important landscape features and resources within an animal's cognitive map might be identified by taking into account the number of recursive

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visits to sites, and the number of consecutive positions at those locations (Bracis et al. 2018). The ability to infer the specific utility of sites from GPS data alone is limited however, relying heavily on assumptions. Ground-truthing sites of clustered GPS positions for behavioural field signs ex post facto, can be an important tool, to better reveal the motives behind an animal's recorded movement (Palacios and Mech 2011, Elbroch et al. 2017) and the behavioural decisions involved in habitat and resource selection (Van Moorter et al. 2013).

A species that shows remarkable variation in space use is the widespread and highly adaptable red fox *Vulpes vulpes* L. (Voigt and Macdonald 1984, Walton et al. 2017). Previous studies have observed that red foxes often focus their activities at discrete resource sites, linked by the necessary movement pathways in between (Macdonald 1983). In this study, we investigated the internal home range movements of 14 red foxes fitted with GPS radio collars within a mosaic of human land-use in south-central Sweden.

The use of frequently visited areas within an animal's home range, not resulting from random or continuous movement, should be statistically clustered (Powell 2000). However, random use of space can also lead to apparent clusters of use in some places, and little use of other places, even though those places are no more, or less, important to the individual animal. By identifying clusters of recorded positions, we evaluated if clusters were created through recursive visits, suggesting a cognitive mapping process, or were simply a by-product of broad habitat preference, or continuous movement over time, creating random clustering patterns.

By ground-truthing the site-specific attributes of cluster locations, we identified key habitats, including landscape features and resources, within the red foxes' home range. We expected red foxes would exhibit cognitive mapping, seen through recursive visits to distinct resource locations. We further predicted that recursive visits would influence the spatial configuration of a home range by constraining space use.

In seasonal, heterogeneous and anthropogenically influenced landscapes; resources vary in predictability, availability and risk, both spatially and temporally. Human activity has been found to facilitate red fox populations increasing their presence in anthropogenic landscapes (Gompper and Vanak 2008). However, persecution of foxes is also common (Reynolds and Tapper 1996). Nocturnality (Díaz-Ruiz et al. 2016), underground denning and surveillance (Wam et al. 2012) are traits that may mitigate against such threats. Therefore, habitats that provide shelter, refuge or vantage points are likely to be important components of the red fox's spatial requirements in anthropogenic environments (Lucherini et al. 1995). On this basis, we further predicted recursive visits to not only be attributed to food sources, but to areas providing safety and shelter. In affirmation of a cognitive map, we also expected foxes to demonstrate recursive movement, navigating via particular routes or strategic points.

Material and methods

Study area

We conducted this study in the southern part of Södermanland county in south-eastern Sweden (58°40′N, 16°22′E). This landscape is a mosaic of productive agricultural land amongst fragments of boreonemoral woodland, commercial conifer plantations and scattered farmyards or human settlements. Mean daily temperatures range from highs of 22°C in July to −6°C in January. Snow cover is irregular, but not uncommon, from December to March. Hunting is a popular pursuit in this region, and a number of feeding sites and bait stations to attract game species, as well as garbage dumps, are found throughout the landscape. Bait stations to attract wild boar *Sus scrofa*, for example, commonly consisted of discarded carcass remains from other large game or livestock, and hay bales or dried pea dispensers, which likely increase localised prey densities.

Fox captures

Between November 2016 and November 2017, we captured and fitted red foxes with GPS radio collars (Tellus 138 Ultralight, 210 g, Televilt, Inc. Lindesberg, Sweden). Foxes were initially captured using baited wooden tunnel traps. Foxes were then immobilized using a mixture of either: 2 mg kg^{-1} ketamine and 0.08 mg kg^{-1} medetomidine, where the medetomidine was later reversed with 0.4 mg kg^{-1} atipamazole; or with 10 mg kg^{-1} tiletamine–zolazepan, for which there is no reversal (Kreeger and Arnemo 2012). Only foxes weighing >5 kg were fitted with GPS radio collars. We sexed, measured and weighed all captured foxes. Total processing time was approximately 25–35 min.

Data collection and analysis

GPS collars were programmed to take six positions per day, at four-hour intervals generally corresponding to 00:00, 04:00, 08:00, 12:00, 16:00 and 20:00 GMT, with a pre-programmed automatic release after 180 days. We limited the GPS data to two seasonal periods: winter (1 Dec–28 Feb) or summer (1 May–31 Aug). These seasonal periods were chosen to investigate seasonal differences and to avoid temporal periods coinciding with the birth and denning period of red foxes, which can influence the number of successful GPS positions due to underground denning behaviour. We further limited our analysis to resident animals only, using calculations of net squared displacement (NSD) as per Bunnefeld et al. (2011) to visually identify patterns of resident movement behaviour from patterns of transient or dispersing behaviour (Bastille-Rousseau et al. 2016). Due to the variable capture and sampling durations of individuals, we only included red foxes having a minimum of 30 days of stable home range use within our above-defined seasonal periods. In total, the number of successful positions available for analysis was 5253, averaging 350 ± 123.3 SD (range = 215–710) across foxes. In general, GPS fix success rate averaged 89.7% (SD = 15, range = 48.6–99.5) across all foxes (Table 2). The mean horizontal dilution of precision (HDOP) of these positions was 1.19 ± 0.71 SD (range = 0.5–21.4.). Lower HDOP values are considered to be more precise (D'Eon and Delparte 2005) and 99.6% of the recorded positions had a HDOP <5.0. Only one recorded position was deemed so distantly outlying it was presumed erroneous and removed.

Using R ver. 3.3.1 (<www.r-project.org>) and the R package 'adehabitatHR' (Calenge 2006), we estimated the spatial extent, that we assumed was readily available to each fox during the study period. We observed that clusters were sometimes located outside the bounds of 95% minimum convex polygon (MCP) estimates. Consequently, they were not deemed appropriate to represent the area available to the foxes. Instead, we used 100% MCPs. However, we used the 95% MCP estimates to investigate the influence of wider exploratory movement excursions on the size of 100% MCPs.

Recursive space use

Clustering of GPS positions was used to identify recursive movement patterns and clumped space use, using the R package 'dbscan' (Hahsler and Piekenbrock 2017). Dbscan is a density based clustering algorithm requiring a pre-defined neighbourhood radius (epsilon neighbourhood (eps)) and a minimum number of positions to be contained within that radius, to define a cluster. We defined a cluster of positions as an eps radius of 55 m around each position and a minimum of six positions within that eps to form an initial core cluster. All positions within 55 m of a core point were included in clusters. We tested different eps values and determined that an eps radius of 55 m produced discrete clusters that were practical to navigate to in the field whilst also maintaining the ability to isolate the identified cause to each cluster. We chose a minimum of six core points to increase the likelihood that clusters were not formed by consecutive positions. Six consecutive positions would indicate that a red fox had remained stationary across a single 24-h period.

It was important to establish that any clustering of the GPS positions was more than might happen by random movement. Therefore, we simulated random distributions of points over the smallest sized 100% MCP estimated from the foxes and quantified the degree of clustering that occurred. Clustering of randomly generated positions used the same parameters as the GPS fox positions, and we repeated the randomisation one thousand times. We were then able compare the proportion of randomly distributed positions forming clusters, to the proportion of GPS positions forming clusters in the real fox GPS data.

Cluster characteristics

We counted the total number of independent visits to each cluster to measure recursive use of cluster locations. Independent visits were defined as a position in a cluster following a preceding position that was not. Clusters were identified both inclusively of all 24-h positions, and separately for diurnal and nocturnal positions. Where there was spatial overlap of diurnal and nocturnal clusters, these were considered as one area when counting revisits. To estimate time spent between recursive visits we also estimated the time interval between each recorded cluster position, inclusive of consecutive positions. The area of each cluster was measured as a 100% MCP, where the 'mcp' function of the R package 'adehabitatHR' was adjusted to a minimum number of three outer positions. To investigate whether the dispersion of recursively used resources is directly linked to the total area traversed by the foxes, we quantified the spatial dispersion of clusters within the fox's landscape by calculating the area of 100% MCPs between the median centre points of each cluster. It was then possible to test for correlation between the dispersion of cluster centres, and the total area traversed by the foxes.

Each individual cluster was visited in the field where a minimum of 12 and a maximum of 116 days (mean = 44 ± 26 SD days) elapsed between the last red fox visit to a cluster and the surveyor's visit to identify cluster cause. We attributed cluster causes to five broad categories: 'food', 'shelter', 'vantage point' and 'route' or 'unidentified'. 'Food' was subdivided into 'Hunting', where there was clear sign of live prey such as burrows, or game and wildfowl feeding stations; or 'Scavenging' where we found food waste or other carrion. 'Shelter' was subdivided into 'Bed' where we found evidence of surface resting sites with signs of fox presence (e.g. hairs), or 'Den' where we found subterranean excavations (earths). Where clusters were located on or around natural high-points, or outcrops in the local topography, we identified these as 'Vantage points'. Positions along paths, roads, clear game trails or necessary routes through gaps and holes in fences were identified as 'Routes'.

Identifying field signs that are exposed to weather, consumption and decomposition (such as carcass remains, especially that of small prey), is likely to be open to error, or a degree of subjectivity and search effort (Palacios and Mech 2011). For assistance in locating prey and carrion remains, or den entrances and beds, a gundog was used in the field. Locations where we were unable to identify a probable use remained as 'Unclassified'. To minimise subjectivity in identification or measurements between clusters, we used the same surveyor and dog to visit at each site.

We recorded the primary habitat within a twenty-meter radius of the cluster centre according to five broadly classified habitat types (Table 1). A 'sightability' index of horizontal vegetation cover was also measured at each cluster using a 30 × 60 cm cover cylinder (Ordiz et al. 2009). We then placed the cover cylinder at the central coordinate, and recorded the percentage of the cylinder visible from a height of fifty centimetres at 10 m in the four cardinal directions. The mean of these four recordings was used as an estimate of horizontal sightability at each location. Ruggedness was estimated within the 20 m radius using three categories:

Table 1. Descriptions of primary habitat types within a twenty-meter radius of the cluster median center point.

Habitat type	Dominant vegetation cover
Forest	Trees >2 m in height
Scrubland	Trees or shrubs ≤2 m in height including planted or regenerating commercial conifer plantations
Parkland	Short grass or pasture containing scattered groups of trees or shrubs.
Agriculture	Pasture and active or harvested arable crops
Human settlement	Areas of regular human activity such as farm-yards, suburban areas or other dwellings

Table 2. Capture and monitoring details for red foxes used in this study. The duration and season of the sampling period (following removal of dispersal events) for each fox individual included in this study. The sex and age class of each fox is provided (F = female, M = male; SA = sub adult, AD = adult) along with the sampling duration, GPS acquisition rate (ACQ), number of successful GPS positions and the spatial extent of those positions in the landscape (measured by both 95% and 100% MCPs). The significantly larger range of Fox F1 is attributed to a number of exploratory excursions beyond her home range.

Fox ID	Sex	Age	Season	Start date (dd/mm/yy)	End date (dd/mm/yy)	Total days	ACQ	No. successful positions	100% MCP (km^2)	95% MCP (km^2)
F1	F	SA	winter	15/01/17	28/02/17	41	98.8%	246	98.5	14.9
M1	M	AD	winter	12/01/17	28/02/17	46	98.6%	278	5.4	3
M2	M	SA	winter	05/12/16	30/01/17	53	93.4%	313	4.9	2.1
M3*	M	AD	winter	27/12/16	27/02/17	63	96.3%	362	11.5	7.1
M4	M	AD	winter	01/12/16	12/02/17	71	97.4%	409	18.3	5.7
M5	M	SA	winter	01/12/16	13/02/17	75	87.1%	390	3.6	1.5
F2	F	AD	winter	01/12/16	15/02/17	77	85.2%	391	4.5	1.6
F3	F	SA	winter	01/12/16	27/02/17	89	60.8%	324	4.1	3.7
F4	F	SA	winter	01/12/16	28/02/17	89	48.6%	258	3.8	2.2
F5	F	AD	summer	01/05/17	06/06/17	36	99.5%	215	5.1	3.9
F6	F	AD	summer	01/05/17	08/06/17	39	96.1%	221	4.3	3.3
M3*	M	AD	summer	01/05/17	22/06/17	52	96.8%	302	4.3	3.3
F7	F	AD	summer	25/06/17	29/08/17	66	95.2%	375	2.4	2.1
F8	F	AD	summer	01/06/17	30/08/17	81	94.6%	459	5.4	4.6
M6	M	AD	summer	01/05/17	30/08/17	122	97.3%	710	6.5	5.7

* Fox monitored over both winter and summer study periods.

1 being flat, 2 being moderate and 3 being rugged terrain (Sahlén et al. 2011). Human settlement locations were identified from Swedish geographic data (Lantmäteriet 2017) and the linear distances were calculated to the nearest 10 m using QGIS 2.18 (QGIS Development Team 2009).

To test if clustering was indeed due to broad habitat type or resource selection, we randomly sampled an equal number of non-clustered positions for each fox. These were equally representative of diurnal and nocturnal clusters. We then measured the same site characteristics, as described above, for these random locations. We tested for any difference in these variables between location types, using a Pearson's χ^2 test.

A classification tree method was used to identify the variables that best classified cluster use as either food, route, shelter or vantage using the package R.Part (Therneau et al. 2017). Beds and dens, or hunting and scavenging, were categorised together as shelter or food, respectively. Clusters of unidentified cause (n = 9) were excluded from this analysis. The data set was partitioned into a 70% training and 30% validation set. Explanatory variables included diel phase, season, sex, habitat-type, distance to human settlement, sightability, ruggedness and canopy openness. We selected the tree with the lowest validation error. Trees built on fewer predictors were chosen over more complex trees of equal prediction accuracy.

Animal capture and handling procedures were approved by the Swedish Animal Ethics Committee (permit number DNR 58-15). Permits to capture wild animals were provided by the Swedish Environmental Protection Board (NV-03459-11).

Results

Fourteen individual foxes were tracked over the study year, including nine foxes during the winter period (female = 4, male = 5) and six foxes during the summer period (female = 4, male = 2; Table 2) n = 15 as one fox (M3) was monitored over both periods. A mean of 42.7% ± 14.3 SD (range = 21.9–64.4%) of positions were found to be clustered as a result of recursive site use. This relatively high proportion of positions in clusters represented a relatively small proportion of the area traversed by the foxes (Table 3, Fig. 1). The average area of clustered positions, per fox, was 0.07 $km^2 \pm 0.05$ SD (range = 0.02–0.16, n = 15). Clustering of fox positions was significantly greater than expected from random occurrence (the null model). Simulations of random points within the smallest red fox MCP confirmed that clustering of positions from real foxes were outside the 5% tails of the randomised density distribution (Fig. 2). The mean density of random points produced by the randomization test within the smallest 100% MCP (2.4 km^2) was 171.1 ± 7.5 SD positions per km^2 (range = 148–198). The minimum density simulated (148.9 per km^2) was therefore greater than the density produced by the majority

Table 3. The average proportion of red fox GPS positions defined as clusters, and the proportional area of clusters within a red fox home range (100% MCPs). For comparison, foxes have been divided into the season of their study period (summer, n = 6; winter, n = 9), as well as all foxes combined (n = 15).

Season	Prop. of positions in clusters			Prop. of 100% MCP covered by clusters		
	Mean	SD	Range	Mean	SD	Range
Summer	39.8%	14.2	(22.8–60.8)	1.3%	0.9	(0.5–2.7)
Winter	44.6%	14.9	(21.9–64.4)	1.4%	1.4	(0.1–4.1)
Combined	42.7%	14.3	(21.9–64.4)	1.1%	1.2	(0.1–4.1)

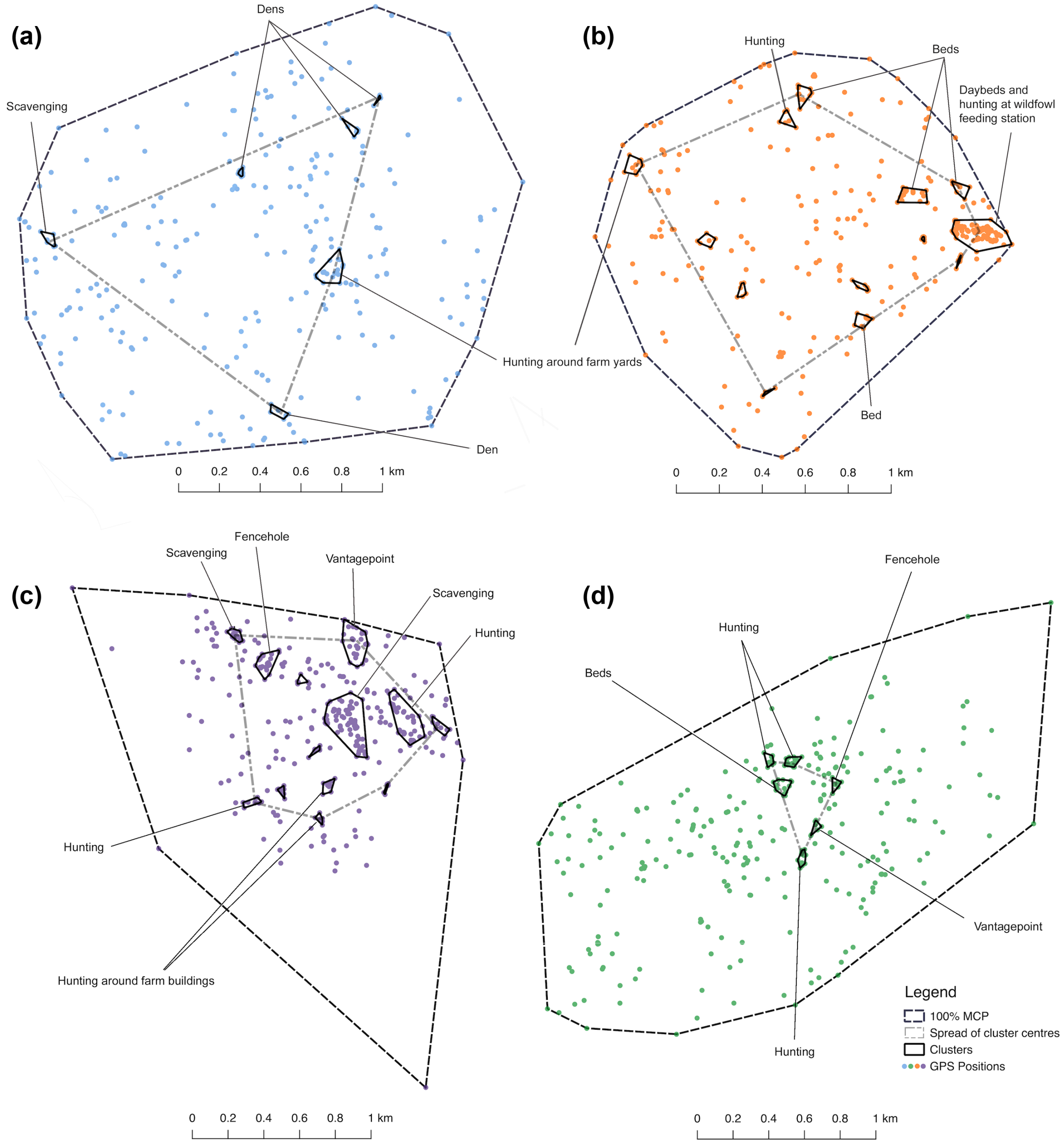

Figure 1. Illustration of the spatial dispersion and proportional area of clustered GPS positions within the 100% MCPs of two female and two male foxes: (a) F3 over 89 days in the winter, (b) F7 over 66 days in the summer, (c) M5 over 75 days in the winter and (d) M3 over 52 days in the summer.

of foxes (mean = 69.3 ± 39.6 SD positions per km^2, range = 2.5–158).

In total 126 individual clusters were identified. These consisted of a median of 10 positions (range = 6–94) with each red fox forming a median average of eight clusters (range = 3–20). Purely recursive clusters (n = 34) consisted of a median of 7.5 positions (range = 6–34). Only one cluster was formed by a single consecutive visit, where fox F8 occupied a den location for eleven consecutive positions (44 h). Clusters containing a mix of recursive and consecutive positions represented the largest proportion, 72.2% (n = 91) of clusters. These clusters contained a median of seven unique visits (range = 3–52) and a median of three (range = 1–53) consecutive positions. Individual red fox re-visitation rates are provided in Table 4. Of the total number of positions forming clusters, 71.3% were identified as unique or recursive visits, and not subsequent consecutive positions. For our four hourly fix schedule, the mean interval between recursive cluster visits was 10.1 h ± 11.8 SD (range = 4–148). This equates to an average rate of

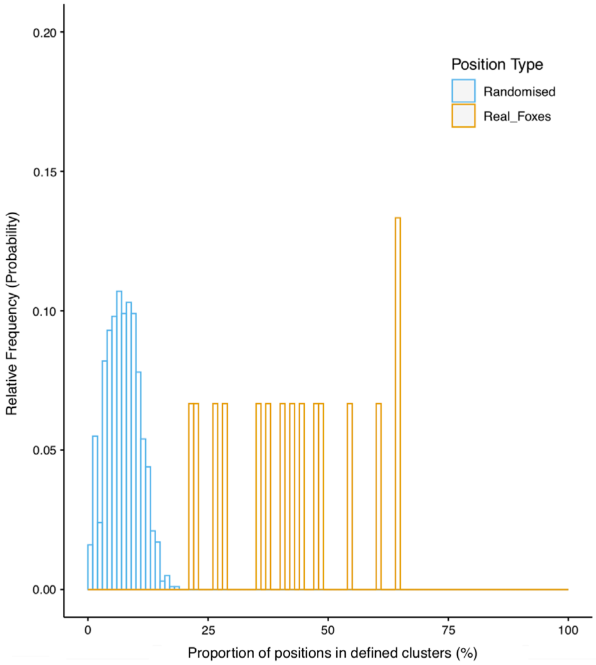

Figure 2. Results of randomisation test where the histogram shows the proportion of positions in defined clusters from real fox position data within their 100% MCP, compared to clustering of 1000 simulations of 402 randomly distributed points within the smallest sized 100% MCP (2.4 km^2).

2.4 (out of six) positions at any cluster per day. Based on 100% MCPs calculated using the cluster centres, cluster locations encompassed an average area of 0.82 km^2 ± 0.92 SD (range = 0.08–3.83 km^2, n = 15). This represented an average of 17.3% ± 17.96 SD (range = 0.16–58.9%) of the total area traversed by individual foxes during their seasonal tracking period (illustrated in Fig. 1). There was no significant correlation between the dispersion of clusters and the total area traversed by the foxes ($r = -0.21$, $p = 0.45$, $n = 15$). Neither were there statistically significant differences in these proportional areas between summer and winter ($t = -0.98$, $df = 5.98$, $p = 0.36$) when sex was pooled, or between males and females ($t = 0.21$, $df = 11.74$, $p = 0.84$), when season was pooled.

The differences in habitat type at clustered positions versus non-clustered positions were not statistically significant ($\chi^2 = 8.84$, $df = 5$, $p = 0.12$, Table 5a) indicating that broad habitat classifications were not influencing clustering. The only notable difference was an 11% greater proportion of single positions in agricultural habitat, which contributed to 42.6% of the χ^2 statistic. There was a significant difference in the attributes of clustered positions compared to those of randomly selected non-clustered positions ($\chi^2 = 91.16$, $df = 6$, $p \leq 0.01$, Table 5b). In comparison to 45% of non-cluster positions, only 7% of cluster positions could not be classified in the field. This difference contributed to 38% of the respective χ^2 statistic. The classification tree that demonstrated the least error in cross validation, classifying cluster utility to 65.7% accuracy, used three variables: habitat type, diel phase and terrain ruggedness (Fig. 3). Following removal of clusters with unclassified utility, and the 30% validation set, sample size was 82. Terrain ruggedness was used in the primary split to predict cluster utility. Nocturnal clusters in forests, parkland and scrub were related to food, except in flat topography where they were predicted as routes. Clusters around buildings and in agricultural or wetland habitats, were most likely to be related to food sources. Field visits revealed signs of high rodent densities and scavenging in these areas. Diurnal clusters in most habitats were attributed to shelter, or, in the most rugged terrain (category 3), to distinct high-points and outcrops, presumably used as vantage points for surveillance (Wam et al. 2012).

Two female foxes recorded comparatively low fix acquisition rates (F3 and F4, Table 2). We assumed that these failures to fix were due to time spent underground in the dens found at their cluster locations, particularly as the failed positions all occurred during the diurnal phase. If this is the case, recursive visits and time spent in shelter locations may be underrepresented. However, we did not find a significant correlation between GPS acquisition

Table 4. Red fox visitation rates to clusters, including total number of positions, number of visits, the number of clustered positions for each individual fox, and the proportion of clustered positions classified as unique visits. The mean number of visits and range of visits by each fox to individual clusters is also included.

Fox ID	Total positions	Visits	Visitation rate	Clustered positions	Visits as prop. of clustered positions	Mean visits to clusters	Range
F1	246	49	19.9%	55	89.1%	12.3	6–20
M1	278	34	12.2%	48	70.8%	6.8	5–8
M2	313	93	29.7%	114	81.6%	10.3	6–28
M3*	362	87	24.0%	113	77.0%	9.7	3–31
M4	409	122	29.8%	164	74.4%	20.3	7–52
M5	390	132	33.8%	175	73.7%	12.0	5–36
F2	391	184	47.1%	210	87.6%	13.1	5–49
F3	324	72	22.2%	88	81.8%	10.3	6–16
F4	258	79	30.6%	86	91.9%	11.3	5–29
F5	215	28	13.0%	46	60.9%	9.3	3–16
F6	221	45	20.4%	65	69.2%	11.3	4–22
M3*	302	36	11.9%	60	60.0%	6.0	5–9
F7	375	101	26.9%	173	58.4%	12.6	4–44
F8	459	104	22.7%	182	57.1%	8.0	1–15
M6	710	136	19.2%	242	56.2%	6.8	2–20
All	5253	1302	24.8%	1825	71.3%	10.7	1–52

Table 5. (a) The percentage of clustered red fox GPS positions versus non-clustered GPS positions in the different habitat classifications. (b) The percentage of clustered and non-clustered positions attributed to specific causes in the field. n = 126 for both clustered and non-clustered positions.

(a)	Settlement	Agriculture	Parkland	Scrubland	Forest	Wetland
Cluster	1.6%	15.1%	8.7%	14.3%	55.6%	4.8%
Non cluster	1.6%	26.2%	3.2%	10.3%	56.3%	2.4%

(b)	Den	Bed	Scavenging	Hunting	Vantage	Route	Unclassified
Cluster	11.9%	25.4%	8.7%	22.2%	16.7%	7.9%	7.1%
Non cluster	0.0%	3.2%	2.4%	11.1%	14.3%	23.8%	45.2%

rates and the percentage of positions recorded in clusters (r = −0.12, p = 0.91, n = 15).

Discussion

We found significant clustering in recorded positions, providing evidence that red foxes use space disproportionately due to the recursive use of discrete resource locations. On average, 43% of total recorded positions were clustered within a small proportion (1.1%) of 100% MCPs (Table 3). These aggregations of positions were significantly greater than would happen by random occurrence (Fig. 2). Non-homogenous space use is in line with previous observations that home ranges are often made up of distinct locations that are occupied more intensively than other locations (Macdonald 1983, Samuel et al. 1985). The relatively small area of clusters suggests that foxes use highly localised resources compared the spatial scale of their potential range (100% MCP). The dispersal of clusters within these areas was not correlated with the total area traversed by the individual foxes, however. This suggests that the foxes did not limit themselves to direct movement between recursively visited resource sites, but that they also demonstrated an individual degree of movement outside the spread of these locations (as illustrated in Fig. 1) probably as exploratory movements beyond commonly used areas (Table 4).

Our habitat classification was too coarse to reveal potential habitat clues as to prey availability. However, other than a greater proportion of single positions in agricultural habitats, there was no general difference in habitat classification between clustered and non-clustered positions (Table 5a). A greater proportion of single positions in agricultural habitats suggest that red foxes frequently occupy these habitats, but perhaps utilise them in such a way that does not form discrete clusters. For example, a fox forag-

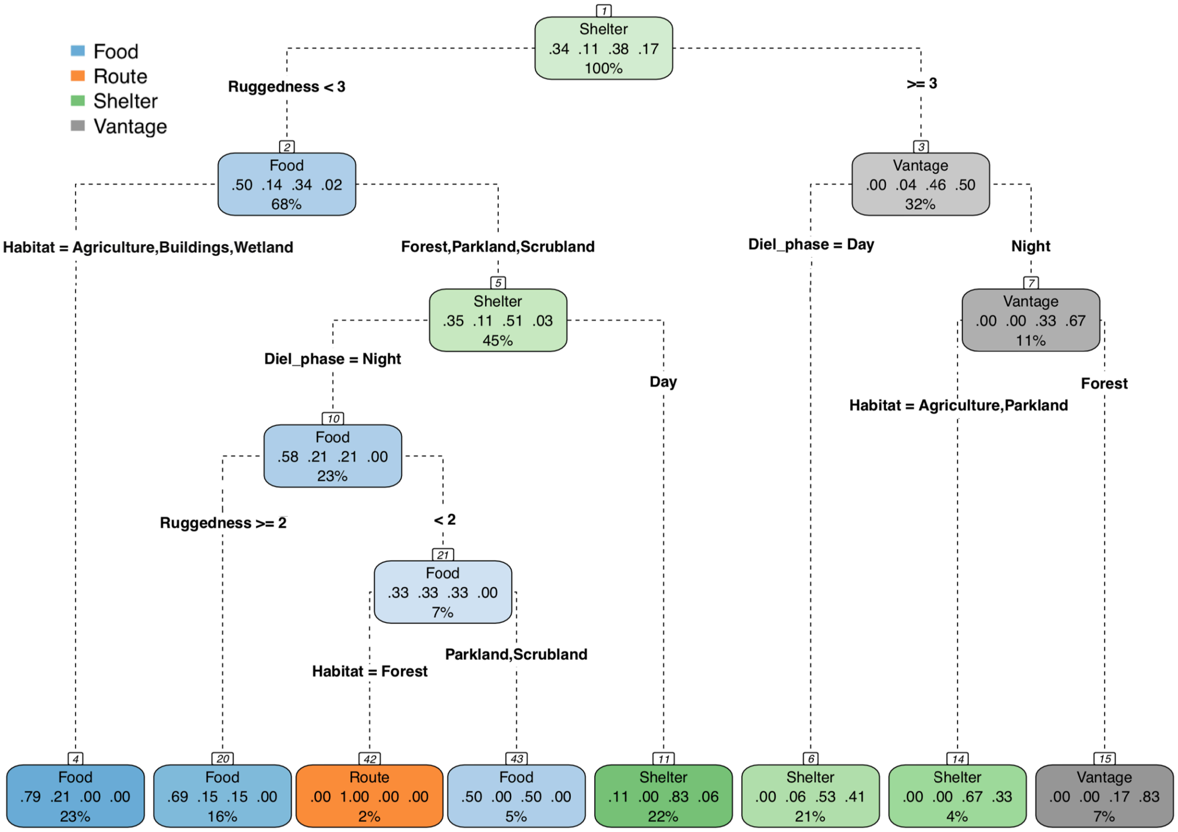

Figure 3. Classification tree predicting cluster utility of 82 red fox clusters identified as food, shelter, route or vantage, by habitat type, site ruggedness and diel phase. Each node details the classification probability of each utility at that node in order: Food, Route, Shelter and Vantage.

ing in a large field may move too quickly or over too great an area, due to search patterns, as to record visits as a discrete cluster. Attributed causes of clustered locations were more discernible in comparison to those of non-clustered positions, however (Table 5b). Specifically, at clusters we discovered more beds, dens and clumped food sources. Construction of classification trees (Fig. 2) revealed that clusters around buildings and in agricultural or wetland habitats, were most likely to be related to food sources. Nocturnal clusters in forests, parkland and scrub were also related to food. The clumped food sources found in these locations, such as garbage dumps, or high rodent densities at farms or baiting stations, highlight how human activity may subsidise opportunistic predators (Gompper and Vanak 2008, Newsome et al. 2014).

Shelter and resting locations have been recognised as an integral home range requirement for the red fox in anthropogenic landscapes. Lucherini et al. (1995) suggest that the location of shelter sites, in relation to that of the food sites determines the size and shape of the red fox's home range. Pandolfi et al. (1997) identified no uniform home range area by red foxes over time, but distinct core areas that were identified as both activity and resting sites. The proportion of clusters and recursive visits that we attributed to both beds and dens, certainly suggest that shelter locations were an important component of the red fox's cognitive map.

We expect food resources to evolve and cease with time to a higher degree than shelter and vantage points, as carrion and prey are unpredictable (Eide et al. 2004) and temporally pulsed (Gomo et al. 2017). Group living may increase fitness if resource sites are heterogeneous and their quality is sufficient for maintenance of multiple individuals (Macdonald 1983). Dynamic interactions and competition between foxes will affect movement and use of localised food. There is likely to be a dominance hierarchy around sites of higher quality; foxes of lower status might have to move about more, and visit less predictable sites (Dorning and Harris 2017). Females, especially those rearing offspring, will require higher quality foraging to meet the energetic demands of breeding (Gittleman and Thompson 1988). We would thus expect reproductive females to demonstrate more frequent visits to predictable food sites or den locations seasonally. However, our small sample sizes prevented us from being able to test for differences between sex and season.

Movement in these dynamic environments allows updates of a memorised landscape to current environmental conditions. Whilst navigating between one resource location to another, foxes will take detours or make exploratory forays to patrol and mark their wider surroundings (Gosling and Roberts 2001), perhaps seeking new foraging or mating opportunities, thus updating their cognitive map. The extent of these movements is highly individual and illustrated by the two male and two female examples shown in Fig. 1. Of particular note is the bounded distance (or time) that these single positions appear to be dispersed around the core areas.

A proportion of clusters were positioned along tracks and necessary movement paths, such as fence holes or culverts, demonstrating route fidelity is also implicit in a cognitive map. However, these aggregations highlight the risk of making false inferences regarding resource selection from GPS positions alone. Discrete clusters of recursive visits are not necessarily indicative of resource locations; they may merely be a by-product of landscape constraints determining the most efficient route between memorised resource sites. The contrary may also be true. Where resources are more thinly dispersed over large patches or landscapes, wider searching or foraging movements may not create discrete cluster patterns, despite regular recursive behaviour. This may explain the high proportion of recorded positions in agricultural habitats that were not identified as clusters according to the study parameters (Table 5a). Only identifying clusters with a minimum number of positions could overlook important, but more recently discovered, resources until they receive the prescribed number of recorded visits. Similarly, additional clustering might also have been missed in habitats where the GPS could not successfully fix position. A cognitive map may feature locations that are seldom visited or indeed avoided completely (Powell and Mitchell 2012). Our representation of a cognitive map is therefore limited to the discrete resource locations where the animal is most likely to revisit, which may not include all of the places it is familiar with or influenced by. We would also expect a cognitive map to be dynamic as new sites are added and others decay over time, in response to changes in environmental heterogeneity, resource availability and social dynamics. However, by identifying recursive movements to both shelter and foraging locations, we find support for cognitive mapping and recursive behaviour leading to bounded multi-modal space-use patterns in heterogeneous landscapes (Van Moorter et al. 2009).

Conclusions

Recursive site use, to both shelter and food resources, played a significant role in optimising red fox movements between distinct core areas, especially as intervals between cluster visits were generally short. Exploratory movement beyond regularly visited locations was also evident, although this varied between individual foxes. We therefore conclude that these patterns support the concept of cognitive mapping enabling recursive resource use, which can lead to emergence of bounded space use, rather than a continuous drifting across the landscape. We propose that by identifying resource locations that are used recursively, it is possible to move a step closer in revealing an animal's cognitive map, or indeed, the movement behaviour underlying home range formation.

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Paper III

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SHORT COMMUNICATION

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 Trewhella 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 Trewhella 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% ± 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

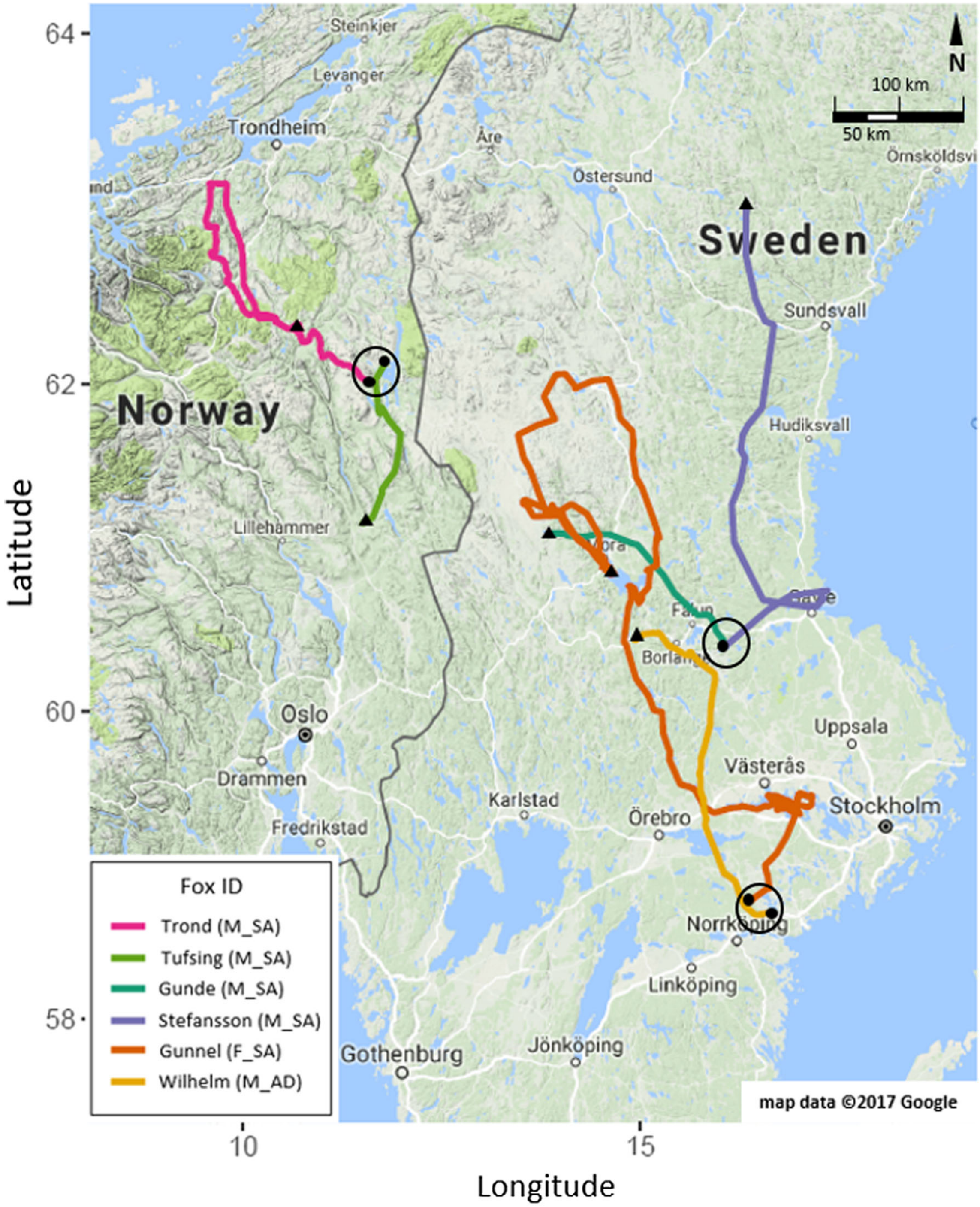

Fig. 1 Long-distance dispersal movements of six GPS-collared red foxes in Sweden and Norway. Solid black circles and triangles indicate initiation (start) and settlement (end) points of dispersal movements, respectively. The three study areas where foxes were initially captured are outlined by black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

Fine scale genetic and spatial structure of a red fox population reveals kin clusters and sex-biased dispersal patterns

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Abstract

The genetic structure of a population can provide important insights into animal movements at varying geographical scales. Individual and social behaviors, such as philopatry and dispersal, affect patterns of relatedness, age and sex structure, shaping the local genetic structure of populations. However, these fine scale patterns may not be detected within broader population genetic structure. Using a combination of SNP genotyping and pairwise relatedness estimates, we investigated the spatial and genetic structuring of 141 red foxes within south-central Sweden at two scales. First, we looked at broad scale population structuring among red foxes at the regional level. We then estimated pairwise relatedness values to evaluate the spatial and genetic structure of male, female and mixed sex pairs for patterns of philopatry and dispersal at a more localized scale. We found limited genetic differentiation at the regional scale. However, local investigations revealed patterns of female philopatry and male biased dispersal. There were significant differences in pairwise geographic distances between highly related same sex pairs with the average distance between related males, 37.8 km, being six times farther than that of related females, averaging 6.3 km. In summary, the low levels of genetic differentiation found in this study illustrates the mobility and dispersal ability of red foxes across scales. However, relatedness plays a strong role in the spatial organization of red foxes locally, ultimately contributing to male biased dispersal patterns.

Keywords: kinship, relatedness, *Vulpes vulpes,* SNPs, GPS, dispersal, inbreeding avoidance, female philopatry, social structure

Introduction

Dispersal is a key driver of gene flow across space, linking populations both demographically and genetically (Clobert et al. 2001). Patterns of dispersal or connectivity arising from physical landscape features (Wright, 1943, Balkenhol et al. 2015) or from behavioral traits such as natal philopatry or territoriality can limit gene flow between groups of organisms, altering the genetic structure of a population (Macdonald, 1983, Bowler and Benton, 2005, van Dijk et al. 2015). Local gene flow patterns, where short distance movements, philopatric behavior or inbreeding avoidance influence patterns of relatedness, age and sex structure, can shape the genetic structure of populations considerably. However, such fine scale patterns may not be detected within broader population genetic structure (Rousset, 2001).

Various genetic methods can provide important insights into animal movements at varying geographical scales by describing how individual behaviors, such as philopatry and dispersal, translates into gene flow (Prugnolle and De Meeus, 2002). While there are still challenges associated with quantifying dispersal in elusive, wild, free-ranging species, advancements in the development of useful, low cost genetic markers (e.g. single nucleotide polymorphisms, SNPs), in combination with rigorous inference methods, offer an expanded framework for interpreting fine scale patterns such as familial relationships, from genetic markers (Beaumont and Rannala, 2004, Latch et al. 2006, Stauffer, 2007, Stephens and Balding, 2009, Banks and Peakall, 2012). Similarly, the use of GPS telemetry for studying animal movements has dramatically increased enhancing our ability to collect detailed movement data from individual animals (Cagnacci et al. 2010). Together, these tools allow for investigation into factors jointly affecting animal spatial and social organization, population dynamics and genetic structuring (Morales et al. 2010).

For many larger species, dispersal movements tend to be relatively short and long distance dispersal, while notable, is uncommon (Nathan, 2005, Jordano, 2017). In mammals, dispersal is often male-biased with females exhibiting philopatric behavior (Greenwood, 1980). When examined at a finer spatial scale, this sex biased dispersal can create different spatial patterns of relatedness between the sexes, with local relatedness higher among members of the more philopatric sex (Prugnolle and De Meeus, 2002). In such philopatric systems, where closely related individuals settle within or close to the home range of their parents, high relatedness among individuals can lead to the emergence of kin structured populations (Kitchen et al. 2005, Croteau et al. 2010, Quaglietta et al. 2013).

The red fox, *Vulpes vulpes,* is a mid-sized canid with variable spatial and social behavior (von Schantz, 1981, Doncaster and Macdonald, 1991, Cavallini, 1996). Red foxes are a highly vagile species, having a geographic range that spans most of the northern hemisphere (Larivière and Pasitschniak-Arts, 1996) and the potential to disperse over long distances (Colson et al. 2017, Walton et al. 2018). In most areas, red foxes form monogamous pairs or small family groups (von Schantz, 1981, Cavallini, 1996). These typically consist of a dominant, breeding pair and subordinate individuals, which are believed to be the offspring of one or both of the dominants (von Schantz, 1981, Baker et al. 2004). However, kinship is rarely confirmed, and red foxes have been shown to exhibit polygynandry, multiple paternity and extra pair copulations (Baker et al. 2004) adding potential complexity to the kin structure of family groups.

Previous population genetic studies indicate that red foxes can exhibit a high degree of gene flow due to their dispersal ability (Gachot-Neveu et al. 2009, Teacher et al. 2011, Mullins et al. 2014, Atterby et al. 2015, Norén et al. 2015). However, detailed studies of how philopatric behavior and dispersal are interacting within populations is largely lacking (Gompper and Wayne, 1996, Koenig et al. 1996, Peakall et al. 2003, Mabry et al. 2013, Galov et al. 2014). Delineating patterns of familial clustering can ultimately lead to a better understanding of red fox social organization, spatial behavior and population dynamics, as well as the mechanisms underlying such patterns. Additionally, as red foxes are known vectors for the spread of parasites and diseases (Vervaeke et al. 2006, Atterby et al. 2015), such knowledge may lend vital information to wildlife management and health authorities aiming at managing a highly diverse and ecologically dynamic generalist species.

Here, we investigated the spatial and genetic structuring of red foxes within south-central Sweden at two different scales. First, we looked at regional scale genetic structuring among red foxes, where we expected gene flow to be high with panmixia occurring over a broad scale due to the high mobility of this species (Norén et al. 2015, Munro and Burg, 2017). We then evaluated the spatial and genetic structure of male, female and mixed sex pairs to compare patterns of philopatry and dispersal at a more localized scale. Here, we predicted that sex biased dispersal due to philopatric female behavior should lead to patterns of kin structuring within a population. The low levels of genetic differentiation found in this study illustrates high mobility and dispersal ability of red foxes across scales. However, relatedness plays a strong role in the spatial organization of red foxes locally, ultimately contributing to male biased dispersal patterns.

Material and Methods

Study area and DNA sampling

This study was conducted within a 13,000 km^2 region in south-central Sweden (58°N-60°N; Fig. 1). Within this region, the northernmost fox trapping sites around Hedemora (60°16′N-

15°59′E) and Grimsö (59°40′N-15°25′E), are separated from our local study area around Kolmården (58°40′N-16°22′E) by approximately 200 km (Hedemora is located ~70 km north of Grimsö and Grimsö is ~130 km north of Kolmården). The northern areas consists of a transitional border zone between boreonemoral forests in the south and boreal forests in the north, where the landscape is generally flat with altitude rising from 75m a.s.l. in the south to 180m a.s.l. in the north. Daily mean temperatures average 15°C in summer to –5°C in winter. The ground is generally snow covered from late December to March. The local study area around Kolmården encompasses approximately 1,800 km^2 within Södermanland County (see inset Fig 1.) representing a fragmented mosaic of productive agriculture areas, boreonemoral forests and scattered human settlements, representing a rural, anthropogenically modified landscape. Daily mean temperatures range from 20°C in summer to –5°C in winter. Snow covers the ground irregularly from December to March.

We collected genetic material (hair, tissue or blood) from red foxes that were live captured as part of a Global Positioning System (GPS) telemetry study during 2012-2019 (see Walton et al. 2017 for details of the capture and handling procedures). We also opportunistically collected red fox scat and tissue samples from deceased, unmarked red foxes found during field monitoring of GPS collared foxes. All live captured foxes were sexed, weighed and marked with plastic ear tags (Rototags, Dalton Supplies, Ltd.). However, only red foxes meeting the necessary weight requirements (≥5kg) were fitted with GPS collars. Age of foxes was approximated, assuming a birth date of 15th April (Englund, 1970), as either pup (<6 months), sub-adult (6 months to <1 year) or adult (>1 year), using the date of capture in combination with the amount of tooth wear and coloration. All capture and handling protocols were approved by the Swedish Environmental Protection Board and the Swedish Animal Ethics Committee (permit numbers NV-03459-11, DNR 70-12, DNR 58-15, DNR 13-47).

DNA extraction and SNP Genotyping

DNA from tissue, blood and hair was extracted using a Qiagen Symphony robot and the QiaSymphony DNA mini kit and QiaSymphony DNA investigator kit, respectively. Feces were manually extracted using Zymo's soil/fecal DNA kit. This kit was chosen after a review of eight different methods/kits.

Table 1. Sample size and age categories of red foxes included in this study. Sex could not be determined from the genetic markers for five foxes in this study. All other individuals were sexed successfully and used in our analysis of pairwise relatedness and distance estimates.

	Age Class				
	Adult	Subadult	Pup	Unk.	Total
Female	**17**	**20**	**10**	**7**	**54**
GPS	15	17	0	0	32
No GPS	2	3	10	7	22
Male	**36**	**28**	**4**	**14**	**82**
GPS	32	27	0	0	59
No GPS	4	1	4	14	23
Unknown	**0**	**0**	**1**	**4**	**5**
Total	53	48	15	25	141

We genotyped individuals on a Fluidigm® Biomark™ microarray platform using the 96.96 dynamic array. The SNP (Single Nucleotide Polymorphism) assays were based on loci shown polymorphic in fox on Illumina's® CanineHD™ 170K Whole-Genome Genotyping BeadChip (marker references listed in Table 1). For the marker ascertainment we used a population of foxes from across Norway (N=24) and Sweden (N=24). The selected somatic markers were not deviating from Hardy Weinberg equilibria expectations and had a minor allele frequency exceeding 0.3. Additionally, we only included markers that clustered well for several DNA sources (tissue, blood, hair, and feces). In addition to 91 somatic markers, we used Sanger sequencing to design three markers that only amplified the Y-chromosome, and two mitochondrial markers for species recognition, for a total of 96 SNP markers.

All genotyping runs included three NTC (No Template Controls) and reference samples. Samples were run in duplicates for quality control (see Table 2). Samples that showed an amplification rate below 90% were discarded. For samples that amplified well (>99%) the error rate fell below 1%. Basic marker statistics are presented in Supplementary Table 1.

Genetic and Spatial Analyses

For analysis of spatial population structure and calculating pairwise relatedness distances described below, we used the last position of each GPS collared animal. Using the last position is a better representation of the area occupied by the animal (i.e. its home range) than the original trapping location, as it allowed for animal movements over time, such as dispersal, to occur, whereas trapping location did not. For red foxes that were trapped but did not receive a collar (i.e. predominantly young foxes under <6 months not meeting the necessary weight requirements), we used the GPS coordinates of the wooden box trap where the individual was captured and subsequently released to represent sample location. For scat or tissue, we used the coordinates taken directly at the site of field collection using a hand held GPS unit. For analyses at the regional and local levels we included only adult and subadult foxes, removing pup samples (n=15) as pups still occupied their natal range, regardless of sex, potentially confounding results. For analyses of fine scale genetic structuring and patterns of kinship within a more localized area, we also removed individuals where we were not able to identify sex (scat samples, n=4). In total, 126 red foxes contributed to the regional analyses and 103 to the local analyses.

To explore the genetic structure of red foxes we ran Genepop 4.2 (Raymond and Rousset, 1995, Rousset, 2008). In Genepop, we calculated basic marker statistics, such as expected heterozygosity (He), observed heterozygosity (Ho) and deviations from Hardy Weinberg equilibrium (HWE) (Supplementary Table 1).

We then ran a spatial principal component analyses (sPCA) in the R package Adegenet (Jombart, 2008) to visualize genetic differentiation geographically, both regionally and locally. The sPCA was run on the full dataset, as well as for subsets of male and female individuals from the southernmost trapping area around Kolmården, Sweden, to explore how distribution of genetic variation varied with sex locally. The K Nearest Neighbor algorithm was used with two neighbors for all runs (Jombart and Collins, 2015). As the information content of the principal components (PCs) of each subset differed slightly, we included different numbers of components. The number of global PCs were 5, 5 and 4 and local PCs 3, 3 and 3 for all foxes, Kolmården females only, and Kolmården males only.

Table 2. Amplification success and error rates of different red fox DNA source materials. There was a negative correlation between amplification success and error. For samples with an amplification rate <75%, error rates may exceed 20%.

Source	Amp. success	Error rate
Tissue	>99%	<0.9%
Blood	>99%	<0.6%
Hair	>92%	<3.4%
Feces	Highly variable	<1.6%*

*Error rate for feces is reported for samples with an amplification success >75%

For comparison, we also ran Structure software (Pritchard et al. 2000) to explore genetic structure using an admixture model and correlated allele frequencies with 100 000 burn-in steps and 100 000 MCMC iterations and 10 replicates for each of the runs for *K* populations = 1-10. Here again, three separate analyses were run. First, all individuals and the subsets of local females and males from the Kolmården area, as described above (Supplementary Fig. 1). The most likely number of clusters (based on LnP(K) and ΔK, Supplementary Fig. 2) was determined using Structure Harvester (Earl and Vonholdt, 2012) and cluster membership was assigned using a cutoff q-value of 0.80.

To determine kinship among individuals, we determined the relatedness coefficient (r) using R.3.3.2 (R-Core-Team 2018) and the R package 'Related'(Wang, 2011, Pew et al. 2015) between all individual pairs going back two generations. The r-value is estimated from similarities in the number of shared identical alleles, in relation to the population level allele frequencies. This allowed us to infer the most probable relationship between individuals. A first-degree pair is expected to show an r-value of 0.5. Such relationships include the individual's parents, full siblings, and offspring. A second degree relative will show an r-value of approximately 0.25, which includes the individual's grandparents, grandchildren, aunts, uncles, nephews, nieces or half-siblings.

To determine if kin were spatially clustered at the local scale, we evaluated the pairwise mean geographic distances among all pairs of first degree relatives ($r \geq 0.40$) for the different sex combinations: female-female, opposite sex, and

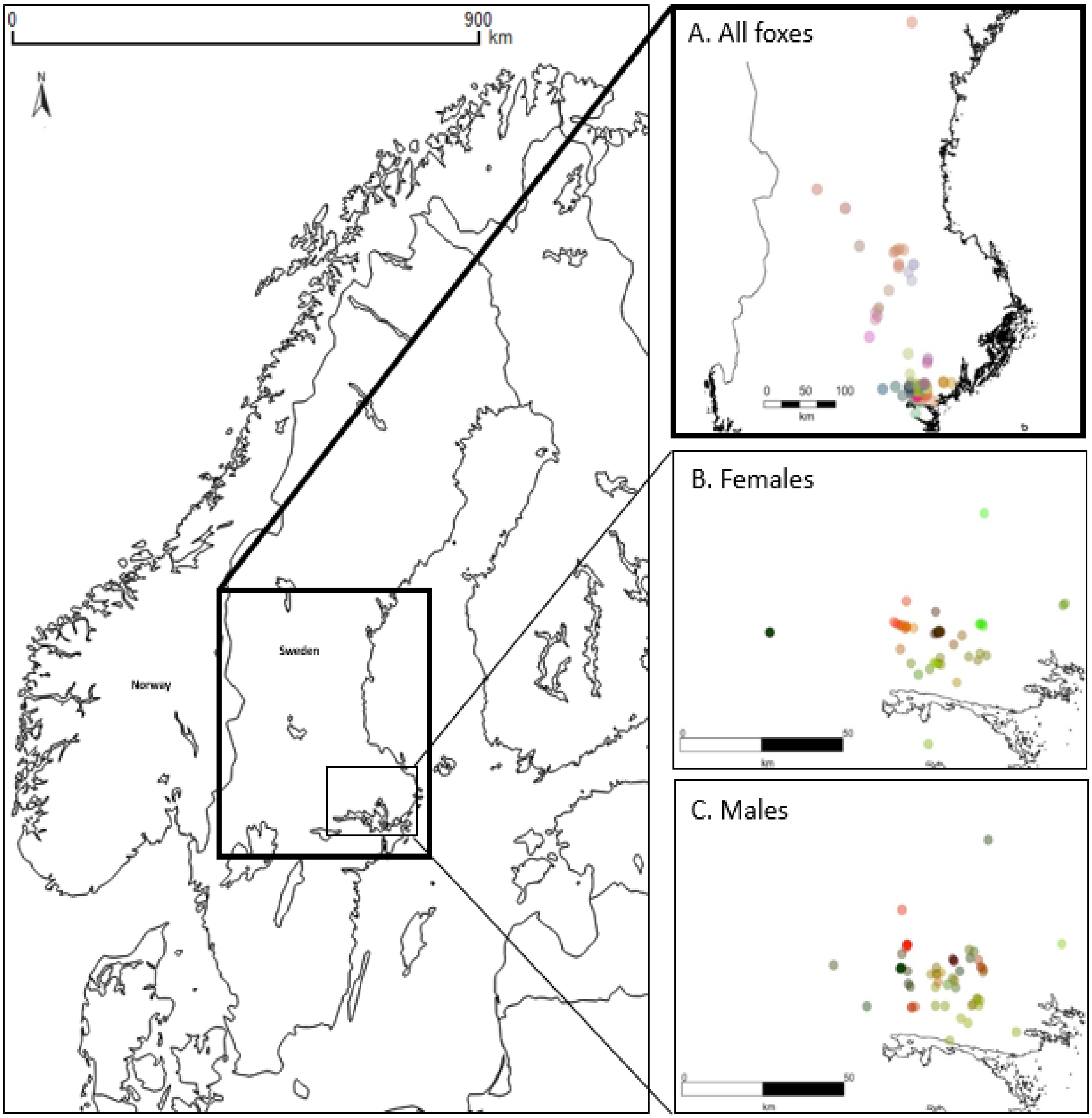

Figure 1. Spatial genetic structure of red foxes visualized by spatial principal component analyses (sPCA). The colors in the maps show the first three principal components only. Colors indicate genetic similarity (similar colors are more genetically similar individuals whereas contrasting colors are more genetically dissimilar) with panels showing different subsets of the population. Panel A represents all individuals included in the study. Panels B and C show local structuring of females and males from the Kolmården area, respectively. Overall, the population displays a high level of mixing, with limited structure, but, the overlapping similar color groupings in panel B indicate females have more localized structure than males.

male-male, using Welch two sample t-tests. We further examined how pairwise distances varied according to differing degrees of relatedness. For this, we categorized all red fox individuals according to their relatedness values where values of 0-0.10 and 0.10-0.20 indicated unrelated or distantly related individuals, 0.21-0.40 intermediate or second-degree relatives and ≥ 0.40 to be first-degree relatives.

Results

Genetic material collected from 180 red fox samples yielded 141 individual genotypes (54 females, 82 males, 5 unknown sex) of which 91 (32 females and 59 males) were fitted with GPS collars (Table 1). The mean amplification success exceeded 99% for tissue and blood extractions, whereas hair was lower at 96%. Feces showed highly variable amplification success, likely correlated to large differences in

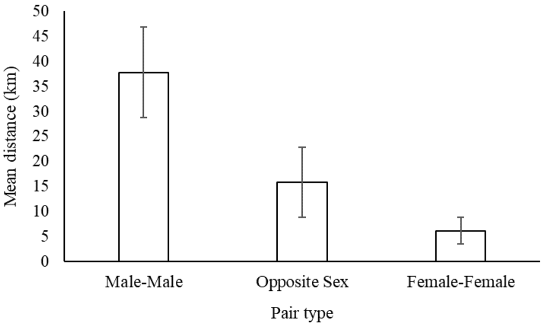

Figure 2. Local scale average pairwise geographic distances ±2SE between highly related (r ≥0.40) pairs of red foxes: male-female (opposite sex), female pairs (female-female) and male pairs (male-male).

Table 3. Mean pairwise geographic distances between highly related adult and subadult red fox pairs (n=124; r≥0.40) within a local area in south-central Sweden. Red foxes under six months of age (pups) and those of undetermined sex were excluded from analysis.

Pair Type	N	Distance (km)	SD
Male-Male	38	37.79	55.54
Opposite Sex	64	15.85	28.49
Female-Female	22	6.17	12.45

the degree of degradation in the field before the DNA could be collected. Error rates were low, but increased for samples with low amplification success. We therefore only included samples with an amplification success of 75% or more (Table 2). This allowed us to confidently separate individuals while simultaneously avoiding the inclusion of unique genotypes caused by genotyping errors (see Creel et al. 2003). Overall, the SNP markers showed high variability, with a mean minor allele frequency of 0.35 and the majority of them conformed to Hardy-Weinberg Equilibrium (HWE) expectations (Supplementary Table 1). Before Bonferroni correction, 11 markers fell outside HWE, and after Bonferroni correction two markers remained significantly outside HWE.

Our sPCA analyses showed low levels of genetic differentiation when analyzing all individuals together at the regional level (Fig. 1A). Here, genetic similarity is indicated by similar colors and contrasting colors are more genetically dissimilar. The Structure analysis suggested genetic differentiation to be limited to three groups at the regional level. Closer examination revealed that 72% of all foxes (n=91) were identified as belonging to one cluster, including all red foxes from the northernmost fox trapping sites Hedemora and Grimsö (n=18) and 73 red foxes from our local Kolmården area. The remaining 35 red foxes split into the other two clusters or were an admixture between clusters (n=9, n=12, n=15, respectively) (Supp. Fig. 1A). Structure results at the local scale indicated that females grouped into two clusters, composed of a small group of highly related females and a large group of predominantly unrelated females and another (Supp. Figs 1B and 1C). Males grouped similarly to the regional level, with three main clusters being most likely.

Locally, the sPCA results of male and female groups showed females configured in a tighter clustering of similar colors, whereas males exhibited more diffuse spatial structure (Fig. 1B and 1C). Geographic distances supported this patterning as well, with female kin being more spatially clustered at the local scale than males. Here, highly related female pairs showed the shortest average pairwise distances, whereas highly related male pairs showed the largest average distances. Opposite sex pairs showed intermediate distances (Fig. 2; Table 3). A t-test identified all pair types to be significantly different from all other pair types, with female pairs and male pairs being most different (t = 3.3661, df = 43.132, p-value = 0.00161). The difference in mean distance between opposite sex pairs and female-female pairs (t = -2.1794, df = 79.144, p-value = 0.03227) and opposite sex pairs and male-male pairs (t = 2.2642, df = 48.766, p-value = 0.02805, Table 3) were also significant. Examining the pairwise distances for all pair types according to their categorized relatedness values showed a similar pattern across all relatedness categories and all pair types (Fig. 3).

Discussion

Our study highlights differing patterns of red fox genetic structure depending on spatial scale and sex. The limited genetic differentiation seen in the sPCA of red foxes at the regional level indicates high levels of gene flow, whereas patterns of relatedness revealed intersexual differences in spatial genetic structure at a local scale. Structure results indicate foxes grouped into three clusters regionally with a limited

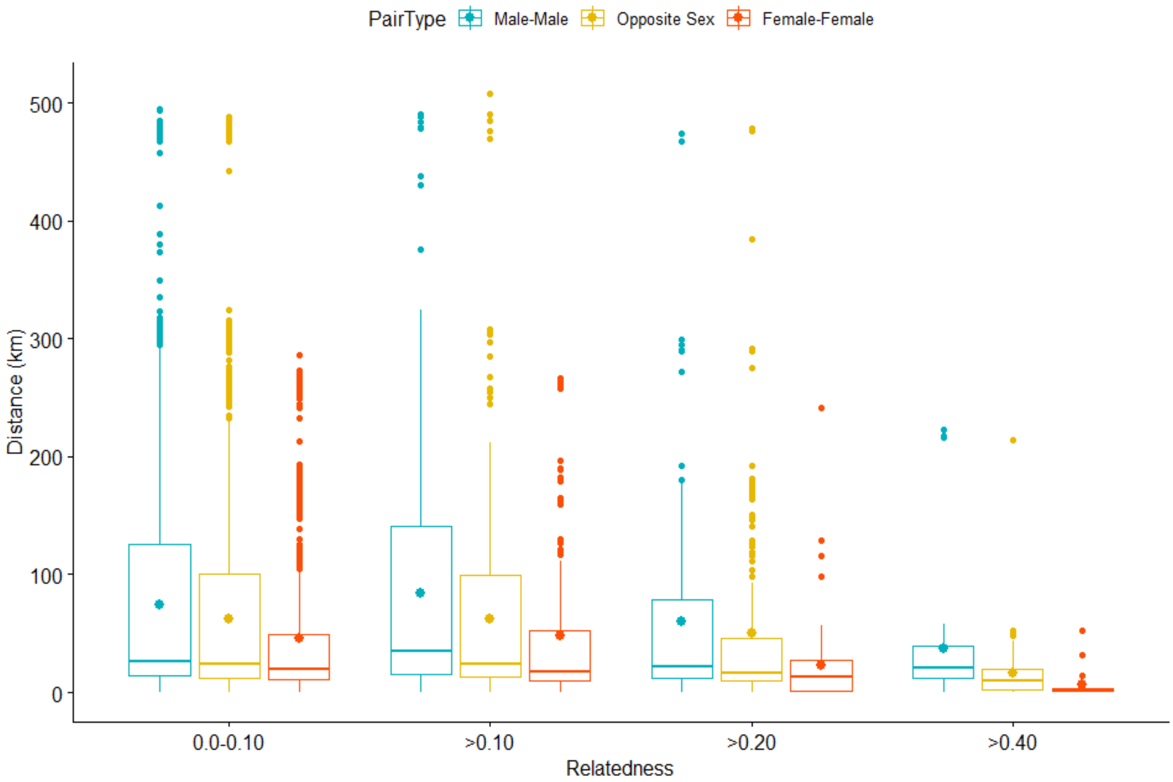

Figure 3. Boxplot showing pairwise distances for all foxes according to pair type: male-male (blue), opposite sex (yellow) and female-female (red) categorized according to their relatedness values. Mean distance values are indicated by the larger colored dot whereas median values are indicated by the line within the box plots. Values of 0-0.10 and 0.10-0.20 indicate unrelated or distantly related individuals, 0.21-0.40 are second generation relatives and those >0.40 are considered highly related individuals (parent-offspring and full sibling).

degree of admixture. Closer inspection of the q-values revealed almost three quarters of the foxes grouping into one cluster. This cluster included all individuals from our northernmost areas, separated by up to 200 kilometers from the rest of the individuals in the same cluster. The remaining foxes separated into two other small clusters. It is possible that these two smaller, distinct clusters are evidence of local scale kinship or familial structuring, as seen in the local scale analysis of only female red foxes in Kolmården (Supp. Fig. 1B). There, we also see two clusters, one large and one smaller distinct cluster. However, we see a third cluster in our local analysis of male red foxes, perhaps due to male immigration from outlying areas via dispersal.

Red foxes are a widespread carnivore showing high genetic diversity throughout their European range (Gachot-Neveu et al. 2009, Teacher et al. 2011, Kutschera et al. 2013, Galov et al. 2014, Atterby et al. 2015, Norén et al. 2015). The low levels of genetic differentiation found between red foxes at the regional level follow expectations that red foxes are a mobile species and dispersal causes gene flow across large spatial scales (Peakall et al. 2003). Our results do not indicate physical barriers to red fox movements within the regional scale of our study (Norén et al. 2015). Similarly, other canid species exhibiting dispersal over long distances also show limited phylogeographic structuring (e.g. grey wolf (*Canis lupus*), coyote (*Canis latrans*) and arctic fox (*Vulpes lagopus*) (Lehman and Wayne 1991, Vilà et al. 1999, Lai et al. 2017).

As restrictions to movement did not appear evident from the Structure and sPCA results at the regional scale, it seems unlikely that natural landscape barriers are limiting gene flow at finer scales. Instead, local scale movement patterns may be more influenced by social rather than physical barriers (Macdonald 1983). The geographic distances between highly related individuals showed spatial patterns

Table 4. Mean geographic distances (km) between red foxes according to their different relatedness values. Here all pair types are pooled. Values of 0-0.10 and 0.10-0.20 indicate unrelated or distantly related individuals, 0.21-0.40 are second generation relatives and those >0.40 are considered highly related individuals (parent-offspring and full sibling).

relatedness	count	mean	sd	median	IQR
>0.40	125	20.8	38.7	10.5	19.8
>0.20	387	49.2	78.1	17.2	35.8
>0.10	1168	67.9	85.1	25	101
0.0-0.10	7498	64.5	82.9	24.6	93.3

indicating significant philopatric behavior among related females with larger geographic separation between related male foxes. The average distance between related male pairs, approximately 38km, was over six times larger than the distance between related female pairs (6km). This confirms our prediction that highly related females show some degree of kin clustering by occurring in closer proximity to related females compared to mixed sex or male red fox pairs.

This philopatric behavior, where female offspring are allowed to settle and breed within or adjacent to their natal range, has been shown to create clustering of related individuals in the landscape (Benton and Bowler 2012). Evolutionarily, females are thought to benefit more than males from being among kin through access to breeding sites (e.g. underground den systems), cooperative social interactions, knowledge of resource areas, or through inheritance of the home range (von Schantz 1981, Macdonald 1983, Baker et al. 1998). In polygynous mating systems such as those in red foxes, inbreeding avoidance (Pusey and Wolf 1996) may contribute to a male biased dispersal pattern, as dispersal is an effective mechanism against inbreeding (Johnson and Gaines 1990) and may be a prerequisite for reproduction or to find a breeding vacancy (Greenwood 1980). Thus, the genetic sub-structuring seen at the local scale is most likely driven by behavioral traits such as male biased dispersal and female philopatry altering gene flow between groups, subsequently shaping local genetic patterns. These genetically identified patterns fit well with dispersal patterns found in other red fox movement studies (Storm et al. 1976, Allen and Sargeant 1993) and for mammals in general (Greenwood 1980). However, these mechanisms likely do not work independently and genetic clustering and female biased philopatry can be expected to differ across populations where different demographic components are at play (Kamler et al. 2013).

The effects of sex biased dispersal on fine scale genetic structure (Banks and Peakall 2012) and dispersal distances (Ronce 2007) has been challenging to study in natural, open populations, in part because real world data sets are often imperfect or difficult to obtain, particularly those of wild populations (Koenig et al. 1996, Nathan 2001). Additionally, a high degree of relatedness among individuals within a population can confound or may not be evident within broader population structure (Anderson et al. 2010, Norman et al. 2017). Here, our results indicate that some of the underlying genetic structure at the regional level may be due to familial clustering. Understanding local spatial patterns of relatedness underlying broader landscape genetic structure can offer important insights into how social structure can contribute to patterns of genetic structure locally.

This study also highlights the use of high resolution SNP genotyping to provide detailed information on the relationships between individuals, in this case allowing for detection of different patterns of gene flow at the population, family and individual kin levels. The power of high resolution genetic markers will likely prove valuable for future studies and provide new avenues for combining genetic methods with movement data. Studies using genetic methods should however, consider the scale they wish to address. For instance, a high level of short distance dispersal events will affect local spatial patterns of genetic differentiation (Rousset 2001) more than a low level of long dispersals (Nathan 2005). Thus, as demographic and behavioral processes can operate at a range of scales to generate genetic structure (Anderson et al. 2010, van Dijk et al. 2015), it is therefore important to consider the scale at which such movements take place and the behavioral aspects that influence such movements.

Limited attention has been given to examining intraspecific patterns of genetic structure at different spatial scales however (Anderson et al. 2010), particularly for carnivores (Gompper 1996; Oehler and Litvaitis 1996). Many species in the order Carnivora show great flexibility in their social systems (Macdonald 1983) which can influence population genetic structuring at a very fine scale. Distinguishing between population structure and the underlying fine-scale social and kinship patterns that affect population genetic structure can ultimately lead to a more thorough understanding of the spatial, social and population dynamics of a species. Yet, these are still among some of the least understood attributes of both individual animals and populations (Sutherland et al. 2000, Nathan 2001, Kokko and López-Sepulcre 2006). Furthermore, populations are not closed. If we assume that our regional population of red foxes is a continuous population (as our regional results might suggest), it is noteworthy that fine scale genetic structuring can occur locally by social mechanisms not linked to the movement ability of the species. This suggests that movement capacity is not a prerequisite for fine scale genetic structuring to occur locally (Campbell and Strobeck 2006, Quaglietta et al. 2013) and that red foxes can be restricted by social barriers.

Two correlates of carnivore spacing behavior are sex and social system (Clobert et al. 2001). By combining animal movement data with patterns of genetic relatedness and allele frequencies in a population we provide new knowledge on how dispersal translates to gene flow (Prugnolle and De Meeus 2002), and we demonstrate the effect both of these factors can have at regional and local scales. In summary, the low levels of genetic differentiation found in this study illustrates the dispersal ability of red foxes across scales, whereas locally, relatedness plays a strong role in the spatial organization of red foxes, ultimately contributing to male biased dispersal patterns and restricted female movements. However, this fine scale structuring occurs by social mechanisms, likely not related to the movement capacity of the species.

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Supplementary Table 1. Statistics of SNPs selected from Illuminas CanineHD Whole-Genome Genotyping BeadChip (172K) based on their performance on 48 ascertainment individuals from across Sweden and Norway. The first two markers are found on the mitochondrial genome and were primarily included as species diagnostics when genotyping non-invasive samples. Markers 3-5 were included for sex diagnostic purposes of non-invasive samples. If a sample amplified for ≥2 markers it was considered male and a female if no markers amplified). **MAF**= Minor Allele Frequency, **H$_O$**= Observed heterozygosity level, **H$_E$**= Expected heterozygosity level, **HWE**= p-value for HWE equilibrium deviation, **Amp. success**= Amplification success. Significant deviations from HWE are noted in bold.

SNP #	Marker reference	Allele(s)	MAF	H$_O$	H$_E$	HWE	Amp. success
1	12s16S_f1	C/T	0.47	na	na	na	1.00
2	12s16S_f2	A/G	0.01	na	na	na	0.99
3	Vv_Y6_54bp	A/G	1*	na	na	na	na
4	Vv_Y6_68bp	C/G	1*	na	na	na	na
5	Vv_Y6_96bp	A/G	1*	na	na	na	na
6	rs21916177	C/T	0.23	0.29	0.35	**0.03**	0.99
7	rs21951676	A/G	0.41	0.52	0.49	0.48	0.97
8	rs21979711	A/G	0.24	0.42	0.37	0.17	0.99
9	rs21998877	A/G	0.35	0.43	0.46	0.58	0.99
10	rs22002910	A/G	0.31	0.41	0.43	0.55	0.95
11	rs22108427	A/G	0.3	0.29	0.42	**0.00**	0.96
12	rs22152882	C/T	0.46	0.45	0.50	0.24	1.00
13	rs22216221	C/G	0.29	0.33	0.42	**0.04**	0.77
14	rs22170273	C/T	0.18	0.26	0.29	0.37	1.00
15	rs22246746	A/G	0.41	0.46	0.48	0.60	0.99
16	rs22272388	C/T	0.36	0.41	0.46	0.20	0.99
17	rs22292152	G/T	0.45	0.46	0.50	0.40	1.00
18	rs22341998	A/G	0.36	0.39	0.46	0.06	0.96
19	rs22459973	C/T	0.31	0.35	0.43	**0.03**	1.00
20	rs22556409	C/T	0.28	0.41	0.40	0.67	0.99
21	rs22573023	A/G	0.38	0.46	0.47	0.86	0.99
22	rs22590008	A/G	0.31	0.35	0.43	**0.02**	1.00
23	rs22597040	C/T	0.35	0.42	0.45	0.46	0.99
24	rs22598480	C/T	0.4	0.52	0.48	0.30	1.00
25	rs22710251	C/T	0.26	0.40	0.38	0.82	0.99
26	rs22752416	A/G	0.32	0.46	0.44	0.56	0.98
27	rs22791735	G/T	0.4	0.47	0.48	0.86	0.98
28	rs22820081	C/T	0.42	0.47	0.49	0.73	1.00
29	rs22900892	A/G	0.24	0.29	0.37	**0.02**	0.98
30	rs22908802	A/G	0.29	0.43	0.41	0.84	1.00
31	rs23087158	C/T	0.43	0.41	0.49	0.06	0.99
32	rs23106825	G/T	0.3	0.46	0.42	0.32	0.99
33	rs23186516	A/G	0.3	0.38	0.42	0.31	0.99
34	rs23192602	A/G	0.38	0.43	0.47	0.27	0.91
35	rs23207600	C/T	0.28	0.37	0.41	0.30	0.99
36	rs23349310	A/G	0.26	0.39	0.39	1.00	0.99
37	rs23364623	C/T	0.49	0.46	0.50	0.40	0.97
38	rs23368164	C/T	0.4	0.43	0.48	0.29	0.98
39	rs23381097	A/G	0.36	0.44	0.46	0.71	0.99
40	rs23406004	C/T	0.3	0.43	0.42	0.84	1.00
41	rs23414537	C/T	0.42	0.45	0.49	0.30	1.00
42	rs23475719	A/G	0.18	0.35	0.30	0.05	1.00
43	rs23490635	A/G	0.47	0.44	0.50	0.18	0.99
44	rs23496810	A/G	0.46	0.46	0.50	0.49	0.96

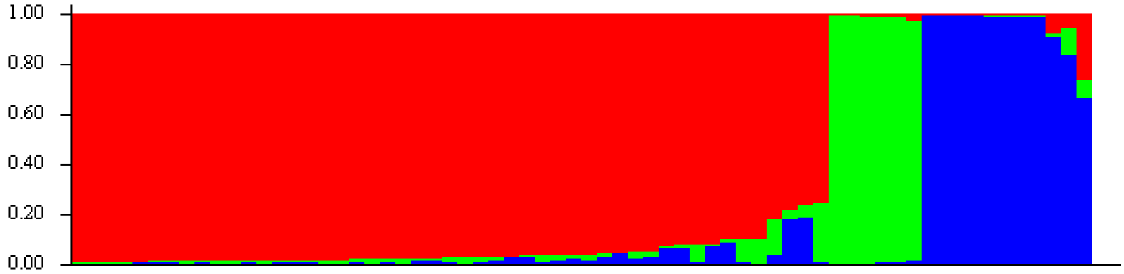
45	rs23497170	A/G	0.4	0.29	0.48	**0.00**	0.98
46	rs23514501	A/G	0.49	0.47	0.50	0.50	0.99
47	rs23580479	A/G	0.41	0.52	0.48	0.49	1.00
48	rs23622809	C/T	0.38	0.42	0.48	0.16	0.99
49	rs23645373	C/T	0.48	0.47	0.50	0.50	0.99
50	rs23664775	C/T	0.49	0.51	0.50	1.00	0.99
51	rs23683521	A/G	0.27	0.39	0.40	0.83	1.00
52	rs23703353	C/T	0.41	0.39	0.49	**0.02**	0.99
53	rs23742691	A/G	0.37	0.41	0.47	0.20	0.98
54	rs23747290	A/T	0.48	0.45	0.50	0.31	1.00
55	rs23821259	A/G	0.37	0.46	0.47	0.86	1.00
56	rs23827829	A/G	0.31	0.40	0.43	0.55	1.00
57	rs23886920	A/G	0.47	0.51	0.50	0.87	1.00
58	rs23969597	A/T	0.5	0.46	0.50	0.39	0.96
59	rs23975367	A/G	0.44	0.41	0.49	0.06	0.99
60	rs23976226	A/G	0.47	0.47	0.50	0.50	0.99
61	rs24004259	A/G	0.31	0.39	0.43	0.33	0.99
62	rs24046888	A/G	0.49	0.37	0.50	**0.03**	0.59
63	rs24127654	C/T	0.35	0.49	0.46	0.58	0.99
64	rs24149555	A/G	0.26	0.37	0.38	0.66	0.98
65	rs24197691	C/T	0.31	0.42	0.43	1.00	0.72
66	rs24237494	C/T	0.35	0.38	0.46	0.06	0.97
67	rs24261914	C/T	0.3	0.36	0.42	0.11	0.99
68	rs24336202	C/T	0.45	0.38	0.50	0.06	0.54
69	rs24372135	A/G	0.3	0.40	0.43	0.54	0.93
70	rs24379754	C/T	0.26	0.27	0.39	**0.00**	0.99
71	rs24429269	C/T	0.41	0.49	0.49	1.00	0.99
72	rs24460576	A/G	0.36	0.45	0.46	0.86	1.00
73	rs24489600	A/G	0.32	0.43	0.44	0.85	1.00
74	rs24502285	A/G	0.41	0.42	0.49	0.12	0.99
75	rs24522505	A/G	0.49	0.49	0.50	0.87	0.99
76	rs24532759	C/T	0.44	0.52	0.49	0.61	0.97
77	rs24559987	C/T	0.33	0.40	0.44	0.25	0.98
78	rs397511402	A/G	0.29	0.39	0.41	0.67	0.93
79	rs853029360	A/G	0.33	0.28	0.44	**0.00**	0.91
80	rs8582623	A/G	0.28	0.39	0.41	0.68	0.98
81	rs8583101	C/T	0.34	0.51	0.45	0.13	1.00
82	rs8631009	C/T	0.48	0.41	0.50	0.03	0.99
83	rs8635392	A/G	0.39	0.49	0.48	0.85	0.84
84	rs8701241	A/G	0.34	0.45	0.45	1.00	1.00
85	rs8713640	A/G	0.17	0.29	0.29	1.00	0.99
86	rs8756252	A/G	0.44	0.42	0.50	0.18	0.60
87	rs8762531	A/G	0.4	0.55	0.48	0.11	0.99
88	rs8856474	A/G	0.24	0.29	0.37	0.01	0.99
89	rs8877836	A/G	0.49	0.54	0.50	0.39	0.96
90	rs8898796	A/G	0.25	0.41	0.38	0.27	0.99
91	rs8930602	C/T	0.25	0.39	0.38	0.82	0.99
92	rs8939454	C/T	0.17	0.26	0.26	1.00	0.61
93	rs8958992	A/G	0.37	0.45	0.47	0.72	1.00
94	rs9018451	A/G	0.34	0.39	0.45	0.14	0.99
95	rs9041333	C/T	0.23	0.36	0.36	1.00	0.99
96	rs9142386	C/T	0.36	0.49	0.46	0.58	0.99
		Means	**0.35**	**0.42**	**0.45**	**--**	**0.96**

* Assays designed to amplify in presence of a Y-chromosome, monomorphic.

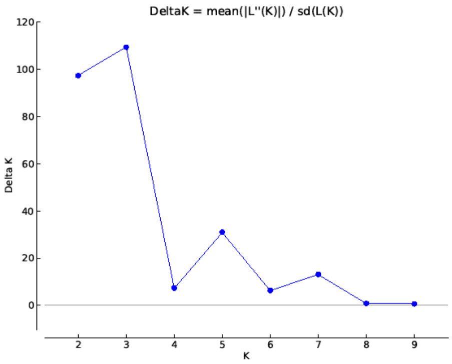
(A). All foxes

(B). Kolmården Females

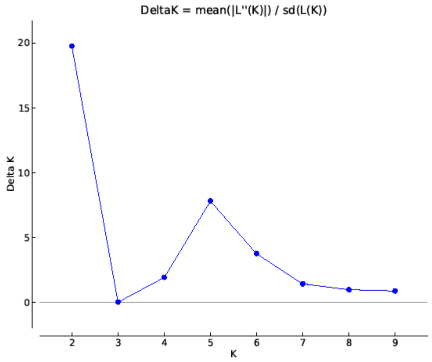
(C). Kolmården Males



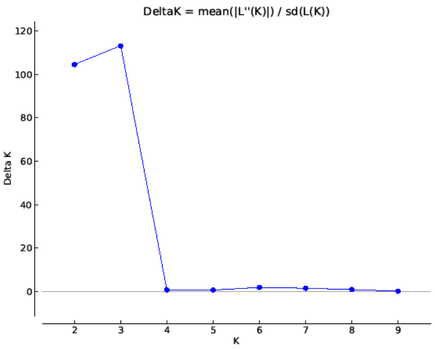
Supplementary Figure 1. Individual genetic clustering in STRUCTURE. Each bar represent one individual. Colors indicate assignment to a particular cluster. Bars containing more than one color represent the degree of genetic admixture in an individual. The most likely number of clusters estimated for all red fox individuals at the regional level by Structure and Structure Harvester was three (K=3) as indicated by the color groupings. At the local level, separate analyses for females (B) and males (C) using Structure and Structure Harvester were run, indicating that the females separated into two different clusters (K=2) while males separated into three clusters (K=3). See Supplementary Figure 2 for delta K values to determine the most likely number of clusters.



(a) All foxes K=3



(b) Kolmården Females K=2



(c) Kolmården Males K=3

Supplementary Figure 2. Delta K values for estimation of most likely number of clusters for (a) all red fox individuals (b) female red foxes from Kolmården (c) and male red foxes from Kolmården.

Paper V

Foxes don’t fit in boxes: variability in movement patterns of the red fox

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Abstract

Animal movement behaviors such as migration, residency, nomadism and dispersal are recognized as important life history attributes across taxa. Interpreting these behaviors is dependent on not just identifying their associated movement patterns, but also the temporal and spatial scales at which these movements occur. However, not all movement patterns are easily classifiable and the distinction between behaviors can be blurred when animal movements show greater variability than anticipated. Here, we tested how well a behaviorally flexible and generalist species, the red fox, fit into common movement classifications of resident, disperser and nomad behaviors. Secondarily, we explored the scale at which red fox movements occurred and how movement classifications differed individually and according to intrinsic factors such as sex and age. We did this by both visually and quantitatively classifying movement trajectories from 112 GPS collared red foxes, using net squared displacement based models. Both the visual and model fitting approaches found evidence of all three movement strategies in red foxes. However, only 53% of red foxes classified consistently as either dispersers or residents between methods. No agreement was found within the nomad category. Visually, 69% of foxes were identified as residents, 27% as dispersers and 4% as nomads. In comparison, both the NSD models classified 43-44% of the foxes as resident, 50% as dispersers and 6-7% as nomads. Even between the quantitative model assessments, varying only by start position, 29% of the classifications did not agree. This inconsistency in classifications likely reveals more variable movement behaviors and suggests that red foxes move in a manner or at a scale that is not ‘typical’ of idealized resident or dispersing behaviors. By identifying common movement patterns exhibited by red foxes and the variation within those movements, we can begin to document different ecologically important red fox movement behaviors. Thus, we caution not oversimplifying animal movements to fit within boxes but to also recognize the behavioral plasticity and individuality within animal movements as being of unique ecological value.

keywords: *Vulpes*, dispersal, nomadism, residency, animal behavior, individual variation, GPS, net squared displacement, exploration, plasticity

Introduction

The ability to move is a key component of animal ecology (Nathan et al. 2008) with broad scale animal movement behaviors such as migration, residency, nomadism and dispersal (hereafter movements) recognized as important life history attributes across taxa (Clobert et al. 2001, Dingle and Drake, 2007; Andersson et al. 1980). Such animal movements are often identified according to their spatiotemporal movement patterns, where quantitative movement metrics such as step length, turning angle or displacement can be used to characterize the observed patterns into movement behaviors (Edelhoff et al. 2016; Morelle et al. 2017). However, not all movement patterns are easily classifiable and the distinction between behaviors can be blurred when animal movements show greater variability than anticipated (Gurarie et al. 2017). An animal's movement trajectory typically encompasses a mix of different movement behaviors at varying spatial and temporal scales. Identifying these behaviors is dependent on not just interpreting the associated movement patterns, but also taking into account the spatio-temporal scale at which these movements occur (Benhamou, 2014; Allen et al. 2016). Advances have been made in identifying common movement metrics and behaviors that extend across taxa (Sutherland, 2000; Abrahms et al. 2017). However, several studies have found a range of individual behaviors within predefined movement classifications (Cagnacci et al. 2016, Gurarie et al. 2017; Spiegel et al. 2017, Ducros et al. 2019). This is hardly surprising as movement behaviors are a dynamic interplay between intrinsic and extrinsic factors, which can vary individually, spatially or temporally, for example, seasonally or annually (Nathan et al. 2008). The behavioral plasticity of individuals to respond to changing environmental and social conditions through movement (eg. partial migration (Bunnefeld et al. 2011, Ball et al. 2001), natal dispersal (MacDonald, 1980)), is important as it may be crucial to their survival and reproduction (Cote et al. 2016; Lai et al. 2016; Couriot et al. 2018; Debeffe et al. 2014; Berger, 2004). However, this variability creates difficulties in quantification and classification of movement patterns, where some individuals may not fit clearly into defined patterns or behavioral categories.

Technological advancements in the collection of high resolution data provides new opportunities to identify movements across many spatio-temporal scales (Cagnacci et al. 2010). However, high volumes of data also present challenges both in complexity and in identifying specific animal behaviors from movement patterns (Morales et al. 2004; Fryxell et al. 2008). Few studies have attempted to test how well a particular species may fit into classifications of common movement behaviors, or to examine the individual variability a species may exhibit, though advances regarding ungulates are well underway (Debeffe et al. 2014; Gurarie et al. 2016; Cagnacci et al. 2016, Eggeman et al. 2016; Spitz et al. 2017; Ducros et al. 2019). Identifying different movement behaviors in animals is thus an important step in understanding their ecology and towards examining particular movement behaviors in greater detail (Bastille-Rousseau et al. 2016; Wheat et al. 2017). One widely used metric to characterize broad scale animal movement patterns is to calculate net squared displacement (NSD) (Bunnefeld et al. 2011; Borger and Fryxell, 2012). Patterns of NSD over time are informative both within and across taxa (Cagnacci et al. 2016; Abrahms et al. 2017) for identifying different movement behaviors such as residency, transience, migration, mixed migration or dispersal (Singh et al. 2012; Bastille-Rousseau et al. 2016; Gurarie et al. 2017; Spitz et al. 2017; Fig. 1). This single metric also links animal movement to behavior and personality (Spiegel et al. 2017; Hertel et al. 2019) and provides meaningful information on rates of behavior switching and the degree of exploration an individual makes from a fixed position over time (Nouvellet et al. 2009).

With this study, we assessed the different movement patterns of a midsized, generalist species, the red fox (*Vulpes vulpes*) to identify their different broad scale movement behaviors. Canids, in particular, show flexibility across a range of behaviors, and red foxes are no exception (MacDonald and Sillero-Zubiri, 2004). As a species, red foxes have exhibited remarkable variation in social structure, home range size, habitat selection and diet (Cavallini, 1996; von Schantz, 1981; Voigt and Macdonald, 1984; Walton et al. 2017). However, red fox movement ecology is one of the least understood attributes of this species. Given that red foxes are a flexible and adaptable species, they are an ideal candidate to investigate how well a species conforms to idealized movement patterns or exhibits variability within movement behaviors.

Here, we used an NSD based approach to classify foxes into resident, dispersing and nomadic behaviors. We did this by visual examination and classification of the movement trajectories from GPS collared red foxes and with a quantitative, model based approach. Secondarily, we explored the scale at which the different movement patterns occurred and how movement classification methods and consistency differed individually and according to intrinsic factors such as sex and age. As behavioral plasticity appears to be a key feature of red fox ecology (Cavallini, 1996; MacDonald and Sillero-Zubiri, 2004), we predicted that this flexibility might also be evident within their movement behaviors, with red foxes showing a high degree of individual variation. However, we expected most red foxes to exhibit common behaviors of residency and dispersal, depending on their sex and age classes. For instance, as dispersal in red foxes is largely known to be biased towards subadult males (Storm et al. 1996) we expected that this behavior will be predominantly seen in juvenile male foxes as opposed to other sex and age classes. Similarly, we expected red foxes classified as residents to be predominantly adult individuals, while nomadic individuals would be a less common classification, restricted to males of either age class (von Schantz, 1981; Meia and Weber, 1995). Finally, we examined the variability of movement patterns shown by red foxes at different scales and discussed factors that can contribute to confounding classifications between different methods.

Methods

Study areas

We studied red foxes in four study areas in Scandinavia, ranging from Hedmark County, Norway, in the north, to Kolmården, Sweden, in the south (62°- 58° N). The areas represent a gradient of landscape productivity and human land use. The northern area is characterized by boreal forests and alpine tundra of low diversity and productivity, whereas the southernmost areas are a mosaic of agriculture areas, boreonemoral forests and human settlements. See Walton et al. (2017) for additional details of the study areas.

Fox capture and handling

Between 2011 and 2019, we captured and fitted red foxes with GPS/GSM radio collars (Tellus Ultralight (210g), Televilt, Inc. Lindesberg, Sweden and Wildcell (250g), Lotek, Newmarket, Ontario, Canada). Foxes were captured throughout the year using baited wooden box traps following the procedures outlined in Walton et al. (2017). We sexed, measured, weighed, and aged all captured foxes. Six foxes were re-collared during our study. Age was roughly defined as sub-adult (<1 year) or adult (>1 year) based on the amount of tooth wear and coloration and an assumed birth date of April 15 (Englund, 1970). GPS collars deployed before October 2015 were programmed to take three positions per day with a pre-set drop-off after nine months. Collars deployed after October 2015 were programmed to take six positions per day with a drop-off after six months. All capture and handling protocols were approved by the ethical guidelines of the Swedish Animal Ethics Committee and the Norwegian Animal Research Ethics Committee.

Movement Classifications

Using the program R 3.6.0 (R Core Team, 2019), we initially, we screened all red fox movement trajectories (N=134 foxes) for errors and removed all two dimensional (2D) recorded positions with a dilution of precision (DOP) >10. We further removed the first 24 hours of positions from each fox to eliminate any capture effect bias in movement behavior (Thiemann et al. 2013). Due to the need to examine movement patterns over time, we only examined individuals with >30 days of monitoring data. Median monitoring duration of the individuals remaining for analysis was 159 days (range 37-371 days, n=112 individuals). To match sampling rates across all foxes, we resampled GPS locations to three locations per day (8 hour time intervals) using the R package adehabitatLT (Calenge, 2011). This allowed us to standardize individual trajectories and facilitate further data analysis (Calenge, 2011). We then evaluated and classified the movements of the remaining 112 red foxes (41 females, 71 males) to characterize resident, nomad and dispersal behaviors.

Visual Classification

Mechanistic models can identify patterns within increasingly complex data, however, visualization can also be an important tool, allowing identification of movement patterns at multiple scales and for identifying any underlying variation within patterns of individuals that do not fit cleanly into broader patterns or classifications (Demšar et al. 2015; Andrienko and Andrienko, 2013). We first calculated NSD as the squared Euclidean distance from an animal's first position to each subsequent position, for each individual fox. We then plotted the time series of NSD in conjunction with each animal's movement trajectory to identify patterns and change points in each trajectory indicative of different animal movement behaviors, focusing only on broad scale movement patterns. Each individual was thus classified using a biologically informed and unsupervised approach according to visual inspection of each animal's movement trajectory and plotting of the associated time series of NSD patterns to differentiate between movement patterns (Supplementary Table 1). We classified a nomadic individual as one showing limited fidelity to a particular range instead using or occupying, multiple ranges over a large geographic area. Alternatively, a nomadic individual is one lacking a clear pattern to movement over a large spatial scale. Resident space use was generally considered bounded with resident individuals showing limited movement between distinct ranges. However, but we allowed for space use to shift over the monitoring period if the spatial scale was limited (ie. multiple separate areas used intensively across a range) and for exploratory excursions outside of the home range to occur. A dispersing individual moved from one range to settle in another range where no range overlap occurred. However, we also allowed for a disperser to show multiple periods of transience between two ranges (i.e. multiple back and forth movements between ranges) before settling at the secondary range. In such cases, these back and forth movements can obscure clear separation between natal and settlement ranges, which we attempted to account for visually. Visual examples of these different movement classifications are presented in Fig. 2 (residents and dispersers) and Fig. 4 (nomads). In this way, we determined the best supported broad scale movement pattern into one of three categories: disperser, resident, or nomad.

Model based classification

Recent advancements to NSD-based analyses have applied model fitting, assessment and assignment of NSD patterns to conceptualizing different broad scale animal movement strategies (Börger and Fryxell, 2012; Edelhoff et al. 2016; Bastille-Rousseau et al. 2016; Spitz et al. 2017). These methods provide a quantitative approach to movement classifications, which we can then contrast with our qualitative visualizations described above. Here, we used the package migrateR (Spitz et al. 2017), which fits each individual's time series of NSD to an a priori statistical model representing idealized conceptualizations of five movement behaviors: resident = asymptotic, disperser = sigmoid, migrant = double sigmoid, mixed migrant = double sigmoid with variable return distance, or nomad = linear (Spitz et al. 2017, Fig. 1), and uses maximum likelihood estimation to determine which of the patterns fit the data best. We restricted movement classifications to the behaviors of dispersal, resident and nomad for model evaluation and selection. We additionally input a species specific restriction into the model, specifying a minimum duration of secondary range occupancy of five days as criteria for quantifying dispersal behavior. We additionally tested secondary range occupancy at 0, 10 and 20 days, however, five days was sufficient to allow us to remove the effects of exploratory movements from dispersal movements without compromising individuals that had limited periods of post-dispersal movement data.

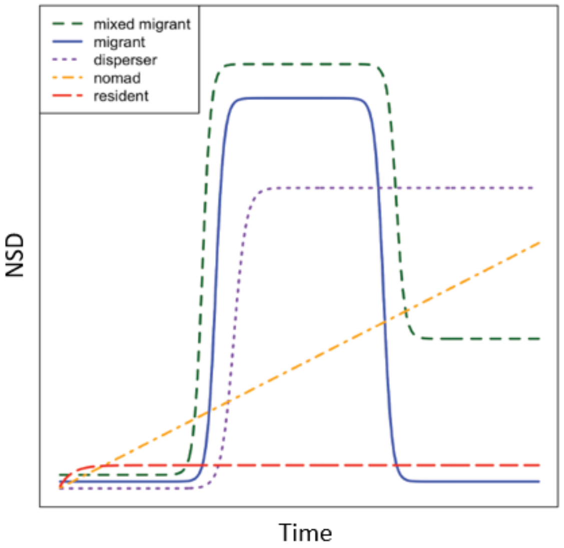

Figure 1. Conceptual illustration of net squared displacement (NSD) based model families representing five a priori movement classifications: mixed migrant, migrant, disperser, nomad and resident. Figure reprinted with permission from Spitz et al. (2017).

One criticism of NSD is its sensitivity to the start position, which can lead to poor model fit or erroneous movement conclusions. This is especially true if the starting position represents an exploratory or dispersal movement or is attributed to a different behavioral state than

Table 1. The number of red foxes classified as dispersing, nomadic or resident according to the three classification methods, Visual, NSD, rNSD. Red fox movement classifications which agreed across the three methods are in bold. The different sex and age classes of red foxes within each movement classification are shown in italics. Sex of female (♀) and male (♂) red foxes are grouped within each category as adult and subadult, respectively.

Method	*Age*	Disperser	Nomad	Resident	total
Visual		**30**	**5**	**77**	**112**
	Adult	*9♂*	*1♀ 3♂*	*27♀ 27♂*	
	Subadult	*5♀ 16♂*	*1♂*	*9♀ 14♂*	
NSD		**56**	**8**	**48**	**112**
	Adult	*11♀ 18♂*	*2♀ 1♂*	*15♀ 20♂*	
	Subadult	*6♀ 21♂*	*3♀ 2♂*	*5♀ 8♂*	
rNSD		**56**	**7**	**49**	**112**
	Adult	*10♀ 20♂*	*2♀ 1♂*	*16♀ 18♂*	
	Subadult	*7♀ 19♂*	*1♀ 3♂*	*6♀ 9♂*	
which agree		**26**	**0**	**33**	**59**

normal movement behavior (Singh et al. 2016). As some red fox captures appeared to occur outside of their 'normal' range use (ie. when on exploratory excursions) thus leading to an increased animal displacement from start position, we further tested for sensitivity in start position by calculating the relative net squared displacement (rNSD) of each fox's movement trajectory. This was done by recalculating the NSD reference position across the initial 15 days of GPS data, and testing for changes to model fit. By fitting the NSD models to the rNSD models we could compare the minimum Aikake's information criteria (AIC) values across dates and select the reference date with the lowest overall AIC score (Spitz et al. 2017). In this way, we attempted to reduce the sensitivity of NSD to start location. We determined the best supported NSD and rNSD models and retained both sets of model classifications for comparison with the visual classifications.

Variability in red fox movement patterns

Following movement categorization of all foxes, we assessed the consistency between the three methods utilized: maximum likelihood model fitted patterns (NSD and rNSD), and visual classification of NSD and movement trajectory patterns (Visual). For those individuals that showed consistent classification across methods we considered their range of values as representing more stereotypical movement patterns (Cagnacci et al. 2016). In contrast, inconsistencies in classification are likely due to individual variation within these patterns. Here, we further explored the variance, mean and maximum NSD and net displacement (ND) values within both consistent and inconsistent movement classifications, as well as between the different classification methods, to better understand the variation and scale of red fox movements. We also assessed classifications according to sex and age of red foxes. By exploring the degree of natural variation within each movement classification and within sex and age categories, as well as the individual variation in red foxes we can assess the fit of broad scale movement behaviors, their classification definitions and utility to this species.

Results

Both the visual and model fitting approaches found evidence of all three movement behaviors in red foxes. However, there was a high degree of variability in movements with only 53% of the 112 red fox trajectories showing agreement across all three methods (Table 1; Fig. 2). Of those that agreed, 56% were classified as residents and 44% as dispersers. No agreement was found within the nomad category.

Visually, 69% of foxes were identified as residents, 27% as dispersers and 4% as nomads. Adult foxes of both sexes were equally and most often classified as residents (54 of 77) although one adult female and 12 adult males showed other behaviors (9 dispersers, 4 nomads). Among the 45 subadult individuals, 21 were

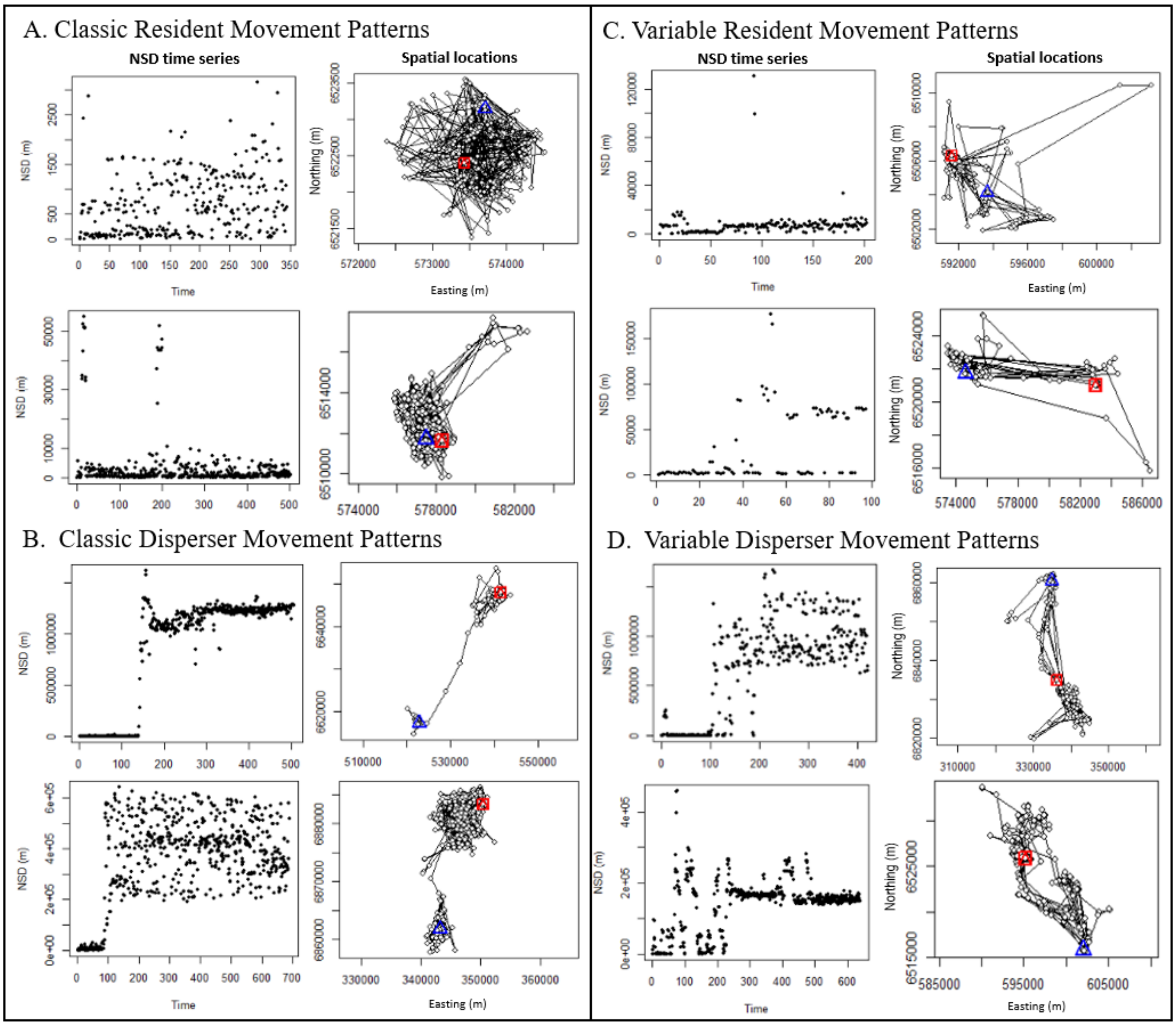

Figure 2. Plots of spatial locations and times series of NSD for red foxes identified as residents and dispersers. Note the different spatial scales of NSD values. The time axis shows all sequential GPS positions per individual, where all individuals were standardized to three locations per day (8 hour intervals). Examples of movement patterns include those which classified consistently (A and B) and those that did not (C & D). Also shown are examples of exploratory movements of resident individuals (A & C) and variability in red fox dispersal patterns, where (B) shows the more traditional one way dispersal movement and (D) shows multiple return movements between start range and settlement range.

dispersers and 23 were residents, while one was classified as nomadic (Table 1).

In comparison, both the NSD and rNSD models classified 43-44% of the foxes as resident, 50% as dispersers and 6-7% as nomads**.** Here as well, resident foxes were predominately adults of both sexes (34 of 49 rNSD and 35 of 48 NSD). However, adult foxes of both sexes also accounted for approximately 53% of individuals classified as dispersers. All sex and age classes were also represented within the nomad category (Table 1).

There were also inconsistent classifications between each of these methods and the visual method, where only 64-65% of both the NSD and rNSD classifications agreed with the visual classifications (Fig. 3; Supplementary Table 2). Five individuals showed no agreement at all between the three methods (Supplementary Fig. 2). Additionally, only 71% of the classifications agreed between the two quantitative methods (80 of 112), which differed only in the reference position of up to 15 locations (see Supplementary Table 1 for rNSD reference position). Among the quantitative classifications that agreed not all of the same

Table 2. Summary of the average maximum (Max), mean and standard deviation (SD) of net displacement (ND) values in kilometers for the different movement classifications which agree and do not agree across methods. Comparison of each method is to the visual classifications. Among resident individuals which agree and don't agree, displacement values are largely similar, indicating spatial scale is used for visual classifying residents while displacement pattern might play a larger role in other classifications.

Method	Classification	Count	Max ND (km)	Mean ND (km)	± SD
Agree	disperser	26	7.30	1.20	1.72
Agree	resident	33	0.42	0.06	0.07
Do not agree	disperser	4	0.68	0.50	0.17
Do not agree	nomad	5	0.54	0.31	0.14
Do not agree	resident	44	0.37	0.07	0.07

individuals were classified into the same movement categories (Supplementary Table 1).

Examining mean, max and variance of squared displacement and net displacement across categories, and among those that agreed and did not agree, further indicated individual level differences (Table 2). The mean variance of net displacement for red foxes whose classifications agreed (n=59) was higher than classifications that did not agree (n=53) (387.2 km ± 218 se vs. 6.3 km ± 2.0 se, respectively). It was also notable that maximum NSD and rNSD values included much lower values in the disperser category than did visual classifications (Fig. 3, Table 2), resulting in more individuals being placed into the disperser category. Additionally, visual classifications place higher NSD values in nomadic categories than the model driven approaches (Fig. 4).

The quantitative approaches (NSD, rNSD) had a tendency to classify more individuals as dispersers (n=26) rather than residents compared to visual evaluation (Fig. 3). These individuals were primarily adult foxes of both sexes (Table 1). Classification of female foxes varied most. Approximately half (20-22 of 42) of the female red foxes classified to categories other than resident according to model based approaches compared to only 6 of 42 females classified visually. All red foxes classified as nomadic according to NSD and rNSD models were identified as residents visually (Fig. 4).

Discussion

Red foxes classified inconsistently, revealing variable movement behaviors and suggesting that red foxes move in a manner or at a scale that is not what we think of as 'typical' of idealized resident or dispersing patterns (Cagnacci et al. 2016; Ducros et al. 2019). This is arguably the most important result of our analysis. However, it is also important to recognize that there are no 'true' reference values with which to compare our model or visual results, ie. there is no 'correct' classification. Each movement trajectory is likely to contain multiple movement behaviors and is open to interpretation depending on the method applied to it and the spatial scale it occurs. The high level of inconsistency between visual and model based quantifications simply highlights the difficulties in quantifying complex animal movement data and the variability within red fox movement patterns.

For red foxes showing consistent classifications between methods, these individuals are likely moving in a manner more indicative of idealized movement patterns (Fig. 2A & 2B). However, the spatial and temporal scales at which an individual's movements take place can influence classification, as seen here (Table 2; Fig. 4). When using NSD to identify migratory behavior in ungulates, individuals showing more limited spatiotemporal movement patterns were more likely to be classified inconsistently as well (Singh et al. 2016; Mysterud et al. 2011). Though red foxes are a comparatively small species, likely moving at differing spatial scales to ungulates, we also found this to be true for red foxes. In cases where mean or maximum displacement was high, individuals were more likely to be consistently classified as dispersers (Table 2; Fig. 3). Thus, consistent NSD based classifications of red fox movement patterns may largely apply to animals that move longer distances, such as dispersing individuals

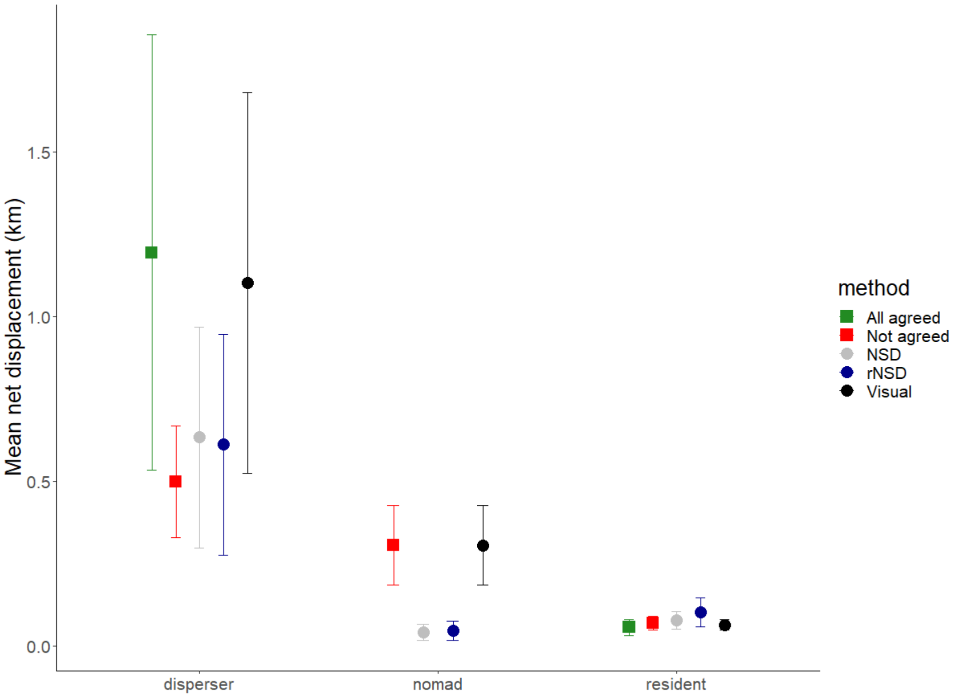

Figure 3. Mean net displacement for individuals classified according to the three different methods (circles) and those individuals showing agreement within movement behaviors or not (squares). Error bars show the standard error of the means. Here, the scale of different movement behaviors indicates that smaller displacement values can encompass multiple behaviors potentially being harder to classify and larger displacement values are more likely classified as dispersers.

exhibiting clear separation between primary and secondary ranges or for highly sedentary resident individuals over long temporal scales. Understanding the spatial and temporal scale of movement behaviors is thus relevant at both an individual and species level and models can be improved with the addition of species-specific ecological knowledge or a scaling factor to help distinguish different behaviors (a priori inputs; Spitz et al. 2017).

Certain life history stages predispose individuals to particular movements more than others (Clobert, 2001) and detection of patterns is likely sensitive to the degree of time spent in different movement categories (Torres et al. 2017). For example, natal dispersal movements of red foxes are more likely to be made by subadult male individuals than other sex and age classes in the population (Storm et al. 1976; Gosselink et al. 2010). Additionally, dispersal movements may be of short duration, whereas nomadic movements may require more time for patterns to develop, thus monitoring duration needs to be sufficient for different movement behaviors to be detected. With the exception of nomadic classifications, 30 days appeared of sufficient duration to identify dispersal and residency behaviors in red foxes (Supplementary Fig. 1). However, while extending monitoring duration may aid in better classifications, it may also allow for more variation and alternate movement behaviors to occur.

For nomads, when examined further, all model based nomadic individuals classified as residents visually (Fig. 4). When spatial scale is not considered, these individuals' resident movements appeared nomadic in pattern. However, when visually examining the spatial scale at which these movements took place, they appear more representative of how red foxes utilized their home ranges, ie. their daily ranging behavior over time. This highlights that similar movement patterns can occur at different spatial scales but represent different behaviors. Thus, for nomadic individuals, both duration of monitoring and the scale at which the movements occur played a role in determining the most appropriate movement behavior.

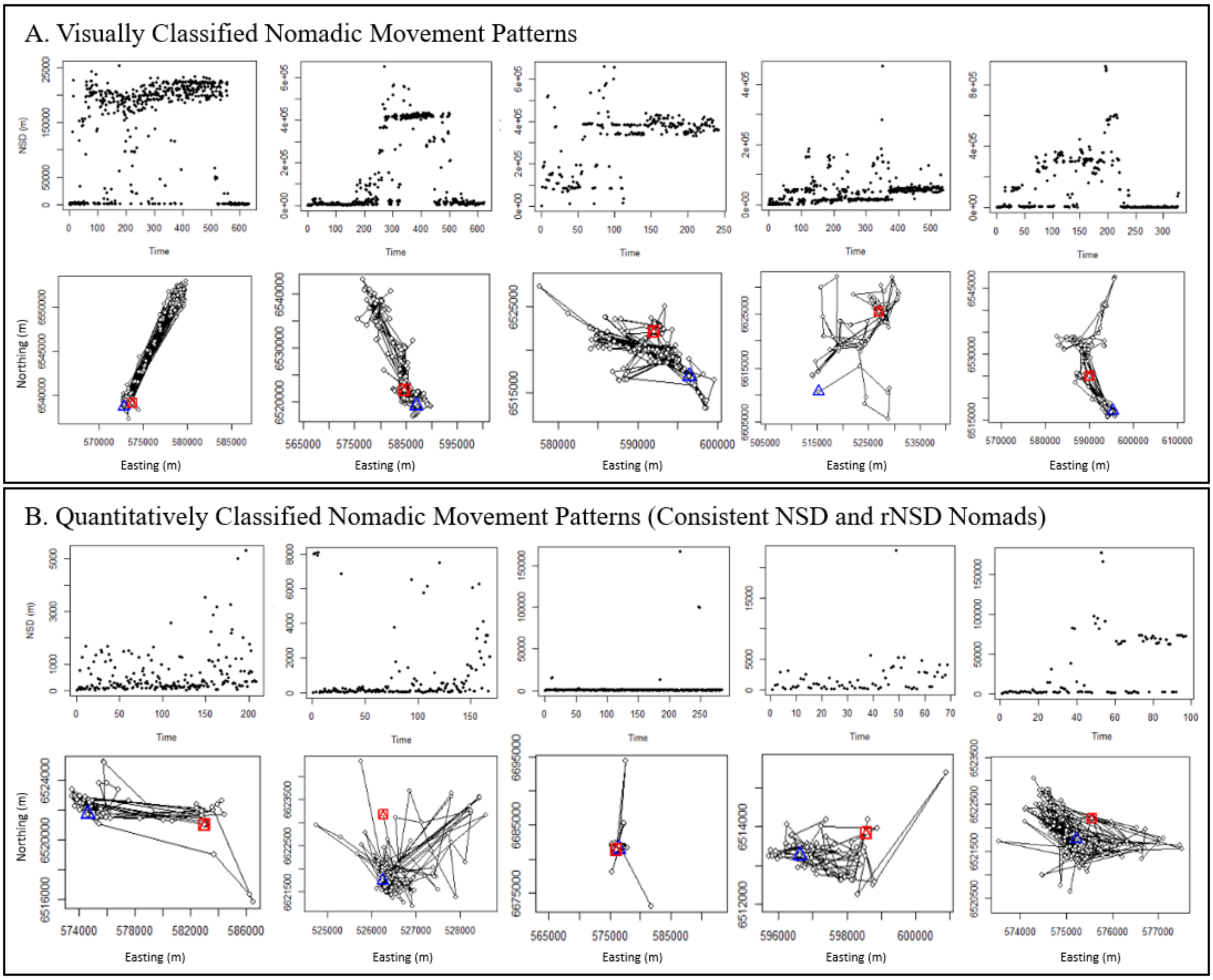

Figure 4. Examples of movement patterns of red foxes classified as nomads (A) Visually and (B) Quantitatively using NSD and rNSD. The quantitatively classified individuals represent the five consistent nomadic classifications (ie. agreed) between the NSD and rNSD methods. There was no agreement between visual and quantitative methods, and all quantitative nomad, classifications were classified as residents visually. Note the differing spatial scales of the NSD time series plots, in square meters, between individuals visually classified as nomads (A) showing a threefold difference in spatial scale compared to the quantitatively classified nomads (B). Each animal's time series of NSD values and movement trajectory are shown, with the blue triangles representing the start position and the red square showing the last position of the trajectories.

Interestingly, a few nomadic red foxes had movements that resembled migrant or mixed migrant behaviors (Fig. 4A), where adult individuals of both sexes moved back and forth between two or more home ranges spending residence time at each. These back and forth movements between ranges should not be confused with migration, as the time scale can range from days to weeks or months of occupancy before return movements, but further research is needed to elucidate such patterns. As migrant or mixed migrant movement categories are not thought to represent red fox ecology, it is notable that these movement patterns are seen and further indicates the degree of variability in red fox movements.

Red foxes can show great variability in movement behaviors. While some red foxes exhibited very stable, sedentary resident behavior, conforming to the idealized resident strategy (Fig. 2A), other resident foxes showed a wider spatial range of area use and exploratory behavior, performing excursions up to 30 km outside of commonly used ranges before returning (Fig. 2C). Exploratory movements are not usually considered a conceptual movement behavior, but given their prominence in red fox movement patterns, we argue that they should be regarded as a common movement behavior of red foxes. Such exploratory movements or 'commuting trips' may allow individuals to keep updated on the status of other species or conspecifics in the area (Wikenros et al. 2017; Temeles, 1994) or the availability of resources allowing individuals to retain their territories or home ranges despite resource shortages inside these areas (hyenas, Hofer and East, 1995; red fox, Tsukada, 1997; beavers, Mayer et al. 2017). Additionally, many male excursions can be linked to the breeding period, potentially in search of extra pair copulations or breeding opportunities (Baker et al. 2004; Soulsbury et al. 2011). The exploratory behavior of red foxes that leads to movements beyond commonly utilized resource areas (ie. the home range) likely contributes to the dynamic nature of home ranges, as well as the variability of red fox movements and inconsistencies in classifications.

Several of our dispersing red foxes also showed alternative dispersal strategies to the stereotypical pattern. For example, several foxes were found to return to their natal range multiple times (in some cases having large separation (>20 km) between ranges (Fig. 2D). These return movements can blur the separation between primary and secondary ranges making classifications following such definitions difficult, particularly when the dispersal distance between ranges is short. Additionally, some resident red foxes appear to use a particular resource area within their home range intensively before moving on to another area of intensive use, leading to spatially distinct area use. We found that such movements within a home range can confound classifications, appearing as residency, dispersal or nomadism (Fig. 3) if spatial scale is not considered. Here too, it is important to consider scale when interpreting movement behaviors.

The variability seen within red fox movements is not surprising given their flexibility in other life history attributes (Von Schantz, 1981, Cavallini, 1996; Walton et al. 2017; Dorning and Harris, 2019). Such variation in movement tactics within a population is not uncommon across taxa (eg. partial migration of ungulates (Ball et al. 2001; Bunnefeld et al. 2011; Cagnacci et al. 2016), tortoises (Bastille-Rousseau et al. 2016; seals (Austin et al. 2004), eagles (Wheat et al. 2017) and arctic foxes (Lai et al. 2017)), as the ability to mitigate the heterogeneity of resources across both time and space through movement is critical for the survival of organisms in all systems (Bauer and Hoye, 2014; van Moorter et al. 2013).

Overall, it is difficult to detect and classify unique and variable behaviors of individuals. The high degree of variability in red fox movements adds complexity to the data, confounding consistent classifications across methods and highlights the importance of identifying intraspecific variability in movement behaviors when assessing and classifying movement patterns (Abrahms et al. 2017; Cagnacci et al. 2016).

Visual inspection of movement patterns allows for the subjectivity to fit outlying behaviors where more rigid quantification methods do not. Collectively, our visual classifications confirmed patterns that are known to occur in red foxes; subadult male biased dispersal patterns (Storm 1976; Greenwood, 1980), a high degree of residency and stability among adult individuals and in particular adult females and only a small proportion of nomadic individuals, which were predominantly male (von Schantz, 1981).

However, such descriptive analysis is not intended as an endpoint, but rather a first step in characterizing different movement behaviors, where additional analysis can occur for individuals classified according to their respective movement behaviors. This allows for simplification of complex animal movement data, which may include multiple movement behaviors at multiple scales (Benhamou, 2014). By isolating a single movement behavior of interest according to the scale at which it occurs (ie. classifying individuals accordingly), we can identify not just the commonalities within the movement behaviors, but assess the degree of variability as well. This will assist in determining how flexible and generalized such pattern definitions need to be to accommodate the natural variability found within a population or species (Nathan et al. 2008). This also makes it possible to look into each behavior collectively or individually (Benhamou, 2014).

Our ability to dissect behaviors from animal trajectories and identify the underlying mechanisms are often hampered by methodological limitations (Nathan et al. 2008, 2012). NSD has proven a useful metric for quantifying larger scale movements in other species and systems, particularly for migratory behaviors in ungulates (Bunnefeld et al. 2011; Singh et al. 2016; Spitz et al. 2017), but perhaps less so for the red fox. Therefore, visual pattern analysis should not be ignored as an important tool for complex data and for matching behaviors to the appropriate scale for highly variable species (Demšar et al. 2015; Andrienko and Andrienko, 2013). This is particularly relevant for a species such as the red fox, as we found that movement behaviors could occur at vastly different scales and that similar movement patterns could represent different behaviors depending on the spatial scale at which they occurred.

This study lends support to the conclusion of Cagnacci et al. (2016) that movement patterns should be considered as a gradient of behaviors rather than as fixed patterns. Our understanding of the behavioral flexibility of animal movements is still in its infancy and current methodologies have not yet caught up with the large volumes of animal movement data being collected (Cagnacci et al. 2010). Extending our knowledge in the field of movement ecology will likely require developing new metrics accounting for 'behavioral plasticity' in movement models (Nathan 2001; Cagnacci et al. 2016), rather than simply removing or smoothing the outlying behaviors of individuals. Visualization thus remains an important tool and is especially important to facilitate data exploration and uncover hidden patterns in data (Dodge, 2016; Benhamou, 2014).

Conclusion

We suggest striving for a middle ground of not oversimplifying animal movements to fit within boxes but to recognize the behavioral plasticity and individuality within animal movements as being of unique ecological value, having individual and population, fitness and evolutionary merit. Determining the appropriate scale at which an animal's movements occur, combined with our understanding of the variability within behaviors will provide a more thorough understanding of how to identify and classify movement behaviors appropriately.

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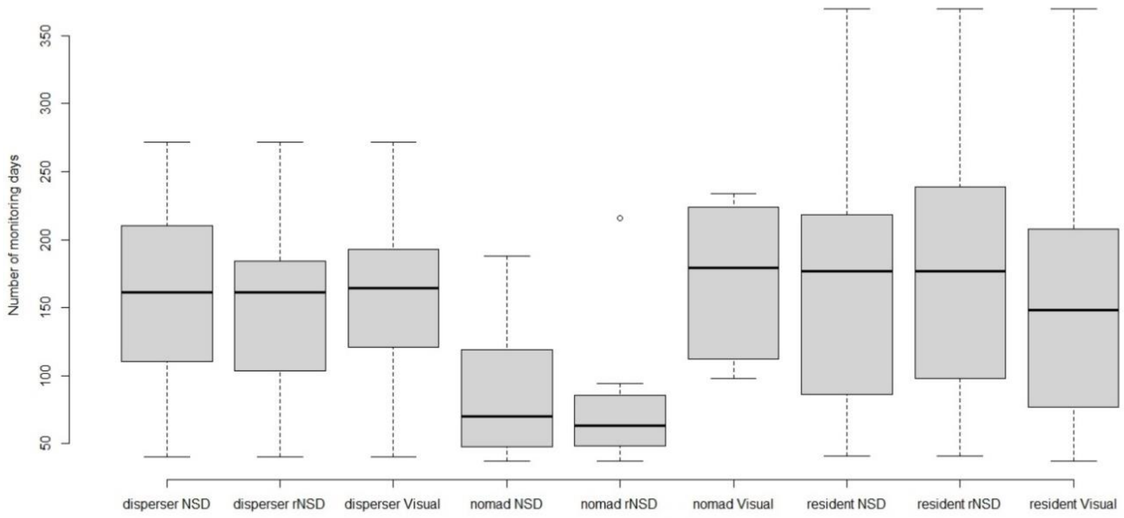
Supplementary Table 1. Movement classifications of red foxes as resident, disperser and nomad, using relative net squared displacement (rNSD), net squared displacement (NSD) and visual inspection of animal trajectories (Visual Class). The recalculated reference position determined for rNSD is provided. Additionally included are the red fox attributes: Sex (M= Male, F= Female) and Age (SA= subadult, AD = adult). Positioning was standardized to three positions per day across all foxes and No. Locs. represents the total number of locations in each animal's trajectory. No. days is the number of days an individual was monitored with start and end dates additionally provided.

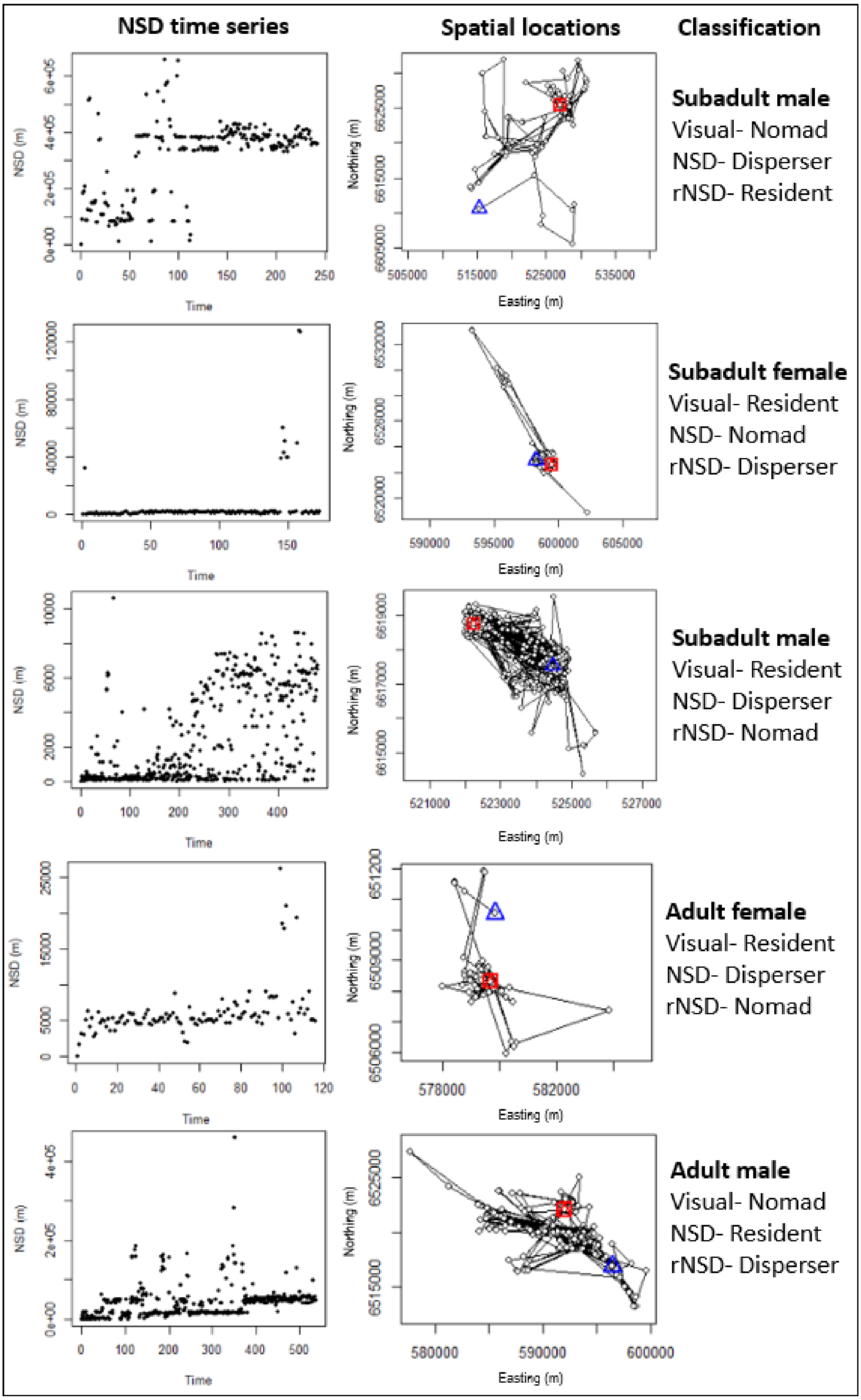
Fox No.	**Sex**	**Age**	**Study Area**	**Date begin**	**Date end**	**No. Locs.**	**No. Days**	**rNSD loc.**	**rNSD model**	**NSD model**	**Visual Class**
1	M	SA	Kolmården	3/16/2018	5/15/2018	165	60	12	resident	resident	resident
2	F	AD	Kolmården	6/28/2013	10/29/2013	288	123	13	resident	disperser	resident
3	F	AD	Kolmården	12/28/2013	9/15/2014	617	261	1	resident	resident	resident
4	M	SA	Kolmården	10/1/2016	1/30/2017	344	121	6	disperser	disperser	disperser
5	M	SA	Hedmark	2/23/2018	10/11/2018	690	230	7	disperser	disperser	disperser
6	M	SA	Hedmark	12/25/2015	5/31/2016	421	158	6	disperser	disperser	disperser
7	M	AD	Kolmården	2/27/2013	11/6/2013	687	252	15	resident	resident	resident
8	F	AD	Kolmården	3/22/2017	6/7/2017	209	77	1	nomad	nomad	resident
9	M	SA	Grimsö	3/4/2012	6/10/2012	242	98	14	resident	disperser	nomad
10	M	AD	Kolmården	11/25/2013	6/29/2014	528	216	13	resident	resident	resident
11	F	SA	Grimsö	1/28/2013	10/24/2013	652	269	13	resident	resident	resident
12	F	SA	Kolmården	12/22/2016	3/3/2017	203	71	14	disperser	resident	resident
13	M	AD	Kolmården	2/15/2018	8/12/2018	520	178	1	resident	resident	resident
14	F	SA	Kolmården	9/6/2013	9/11/2014	881	370	5	resident	resident	resident
15	F	AD	Kolmården	3/31/2018	6/23/2018	236	84	8	resident	resident	resident
16	F	SA	Kolmården	10/26/2016	4/21/2017	429	177	13	resident	resident	resident
17	M	SA	Grimsö	12/19/2013	2/20/2014	168	63	12	nomad	nomad	resident
18	M	AD	Kolmården	2/2/2016	5/24/2016	328	112	15	disperser	disperser	nomad
19	M	AD	Hedmark	12/22/2011	2/4/2012	98	44	8	resident	resident	resident
20	M	AD	Hedmark	11/6/2014	1/11/2015	178	66	15	disperser	disperser	resident
21	M	SA	Hedemora	11/22/2014	1/29/2015	185	68	5	disperser	disperser	disperser
22	F	SA	Kolmården	10/4/2017	11/30/2017	173	57	6	disperser	nomad	resident
23	F	AD	Hedmark	1/31/2013	6/15/2013	336	135	3	resident	resident	resident
24	M	SA	Grimsö	11/27/2014	7/1/2015	480	216	2	nomad	disperser	resident
25	M	AD	Kolmården	12/1/2015	7/12/2016	632	224	13	disperser	disperser	nomad
26	M	AD	Kolmården	12/4/2016	5/7/2017	451	154	6	disperser	disperser	disperser
27	M	AD	Kolmården	1/25/2016	7/12/2016	328	169	3	disperser	resident	resident
28	M	AD	Kolmården	3/22/2017	9/16/2017	532	178	14	resident	disperser	resident
29	M	AD	Kolmården	11/9/2015	5/7/2016	502	180	7	disperser	disperser	disperser
30	M	SA	Grimsö	12/13/2014	9/6/2015	741	267	8	resident	disperser	disperser
31	M	SA	Kolmården	3/21/2018	7/16/2018	344	117	3	disperser	disperser	resident
32	M	SA	Hedemora	2/12/2014	6/1/2014	295	109	13	disperser	disperser	disperser
33	F	AD	Kolmården	5/31/2013	11/7/2013	368	160	1	disperser	disperser	resident
34	F	SA	Kolmården	3/4/2017	8/30/2017	534	179	13	disperser	disperser	disperser
35	F	AD	Hedmark	4/8/2018	7/15/2018	280	98	10	resident	disperser	resident
36	M	AD	Kolmården	10/30/2014	6/26/2015	619	239	11	resident	resident	resident
37	M	SA	Grimsö	12/6/2015	6/2/2016	506	179	15	disperser	disperser	disperser
38	F	SA	Kolmården	10/25/2016	4/22/2017	411	179	15	disperser	disperser	resident
39	M	AD	Kolmården	11/18/2017	2/10/2018	255	84	6	disperser	disperser	disperser
40	F	AD	Kolmården	10/5/2017	12/4/2017	142	60	11	resident	resident	resident
41	F	AD	Grimsö	12/8/2015	6/13/2016	447	188	11	resident	nomad	resident
42	F	AD	Kolmården	8/18/2016	2/15/2017	503	181	13	resident	resident	resident
43	M	AD	Kolmården	4/5/2013	11/3/2013	562	212	10	resident	disperser	resident
44	M	AD	Kolmården	5/9/2014	1/25/2015	519	261	5	disperser	resident	resident
45	M	SA	Kolmården	11/1/2013	3/29/2014	341	148	5	resident	resident	resident
46	M	AD	Kolmården	11/12/2016	5/11/2017	523	180	6	disperser	disperser	disperser
47	M	AD	Kolmården	1/28/2015	9/29/2015	645	244	5	resident	resident	resident
48	M	AD	Kolmården	12/4/2018	5/15/2019	480	162	4	disperser	disperser	disperser
49	M	SA	Kolmården	8/22/2018	10/1/2018	117	40	1	disperser	disperser	disperser
50	M	SA	Hedemora	11/16/2014	8/10/2015	659	267	4	resident	disperser	resident

Fox No.	**Sex**	**Age**	**Study Area**	**Date begin**	**Date end**	**No. Locs.**	**No. Days**	**rNSD loc.**	**rNSD model**	**NSD model**	**Visual Class**
51	F	AD	Kolmården	6/2/2017	11/26/2017	472	177	5	resident	resident	resident
52	F	SA	Hedemora	3/3/2015	6/5/2015	285	94	8	nomad	nomad	resident
53	M	AD	Kolmården	3/17/2018	5/31/2018	226	75	9	resident	resident	resident
54	F	AD	Grimsö	2/27/2017	8/24/2017	463	178	14	resident	resident	resident
55	M	AD	Kolmården	2/21/2014	11/17/2014	731	269	15	resident	disperser	resident
56	F	AD	Kolmården	2/10/2015	7/18/2015	361	158	4	resident	resident	resident
57	F	AD	Kolmården	1/16/2019	4/6/2019	215	80	9	resident	resident	resident
58	F	SA	Kolmården	11/8/2014	8/7/2015	686	272	10	disperser	disperser	disperser
59	M	SA	Kolmården	3/30/2014	11/8/2014	638	223	8	resident	resident	disperser
60	M	AD	Hedmark	12/24/2012	3/15/2013	154	81	15	disperser	resident	resident
61	M	SA	Kolmården	10/16/2012	7/13/2013	710	270	1	disperser	disperser	disperser
62	F	AD	Kolmården	5/13/2019	7/8/2019	170	56	2	resident	resident	resident
63	F	AD	Kolmården	6/26/2017	11/10/2017	398	137	7	resident	disperser	resident
64	F	SA	Kolmården	10/31/2015	3/23/2016	361	144	6	resident	nomad	resident
65	F	AD	Kolmården	6/1/2016	11/11/2016	472	163	10	disperser	disperser	resident
66	M	SA	Kolmården	8/14/2016	2/12/2017	513	182	3	disperser	disperser	disperser
67	F	AD	Hedemora	3/18/2015	10/6/2015	399	202	8	resident	resident	resident
68	F	SA	Hedemora	3/14/2015	7/14/2015	323	122	6	resident	disperser	disperser
69	F	AD	Kolmården	3/21/2017	7/9/2017	275	110	12	disperser	resident	resident
70	M	SA	Kolmården	9/30/2014	2/3/2015	235	126	4	disperser	disperser	disperser
71	M	SA	Hedemora	1/17/2014	5/11/2014	280	114	1	disperser	disperser	disperser
72	M	AD	Kolmården	12/25/2016	6/22/2017	533	179	7	disperser	resident	resident
73	M	AD	Kolmården	12/6/2017	7/15/2018	622	221	2	disperser	resident	resident
74	F	SA	Kolmården	1/21/2013	6/24/2013	307	154	11	disperser	resident	disperser
75	M	AD	Hedemora	2/18/2015	9/14/2015	584	208	1	resident	resident	resident
76	M	AD	Kolmården	11/12/2015	1/5/2016	157	54	15	resident	resident	resident
77	M	SA	Kolmården	2/19/2014	11/16/2014	714	270	11	disperser	disperser	resident
78	F	AD	Kolmården	1/22/2018	6/6/2018	396	135	1	disperser	disperser	resident
79	M	SA	Kolmården	8/27/2013	11/23/2013	111	88	4	disperser	resident	resident
80	M	AD	Kolmården	11/20/2015	5/17/2016	537	179	10	disperser	resident	nomad
81	M	SA	Kolmården	1/22/2015	7/18/2015	450	177	9	disperser	resident	resident
82	M	AD	Kolmården	12/7/2018	1/17/2019	119	41	10	resident	resident	resident
83	M	SA	Kolmården	8/12/2014	10/5/2014	155	54	3	disperser	disperser	resident
84	M	SA	Kolmården	10/13/2014	11/20/2014	69	38	5	nomad	nomad	resident
85	M	AD	Hedemora	11/21/2015	2/29/2016	294	100	14	resident	resident	resident
86	F	AD	Kolmården	10/30/2017	2/5/2018	291	98	2	disperser	resident	resident
87	M	SA	Hedemora	2/11/2015	4/11/2015	169	59	9	resident	resident	resident
88	M	AD	Kolmården	3/29/2015	12/23/2015	723	269	1	resident	resident	resident
89	M	SA	Grimsö	2/22/2017	7/12/2017	401	140	10	resident	resident	resident
90	M	AD	Kolmården	12/6/2017	2/18/2018	220	74	14	disperser	disperser	resident
91	M	SA	Kolmården	9/3/2014	1/29/2015	339	148	6	disperser	disperser	disperser
92	F	AD	Kolmården	3/8/2013	12/2/2013	573	269	5	disperser	resident	resident
93	M	AD	Kolmården	12/1/2015	1/7/2016	97	37	6	nomad	nomad	resident
94	F	AD	Kolmården	10/15/2014	12/13/2014	116	59	9	nomad	disperser	resident
95	M	AD	Kolmården	10/10/2014	3/26/2015	405	167	13	disperser	disperser	disperser
96	M	SA	Hedemora	2/18/2014	6/2/2014	67	104	4	resident	resident	resident
97	F	SA	Hedmark	2/8/2013	11/2/2013	596	267	10	resident	disperser	resident
98	F	AD	Hedmark	3/8/2016	8/1/2016	327	146	2	disperser	disperser	resident
99	M	AD	Hedmark	12/12/2015	1/29/2016	35	48	11	disperser	disperser	resident
100	M	AD	Kolmården	11/22/2014	5/31/2015	502	190	5	resident	resident	resident
101	F	AD	Hedmark	12/5/2015	5/27/2016	502	174	12	disperser	disperser	resident
102	F	AD	Hedmark	11/18/2015	5/24/2016	499	188	6	disperser	resident	resident
103	M	AD	Kolmården	11/14/2015	5/25/2016	547	193	5	disperser	disperser	disperser
104	F	SA	Kolmården	1/14/2015	10/7/2015	698	266	9	disperser	disperser	disperser
105	M	AD	Kolmården	2/24/2015	11/17/2015	726	266	12	resident	disperser	resident
106	M	SA	Kolmården	8/29/2017	10/11/2017	116	43	13	disperser	disperser	disperser
107	F	AD	Kolmården	3/6/2017	5/18/2017	179	73	13	resident	disperser	resident
108	M	AD	Hedmark	4/30/2016	6/18/2016	148	49	10	disperser	disperser	disperser

Fox No.	Sex	Age	Study Area	Date begin	Date end	No. Locs.	No. Days	rNSD loc.	rNSD model	NSD model	Visual Class
109	M	SA	Hedmark	11/13/2011	6/8/2012	542	208	13	disperser	disperser	disperser
110	M	AD	Kolmården	1/3/2015	9/12/2015	700	252	2	resident	resident	resident
111	M	AD	Kolmården	12/27/2015	7/1/2016	554	187	12	disperser	disperser	disperser
112	F	AD	Kolmården	9/1/2013	4/23/2014	623	234	13	disperser	disperser	nomad



Supplementary Figure 1. Boxplots showing the distribution of the monitoring durations (days) for each movement classification and method. The interquartile ranges are given by the grey boxes with the median values represented by the black lines. From left to right, dispersers, nomads and resident individuals are listed by methods (NSD, rNSD and Visual). With a model driven approach, individuals with shorter monitoring durations are more likely to be classified as nomads (or confound classification into alternative categories) than visually classified individuals or other movement categories. Thus, sampling duration is likely to play a role in classification consistency.



Supplementary Figure 2. The movement trajectories and NSD time series patterns for the five red fox individuals that showed no agreement across all three methods. The age and sex of each fox is given in bold along with the movement classification according to the different methods (Visual, NSD or rNSD). Note the spatial scale, in square meters, of the NSD time series plots. The blue triangles represent the start position and the red squares shows the last position in each animal’s movement trajectory.

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The red fox *Vulpes vulpes* has one of the largest geographic ranges of any wild terrestrial mammal and is a commonly recognized species in Scandinavian ecosystems. However, our understanding of red foxes in rural and human modified landscapes is constrained by a lack of knowledge about how foxes use these landscapes.

This thesis represents one of the first GPS telemetry studies of red foxes, tracking the movements of 134 red foxes within four study areas across Norway and Sweden. In this thesis, I investigated the spatiotemporal movement patterns of red foxes along a landscape gradient of human influence using individual based GPS telemetry data from red foxes collected in Norway and Sweden between 2011- 2019.

Using GPS technology highlights the ecological plasticity of the red fox. Red foxes showed a high degree of individual variation and much larger home ranges than previously recorded, partially explained through environmental factors along a landscape gradient. Red foxes also did not move or use space randomly but repeatedly revisited previously used resource locations linked by directed or exploratory movements in between. Red foxes also demonstrated their ability to traverse between populations and across landscapes, as highlighted by six long-distance dispersal events, representing some of the longest dispersal distances recorded for red foxes. However, locally, spatial organization in red foxes occurred by social mechanisms not linked to their movement ability or dispersal capacity.

This information increases our understanding of red fox movement behaviors and their interactions with social and environmental factors at multiple spatial scales, with implications for future research, management and demographic and disease modeling.