

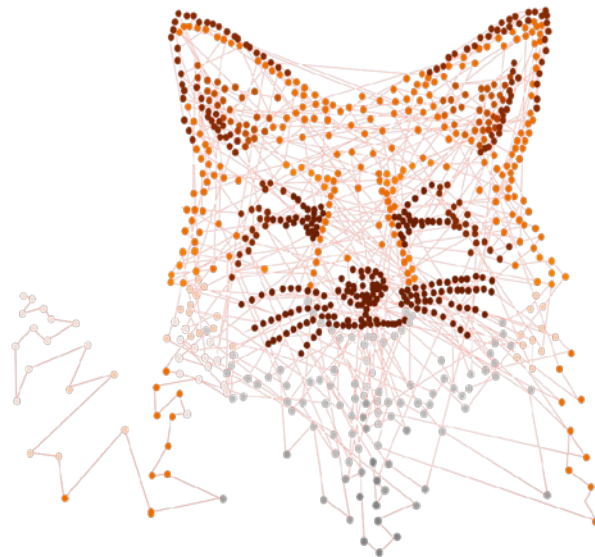
Faculty of Applied Ecology and Agricultural Sciences

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Master's thesis

Navigating the Red Fox's Cognitive Map:

How recursive use of resource locations influence movement patterns
and the notion of a home range.



Master in Applied Ecology

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Abstract

The size and location of an animal's home range is considered fundamental to the understanding of a species' dispersion and spatio-ecological requirements. Recent studies suggest that memory and recursive movement strategies have been overlooked in the shaping of home range patterns. It has been proposed that the most apt definition of a home range is: that part of animal's cognitive map of its environment that it chooses to keep updated. By following fourteen GPS collared red foxes, I investigate how recursive movement and fine scale site or route fidelity, implicative of a cognitive map, shapes red fox space-use patterns. Red foxes showed significant clustering in recorded positions. An average of 43% of fixes were found in clusters that covered a proportional area of only 1.1% of their total range; providing evidence that red foxes use space disproportionately and demonstrate strong recursive use of specific resource locations. Clusters were attributed to clumped food sources, bed or den sites, routes and vantage points in the landscape. Cluster habitat and utility was strongly linked with diel phase. Foxes were more active at night and demonstrated recursive movement to food sources in habitats of greater exposure to humans, under cover of darkness. During the day, foxes were less active and demonstrated extended residence time at established shelter locations. These were in dense vegetation or rugged terrain further from human habitation or farmyards. Foxes demonstrated limited movement time away from cluster locations. My results indicate that memory and an associated cognitive map play a prominent role in optimizing red fox movement patterns in rural landscapes.

Keywords: home range, memory, recursive movement, cognitive map, nocturnality, land use, space use, resource selection, red fox, *Vulpes vulpes*.

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1. Introduction

The geographic area traversed by an animal for all normal activities is referred to as a ‘home range’, a concept put forward by Burt (1943). The size and location of what is considered to be an animal’s home range is a commonly reported attribute in wildlife studies, as it is considered fundamental to the understanding of a species’ dispersion and spatio-ecological requirements. If we also presume that home range movements and behaviour are a product of an animal’s memory, sense of place and decision-making process, then a home range represents the interplay between an environment and an animal’s understanding of that environment, i.e. its cognitive map (Peters 1978, Fabrigoule and Maurel 1982, Powell 2000).

Estimated home range size varies considerably within and between different taxa, which has been linked to a number of explanatory factors. For carnivore species these include: body mass (Gittleman and Harvey 1982), population density (Šálek et al. 2015), resource availability, seasonality or environmental productivity (Walton et al. 2017), sex (Aronsson et al. 2016), reproductive status (Travaini et al. 1993), social structure, territoriality (Dahle and Swenson 2003, Loveridge et al. 2009) and perhaps even individual temperament (Spiegel et al. 2017). The relative importance of each of these elements on home range size remains unclear however, as it is difficult to dissect their many synergistic effects. Facilitated by recent advances in telemetry technology, particularly that of GPS tagging (Tomkiewicz et al. 2010), a variety of estimation methods have evolved to quantify the operational dimensions of a home range. There is criticism however that ‘the technological cart’ may have been ‘ahead of the conceptual horse’, and many previous studies missed how actual animal behaviour builds home ranges (Powell and Mitchell 2012)

An animal’s spatial memory of resource locations will also influence that animal’s movement and resource selection decisions (Fagan et al. 2013). Recursive movement patterns are a widespread trait in animal behaviour (Bracis et al. 2018), thought to be linked with optimal foraging strategies, such as trap-lining (Berger-Tal and Bar-David 2015) or food caching (Macdonald 1976). If site and route fidelity is essentially the repeated use of, or travel to and from memorized resources, it is reasonable to assume that memory and experience play a fundamental role in constraining space-use patterns. Mechanistic movement models which incorporate memory-like components, successfully demonstrate

the emergence of bounded space-use characteristics that are definitive of a ‘home range’ (Van Moorter et al. 2009, Gautestad 2011).

A common procedure to analyse space use within a home range from animal movement data, is to compute a Utilization Distribution using Kernel Density Estimates (KDEs), Minimum Convex Polygons (MCPs) or Local Convex Hulls (LoCoHs) (Getz et al. 2007). These methods 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 rest places, may appear of higher utility than sites that are as frequently visited, but for much shorter durations. By distinguishing between the number of recursive visits to patches, and the number of consecutive positions at those locations, important landscape features and resources in an animal’s space might be identified, that might otherwise have been overlooked or misinterpreted.

A species that shows remarkable variation in home range size is the increasingly widespread carnivore, the red fox *Vulpes vulpes* L. (Voigt and Macdonald 1984, Cavallini 1996, Walton et al. 2017). As a generalist mesopredator the red fox is a highly adaptable and opportunistic species that does not conform to any strictly defined niche. The diverse range of habitats the red fox occupies is testament to its adaptive capacity, illustrated by their well-established presence, at relatively high densities, in many of the world’s densest human population centres (Harris and Rayner 1986, Šálek et al. 2015). Red foxes are also seen to thrive particularly well in areas of farmland and forestry (Pasanen-Mortensen and Elmhagen 2015). Human activity can facilitate red fox populations either through direct food provision, or indirectly through activities and habitat re-structuring which support increased densities of prey species (Gompper and Vanak 2008). The heterogeneous mosaics of habitat patches and edges that are commonly associated with agricultural regions, are also implicated as a key benefit to red foxes in these landscapes (Kurki et al. 1998). With increasing human land-use modifications and reduced seasonality at northern latitudes, it is foreseeable that the red fox’s current range of occupation is likely to persist, or even expand (Elmhagen et al. 2015). Where the red fox’s range has expanded to previously unoccupied landscapes, the species has proven highly invasive (Lowe et al. 2000, Tannerfeldt et al. 2002). Consequently, persecution of foxes is a common management tool in rural areas to minimise predation on livestock or game species (Reynolds and Tapper 1996, Trewby et al. 2008, Lozano et al. 2013). Inherently vulpine traits such as nocturnality (Díaz-Ruiz et al. 2016), underground

denning and surveillance, may mitigate against such threats, and 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).

There is accumulating evidence suggesting that the red fox plays a significant role in the food webs of many ecosystems (Lindström 1980, Marcstrom et al. 1988, Storch et al. 1990, Lindström et al. 1994, Kurki et al. 1998, Leckie et al. 1998, Dell'Arte et al. 2007, Goszczyński et al. 2008). The species is also a vector for a number of zoonotic diseases (Steck and Wandeler 1980, Murray et al. 1986, Saeed et al. 2006, Lind et al. 2011). As such, the ecology of the species warrants attention.

The highly individual behaviour and home range patterns observed in red foxes provide an opportunity to investigate if emergent 'home range' patterns are a product of recursive activity and movement implicative of a cognitive map. The high degree of local variation in red fox home range estimations is often attributed to complexities and intraspecific variation in their social structure and territoriality (White and Harris 1994, Cavallini 1996). Following observations that red foxes often focus their activity at discrete resource sites, linked by the necessary movement pathways in between, Macdonald (1983) proposed the resource dispersion hypothesis (RDH). He suggested that spatial dispersion and richness of food patches determines home range size. Lucherini et al. (1995) find support for this hypothesis, but suggest the additional importance of shelter.

By following foxes fitted with GPS radio collars within a mosaic of human land-use in southern Sweden, I look for evidence of recursive movement patterns and site use by identifying clusters in recorded positions. I predict that a significant proportion of red fox movements will be constrained by recursive visits to distinct resource patches. Because red foxes are widely understood to be nocturnal in response to optimal hunting conditions and human disturbance, I also test the influence of diel phase. I predict that foxes will demonstrate recursive movement to food sources under cover of darkness. I expect these resources to be in habitats of greater exposure to humans, and consequently I predict that residence-time at these locations will be short. During the day, I predict that foxes will demonstrate extended residence time at established shelter locations. I expect these to be in dense vegetation, in rough ground and further from human habitation or farmyards. In affirmation of a cognitive map I also expect that foxes will demonstrate recursive movement via particular routes and strategic points.

2. Materials & Methods

2.1 Study Area

I conducted this study in the Southern part of Södermanland county in south-eastern Sweden ($58^{\circ}40'N$, $16^{\circ}22'E$; Fig. 1). This landscape is a mosaic of productive agricultural land amongst fragments of boreonemoral woodland (Rydin et al. 1999), commercial conifer plantations, and scattered farmyards or human settlements. The area lies at an average altitude of twenty-four meters above sea level. Mean daily temperatures range from highs of $22^{\circ}C$ in July to $-6^{\circ}C$ in January. Snow cover is irregular but not uncommon from December to March. Hunting is a popular pursuit in this region, and to attract game species, a number of feeding and bait stations are found throughout the landscape. Bait stations to attract wild-boar, *Sus scrofa*, commonly consisted of discarded carcass remains from other large game or livestock, and hay bales or dried pea dispensers designed to increase localised prey densities.

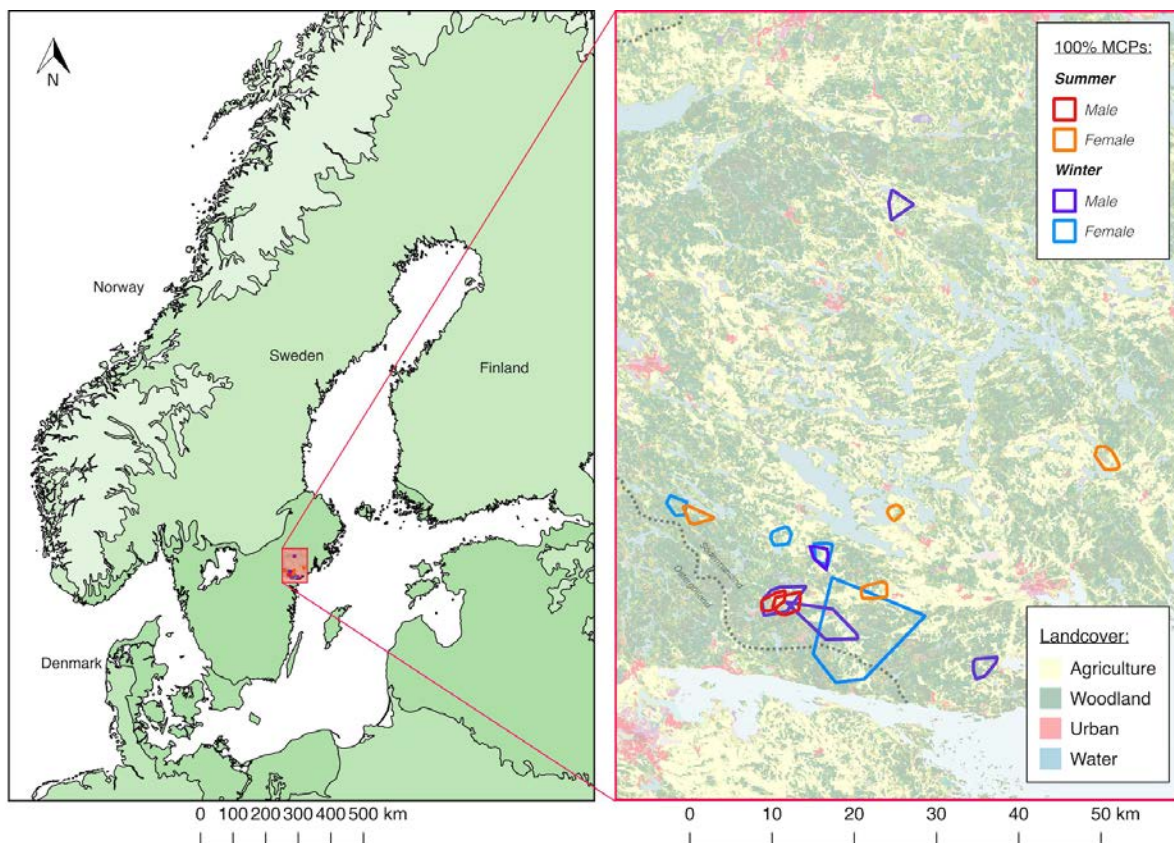


Figure 1: Map of the study area in South-eastern Sweden. Shades of green in left hand panel represent gradient in landscape productivity. Right hand panel shows smaller scale map of broad land use types in the area (Naturvårdsverket 2014); and 100% Minimum Convex Polygons represent the area traversed by individual foxes during the different study periods. Polygon colour represents season and sex of individual.

2.2 Fox Capture, Immobilization & Fix Shedule

Between November 2016 and 2017 14 foxes were captured and fitted with GPS radio collars (Tellus 138 Ultralight, 210g, Televilt, Inc. Lindesberg, Sweden). Animal capture and handling procedures were approved and followed the ethical guidelines required by the Swedish Animal Ethics Committee (permit number DNR 58-15). Additional permits to capture wild animals were provided by the Swedish Environmental Protection Board (NV-03459-11). Foxes were initially captured using baited wooden trap boxes, (see Värmlands Tunnel Trap described in Opdahl (2014)). Foxes were then immobilized using a mixture of either: 2mg/kg ketamine and 0.08mg/kg medetomidine, where the medetomidine was later reversed with 0.4mg/kg atipamazole; or with 10mg/kg tiletamine-zolazepan, for which there is no reversal (Kreeger 2012).

Captured animals were sexed, measured, weighed and aged. Age was defined as sub-adult (<1 year) or adult (>1 year) based on month of capture the amount of tooth wear and colouration (Harris 1978). Only foxes of weight greater than 5kg were fitted with GPS radio collars. Total processing time was approximately 25-35 minutes.

Collars were programmed to take 6 positions per day, with the collar pre-programmed to automatically release after 180 days. Time was recorded in Greenwich Mean Time (GMT) without Daylight Saving Time (DST) in effect (Note: Local time is GMT +1 hour in winter, GMT + 2 hours in the summer). Positions were recorded at for hour intervals corresponding to 00:00, 04:00, 08:00, 12:00, 16:00 and 20:00 GMT for the majority of foxes. However, a number of positions recorded at 23:00, 03:00, 07:00, 11:00, 15:00 and 19:00 GMT at various stages in the study period. Of the 5993 scheduled positions 12.3% failed to record, most likely due to the influences of topography, or overhead cover whilst denning (Cain III et al. 2005). Only one recorded position was so distantly outlying it was presumed erroneous and removed.

2.3 Study Period and Number of Foxes

To focus on animals with stable home range use, I analysed net squared displacement (NSD) of the foxes from their capture point, as per Bunnefeld et al. (2011) in order to discount time periods where individuals were either dispersing or transient. Where foxes displayed a relative degree of stability and fidelity to a particular stay-region, for at least 30 days, I

extracted this period of positions for use in further analysis. I limited individual fix samples to maximum of 90 days per fox. However, one male fox (ID: Frans) was followed for 122 days, covering the entire extent of the study's summer sampling period, to further explore the effect of greater fix numbers on the degree of clustering. To detect temporal changes in behaviour, positions were analysed over two contrasting seasons: the 1st December to 28th February in the winter, and the 1st May to the 31st August in the summer. Position data that met these constraints was available for nine individual foxes over the winter period (female = 4, male = 5), and six foxes over the summer (female = 4, male = 2). One male fox (ID: Mattias) was active in both the summer and winter study periods.

2.4 Circadian Rhythm in Activity

Unless otherwise stated, all analysis (and use of specified 'packages') were carried out in the R 3.3.1 (R Core Team 2016).

Using activity loggers integrated in each GPS radio collar, I was able to estimate the degree of physical movement in the foxes at each GPS position. Collars logged the number of seconds the collar was moving in the horizontal (x) and the vertical (y) direction, during the time to fix for each position (30-59 seconds). The sum of movement in both the x and y direction, was divided by the time to fix, and plotted against the scheduled hour of each fix (maximum possible measurement = 2). Following the observed patterns in fox activity over the twenty-four hour period, I then segregated GPS positions by diurnal or nocturnal phase to distinguish between times of active or passive behaviour in later analysis. These categories were assigned according to the time of each fix and the sunrise and sunset times at **58°73'N, 16°49'E** using the R package 'maptools' (Bivand and Lewin-Koh 2007). This package uses data and algorithms provided by NOAA (the National Oceanic & Atmospheric Administration – US Department of Commerce). I used a Welch two sample t-test to determine statistical significance between the mean diurnal and nocturnal activity measurements.

Mean sunrise to sunset times in the winter study period was 07:12 to 14:47 GMT. Mean sunrise in the summer study period was at 2:14 GMT, setting at 19:26 GMT. The fix schedule consisted of a mean ratio of 2.1 daytime positions to 3.9 night-time positions in winter. The longer daylight hours of summer shifted this ratio to 4.4 fixes in the day to 1.6 at night.

2.5 Clustering and Home Range Metrics

2.5.1 Minimum Convex Polygons

I used the 'adehabitatHR' package (Calenge 2006) in R to generate 100% and 95% MCPs. This was carried out inclusive of both diel phases, and also separately for diurnal and nocturnal positions. Area estimates of the diurnal and nocturnal MCPs were compared using a paired t –test. MCPs are not used in this study as an estimate of home range size but rather to estimate the extent of the area assumed available to each fox, following second order habitat selection (Johnson 1980). 95% MCPs were calculated to reduce the effect of any outlying positions that may cause overestimation of this extent.

2.5.2 Clustering

I identified clustering of GPS positions for each fox using the R package 'dbscan' (Hahsler 2017). Clusters were distinguished from 'noise' using the following parameters: I set the Epsilon Neighbourhood (eps) to a radius of 55 meters around each fix; and I required a minimum of six positions within that eps to form an initial core cluster. All of the points within 55m of a core point were included in clusters. I chose a minimum of six core points to increase the likelihood that clusters were not formed by consecutive positions over a single period. Foxes would have had to either spent longer than a whole day and night within the eps (0.95 ha), which I expected to be rare, or they must have left and returned to that area over a number of days.

To measure recursive use of cluster locations, I counted the total number of independent visits to each cluster. Independent visits were defined as: any positions in a cluster following a preceding position that was not. I then counted the number of consecutive positions at each cluster, and by dividing the total number of positions in each cluster by the number of independent visits, I calculated a mean number of positions per visit to each cluster. Clusters were identified in the data both inclusively of all twenty-four hour positions, and also separately for daytime and night-time positions. I therefore identified overlapping day and night clusters as one area whilst counting departures and revisits. To estimate time spent between recursions, I also counted the fix interval between each recorded cluster position, inclusive of consecutive position.

The spatial area of each cluster was calculated by generating 100% MCPs of each individual cluster of positions using the ‘adehabitatHR’ package. I found it necessary to modify the ‘mcp’ function, by reducing the minimum number of outer positions to three.

Random use of space can lead to apparent clumps 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. Therefore to identify core areas in an animal’s home range, use of space over that area must be statistically clumped and not random or even (Powell 2000). On this basis, it was important to establish that any clustering in the GPS positions was more than might happen by random occurrence. To check this, I simulated random distributions of points over three different sized polygons; and quantified the degree of clustering that occurred by chance. I then compared this to the spatial clustering in the fox positions. I used the dimensions of the smallest, the median and the largest sized 100% MCPs, and ensured that the number of random points within these polygons was greater or equal to the number of positions analysed for the foxes (see Fig. 5a). Mean number of simulated positions within polygons was 402 ($SD = 17.81$, range = 346 – 477). I removed any random positions that fell outside these polygons. I identified clustering of the randomly generated points using the same parameters I used on real fox positions, and repeated the randomisations one thousand times per polygon. I was then able compare the proportion of positions in randomly created clusters, to those produced by the real foxes. The statistical significance of any difference was tested using a Welch two sample t –test.

2.6 Ground truthing and cluster characteristics.

I calculated the median location of each daytime and night-time cluster, and randomly sampled an equal number of non-cluster positions for each seasonal fox dataset. I then visited the coordinates for each of these locations, where I measured a number of habitat characteristics and inferred utility by identifying local habitat characteristics, or field signs if found. By sampling and visiting non-clustered positions, I was able to compare the habitat characteristics of sites where the fox had not recorded recursive or consecutive positions to where they had. Any difference was tested using a Pearson’s χ squared.

I attributed the fox’s utility of each location by field observations and spoor identification. Each location was attributed to five broad categories: ‘**Food**’, ‘**Shelter**’, ‘**Vantage Point**’, ‘**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 I found food waste or other carrion.
- **'Shelter'** was subdivided into **'Bed'** where I found evidence of surface resting sites with signs of fox presence (e.g. hairs), or **'Den'** where I found subterranean excavations (earths).
- Where positions were located on or around natural highpoints, or outcrops in the local topography I 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 I was unable to identify a probable use remained as **'Unclassified'**.

For assistance in locating prey and carrion remains, or den and bed entrances, I was accompanied at each location by a gundog. In addition to cluster utility, the primary habitat type within a twenty-meter radius of the cluster median was broadly classified as either:

- **Forest:** where dominant vegetation cover consisted of trees over two meters in height.
- **Scrubland:** where dominant vegetation cover was trees or shrubs up to 2m in height including planted or regenerating commercial conifer plantations.
- **Parkland:** Where dominant vegetation was 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 farmyards, urban areas or other dwellings.

I measured horizontal vegetation cover / 'sightability' at each location using a 30x60cm cover cylinder as described in Ordiz et al. (2009). I placed the cover cylinder at the central coordinate of each location. From a crawling height of fifty centimetres, ten meters in the four cardinal directions from the central cylinder, I recorded the percentage of the cylinder visible through the horizontal vegetation cover. The mean average of these four recordings was taken as an estimate of horizontal sightability at each location. From a crouching position, I estimated vertical canopy cover in five categorical measures of visible sky: <20%, 20-40%, 40-60%, 60-80% and 80-100%, in order of densest canopy cover to most open. I estimated site ruggedness within the 20m radius to three categories as specified in Sahlén et al. (2011), 1 being flat, 2 being moderate and 3 being rugged terrain.

Finally, I measured linear distance to the nearest human activity centre, i.e. active residence or farm yard in QGIS 2.18 (QGIS Development Team 2009) to the nearest 10m using coordinates for settlement locations identified from Lantmäteriet geographic data.

2.7 Analysis of cluster utility

To explore the relationships and interactions between site-specific landscape characteristics and attributed cluster utility, I employed classification trees to identify the variables that best divided cluster utility into homogeneous sets. This was carried out using the Package R.Part (Therneau et al. 2017). I then used these models to predict cluster utility from the associated habitat metrics. Beds and dens, or hunting and scavenging, were broadly categorised as food or shelter, and clusters of unidentified utility were excluded from this analysis. Explanatory variables included, diel phase, season, sex, habitat-type, distance to human settlement, sightability, ruggedness and canopy openness. The data set was shuffled and partitioned into a 70% training set and 30% validation set. Using the training dataset I created models that incorporated combinations of each of these variables. These were then validated for accuracy by testing them on the validation dataset. I then selected the tree with the lowest validation error that distinguished between all identified utility classes. On this condition, trees built on fewer predictors were chosen over more complex trees of equal prediction accuracy. The best tree was then used to predict the utility of clusters of unidentified utility.

2.8 Analysis of recursive use and cluster residence time

I employed generalised linear mixed models (GLMMs) to test recursive movement and residence time as a function of diel phase, season, sex, and habitat characteristics. Age was discounted from analysis, as no sub-adults were collared over the summer. Individual fox identity was included as a random effect, to account for the non-independence of observations according to individual characteristics. The response variable was either the number of visits to a cluster location, or the count of consecutive positions at each cluster. Models to predict number of consecutive positions were fitted to a Poisson distribution through a log link function. However, the models to predict the number of visits to a cluster location were fitted with a negative binomial distribution, to reduce dispersion of the residuals. For number of visits, I included the sampling duration for each fox as an offset in the models, to standardise visits to each cluster per sampling effort. For the number of

consecutive positions, I included the total number of positions at each cluster as an offset. Fixed explanatory effects included: diel phase, season, sex, habitat type and cluster utility as categorical variables, distance to human settlement, sightability, ruggedness and canopy openness as continuous variables. Categorical variables, habitat type and cluster utility, were not combined in models due to insufficient sample size in each category. Continuous variables were centred and scaled by subtracting the mean and dividing by the standard deviation. I tested for correlations between the continuous explanatory variables using Pearson's correlation coefficients. I did not combine correlated variables in the same model if $|r| > 0.5$. One outlying cluster location, created by 11 consecutive positions and no recursive visits, was removed from the dataset prior to modelling to reduce over dispersion.

Analyses were carried out in R 3.0.1 with the lme4 (Bates et al. 2014) or glmmTMB (Magnusson et al. 2017) packages. I assessed whether final models were affected by over-dispersion, accepting dispersion parameter levels between 0.5 and 1.5 (Zuur et al. 2009). Model residuals were plotted, whilst taking random effects into account, using the R package DHARMA (Hartig 2017). Using the package MuMIn (Barton 2018), I calculated marginal R^2 values (R^2_m) to assess the percentage of the variation in the residence time explained by the fixed effects only. I then utilized a small sample size corrected version of Akaike Information Criteria (AICc) to select the most parsimonious model for interpretation. I considered all models with $\Delta AICc < 2$ to be equally supported by the data. Where several models were considered, I computed model-averaged parameter estimates and assessed the relative importance of each parameter by summing Akaike's weights across these models.

3. Results

3.1 Number of Foxes

A total of fourteen fox individuals were tracked over the study year, including nine foxes during the winter period (Female = 4, Male = 5) and six during the summer period (Female = 4, Male = 2). From a combined total of 999 telemetry days, mean average study period per fox was $67 \text{ days} \pm 23.4 \text{ SD}$ (Range = 36 - 121.7), this consisted of a mean of $350 \pm 123 \text{ SD}$ positions per fox (Range = 215 - 710). Individual fox sampling details are listed in Appendix 1.

3.2 Circadian Rhythm in Activity

Mean average collar activity measurements were significantly lower during daylight hours than at night ($t = -23.3$, $df = 5237.5$, $p < 0.0001$, Fig. 2). This greater median activity measurement of 0.3 (Interquartile range = 0.0–0.6) at night compared with 0.00 (IQR= 0.0 – 0.26) during the day indicates a circadian rhythm where foxes are strongly nocturnal; making movements at night and resting during the day (Fig. 2).

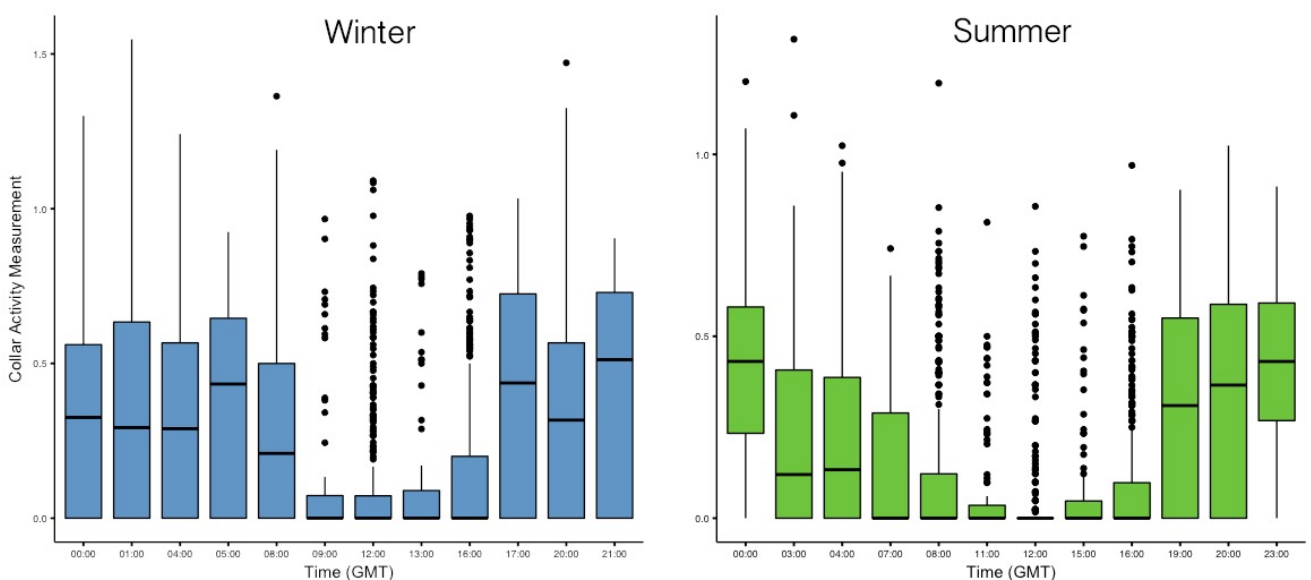


Figure 2: Collar Activity Measurement (X+Y movement / time taken to fix) over the recorded fix times during the summer and winter study periods. Time is recorded in GMT regardless of season. Individual fox activity measurement are combined.

3.3 Clustering and Home Range Metrics

3.3.1 Minimum Convex Polygons

100% MCPs ranged from 2.4 km² to 98.5 km² (*Mdn* = 4.9 km², IQR = 4.2 – 6.0). 95% MCPs ranged from 1.5 km² to 15 km² (*Mdn* = 3.3 km², IQR = 2.2 – 5.2). Individual MCP sizes are listed in Appendix 1 and 100% MCP shapes are illustrated in Fig. 1. Nocturnal positions occupied a median area of 4.4 km² (IQR = 3.8 – 5.4, 100%MCP), ranging from 2.2 to 98.5 km². This was greater than the median area for diurnal positions of 4.1 km² (IQR = 1.2 – 5.9, 100%MCP) which ranged from 0.02 to 36.9 km².

Using 95% MCPs, to confirm that this difference was not biased or confounded by a proportionally small number of outlying positions or excursions during either diel phase, I found that nocturnal positions occupied a greater median area (*Mdn* = 3.1 km², IQR = 2.2 – 4.5) than diurnal positions (*Mdn* = 2.2, IQR = 0.9 – 3.3 km²). Using a paired t- test I found a notable differences in these areas between day and night, dependent on season:

Difference in 95% MCP area between day and night in summer was not significant ($t = -0.62$, $df = 5$, $p = 0.57$), although it was in winter ($t = 2.38$, $df = 8$, $p = 0.04$). During the winter study period the extent of positions in the landscape, was significantly wider at night than during the day (Fig. 3).

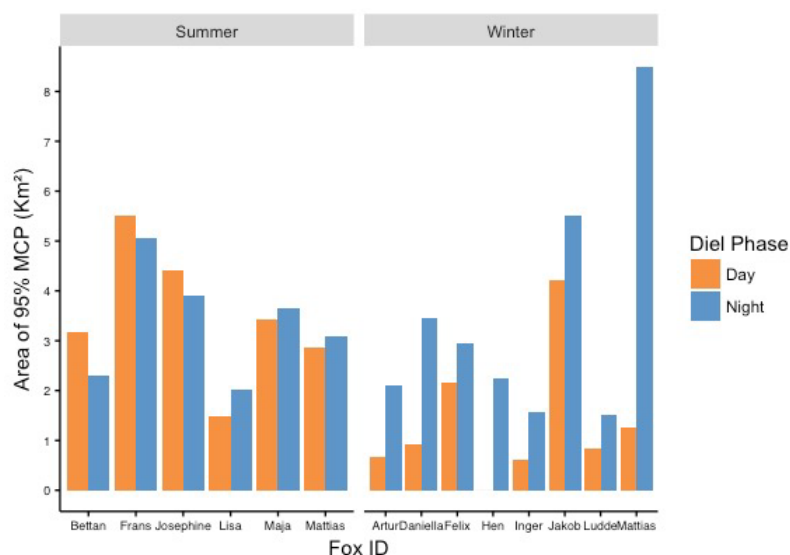


Figure 3: The extent of 95% MCPs (Km²) of nocturnal and diurnal positions for each fox. For visual clarity in figure, fox with (Charlotte.) large outlying MCP area is not illustrated: Day = 5.5Km², Night = 16.5Km² (95%).

Difference in 95%MCP of nocturnal positions between summer and winter was not significant ($t = -0.94$, $df = 9.22$, $p = 0.37$). I did find significant difference in the relative distribution of diurnal positions between seasons however ($t = 2.71$, $df = 10.75$, $p = 0.02$). The extent of diurnal positions was significantly wider during the summer than in winter (Fig. 3).

3.3.2 Clustering

A mean of 42.7% of the total positions per fox were clustered. This relatively high proportion of positions in clusters represented a small proportional area of the total MCP area (Table 1). Identifying clusters in the simulations of random points, confirmed that clustering of positions from real foxes, was significantly greater than would be expected by random occurrence ($t = 10.86$, $df = 14.01$, $p = <0.0001$, Fig. 4b).

A median average of eight clusters was identified per fox (IQR = 6.0 – 13.5). Individual clusters consisted of a median of 10 positions (IQR = 7 -15). The median number of positions in diurnal clusters was 11 (IQR = 7.5 - 15), and similarly, nocturnal clusters included a median of 10 positions (IQR = 7 - 14). Six was the minimum number of positions required to classify as a cluster.

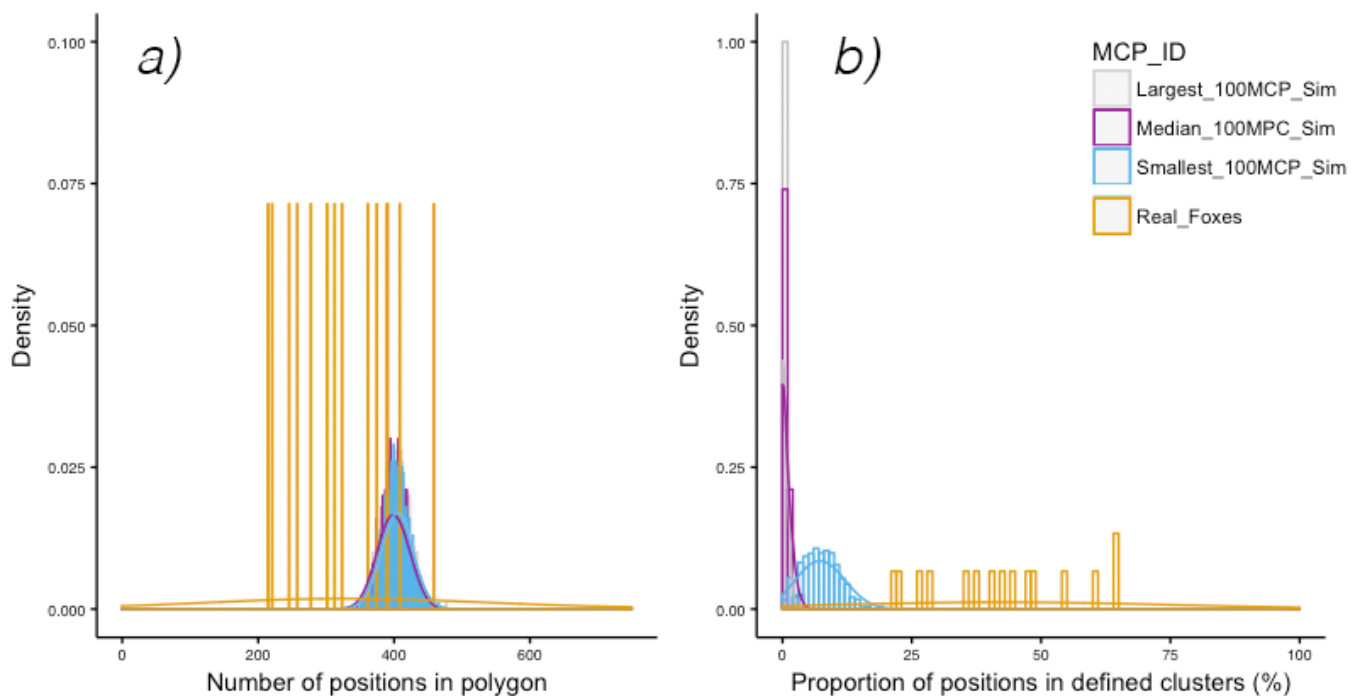


Figure 4: Histograms showing the frequency density of: a) The number of positions from real foxes compared to simulations of randomly distributed points in the smallest, median and largest 100%MCPs. b) The proportion of positions in defined clusters from real fox position data compared to the simulated random positions.

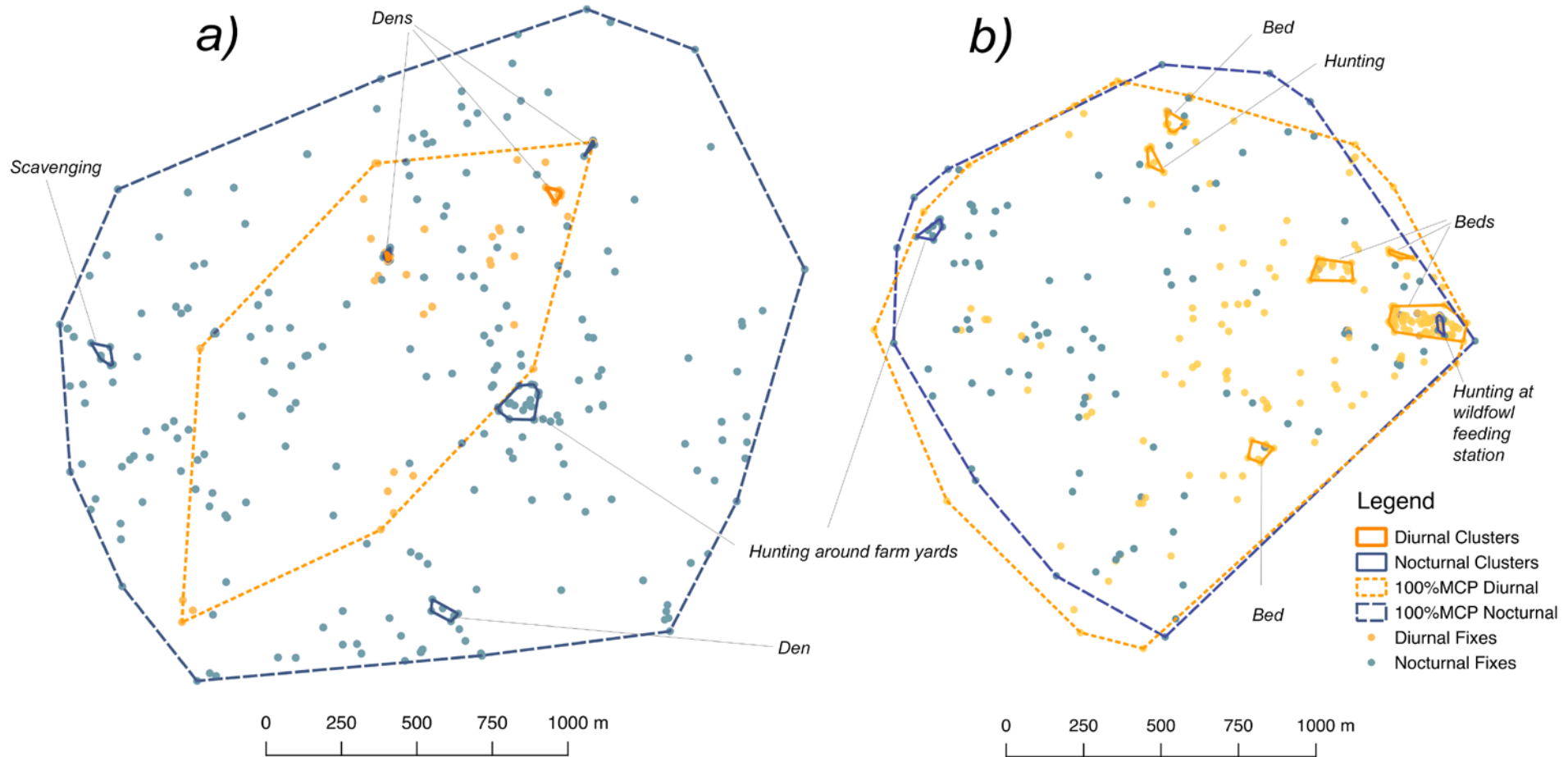


Figure 5: The extent of diurnal and nocturnal positions (100%MCPs) for two representative female foxes tracked over the two study seasons: a) 'Daniella' in the winter, and b) Lisa' in the summer. Figure illustrates contrasting ratio in diurnal/nocturnal range over both seasons, and proportional area of clustered positions.

Table 1: Mean proportion of nocturnal and diurnal positions in defined clusters, compared to the proportional area of clusters. For comparison, foxes have been divided by the season of their study period. Diel phase 'All' details clusters identified in positions unsegregated by diel phase.

Season	Diel Phase	Proportion of positions in clusters			Proportion of 100% MCP covered by cluster area			Proportion of 95% MCP covered by cluster area		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Summer (N=6)	Diurnal	41.2%	15.3	(24.5 - 60.3)	0.9%	0.5	(0.5 - 1.7)	1.2%	0.8	(0.6 - 2.6)
	Nocturnal	8.9%	8.8	(0.0 - 19.0)	0.1%	0.7	(0.0 - 0.2)	0.1%	0.1	(0.0 - 0.2)
	All	39.8%	14.2	(22.8 - 60.8)	1.3%	0.9	(0.5 - 2.7)	1.5%	0.98	(0.6 - 3.0)
Winter (N=9)	Diurnal	33.9%	27.1	(0.0 - 85.7)	1.3%	2.9	(0.0 - 9.0)	0.7%	0.8	(0.0 - 2.5)
	Nocturnal	35.2%	13.9	(13.7 - 54.9)	1.1%	1.2	(0.0 - 3.0)	2.5%	2.9	(0.2 - 7.6)
	All	44.6%	14.9	(21.9 - 64.4)	1.4%	1.4	(0.1 - 4.1)	3.4%	3.6	(0.5 - 10.0)
All Seasons (N=15)	Diurnal	36.8%	22.7	(0.0 - 85.7)	1.1%	2.2	(0.0 - 9.0)	0.9%	0.8	(0.0 - 2.6)
	Nocturnal	24.6%	17.8	(0.0 - 54.9)	0.7%	1	(0.0 - 3.0)	1.5%	2.5	(0.0 - 7.6)
	All	42.7%	14.3	(21.9 - 64.4)	1.1%	1.2	(0.1 - 4.1)	2.7%	3.1	(0.5 - 10.0)

3.4 Cluster Utility and Characteristics

The differences in habitat type at clustered positions compared to non-clustered positions were not statistically significant ($\chi^2 = 8.84$, $df = 5$, $p = 0.12$, Table 2). The only notable difference was the greater proportion of single positions in the agricultural habitat.

Table 2: The percentage of clusters vs. non-clustered positions in the different habitat classifications. 126 clusters and 126 non-clusters.

	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%

I found significant differences between a number of the habitat variables measured at clusters and the diel phase of that cluster (Fig. 6). In nocturnal clusters terrain was generally more rugged ($t = 2.46$, $df = 122.29$, $p = 0.015$); distance from farms and houses was less ($t = 2.89$, $df = 123.89$, $p = 0.005$); and sightability was greater ($t = -3.73$, $df = 121.97$, $p < 0.001$). I did not find a significant difference in canopy openness between diel phases ($t = -1.33$, $df = 119.87$, $p = 0.19$).

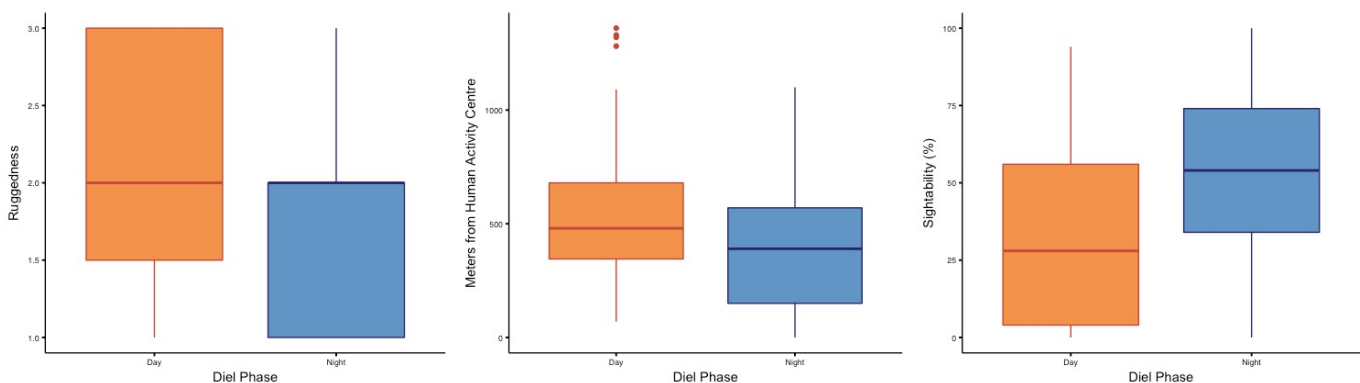


Figure 6: Ruggedness, distance from humans activity centres, and horizontal vegetation cover (sightability) at cluster locations in relation to diel phase. (ruggedness: 1 = flat, 2 = moderate and 3 = rugged terrain)

There was a significant difference in the utility attributed to clustered positions compared to those of randomly selected non-clustered positions ($\chi^2 = 91.16$, $df = 6$, $p = < 0.01$, Table 3).

Table 3: The percentage of clusters and non-clustered positions attributed to specific causes in the field. $N = 126$ clusters and 126 non-clusters.

	Shelter		Food		Vantage	Route	Unclassified
	Den	Bed	Scavenging	Hunting			
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%

The classification tree that demonstrated the least error in cross validation, predicting cluster utility to 65.7% accuracy, used three variables habitat type, diel phase and terrain ruggedness (Fig. 7). Following removal of clusters with unclassified utility, sample size was 82.

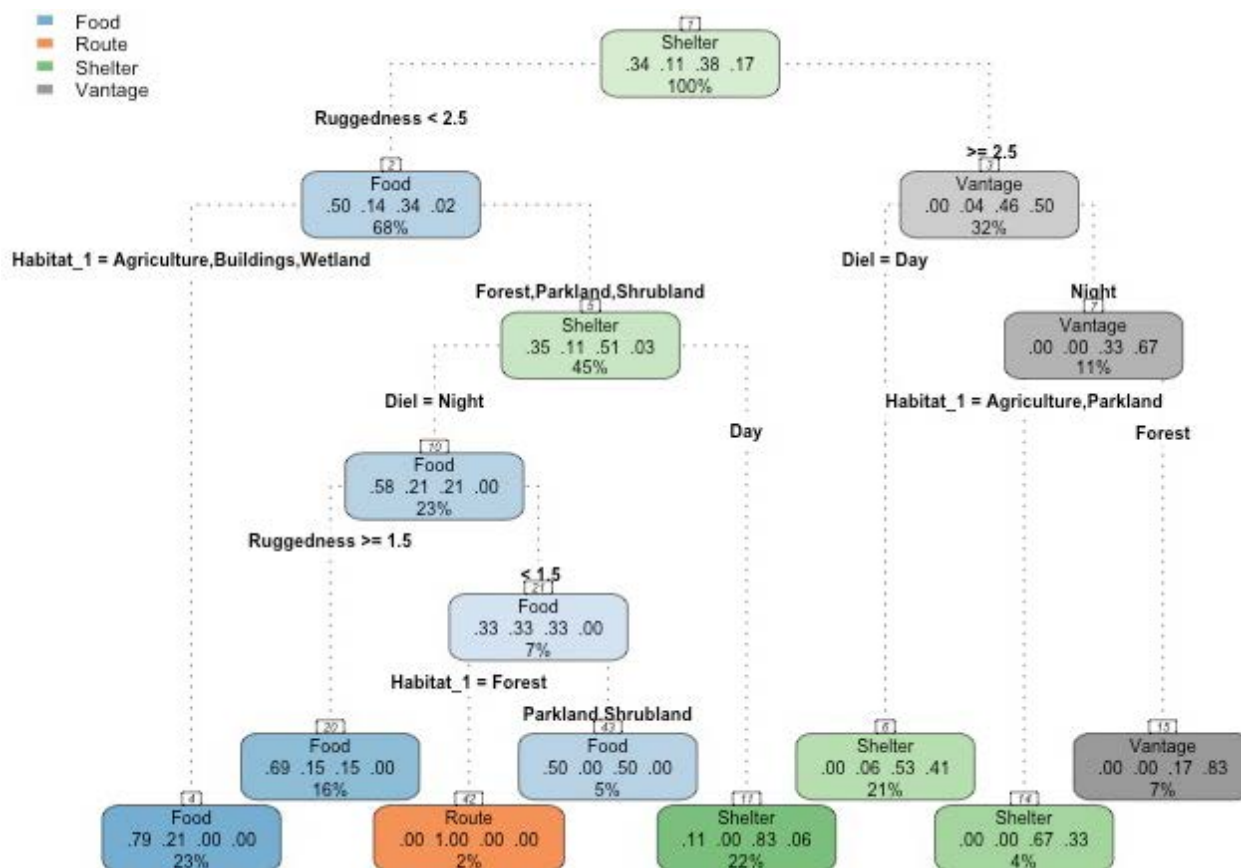


Figure 7: Classification tree predicting cluster utility (Food, Shelter, Route or Vantage) by habitat type, site ruggedness and diel phase. Each node details the classification probability of each utility at that node in order: **Food, Route, Shelter, and Vantage**. $N = 82$

Terrain ruggedness was used in the primary split to predict cluster utility. Clusters in the most rugged terrain (>2.5) are predicted to be either a vantage points or shelter. Clusters in

flatter terrain (<2.5) are predicted as food or, if located in forest, parkland or shrubland during the day, as shelter. Nocturnal clusters in flat forest locations were predicted to be routes. Using the habitat metrics at clusters of unclassified utility, the classification tree (Fig. 7) predicted the nine unclassified clusters as two routes, three food sources and four shelter locations.

3.5 Recursive use and residence time at clustered positions

Because diel phase, season and age were significantly correlated ($|r| \geq 0.5$, $p = <0.001$), as was ruggedness and site utility ($r = 0.56$, $p = <0.001$), I did not combine these variables together in any one model.

3.5.1 Recursive Use

Table 4: Evaluation of GLMMs to assess the relationships between intrinsic and extrinsic factors on the number of visits to a cluster location. The five best models and the Null model are included for comparison. All models are negative binomial distributed and include Fox ID as a random effect. Candidate models included Sex, Season, Diel Phase, Sightability, Canopy Openness, Distance to Human Habitation, Ruggedness, Habitat type and Utility as fixed factors.

# Visits ~	df	AICc	Δ AIC
Ruggedness	4	812.6	0.00
Ruggedness + Season	5	812.9	0.37
Ruggedness + Sex	5	813.1	0.55
Ruggedness + Diel phase	5	813.5	0.94
Ruggedness + Sightability	5	814.7	2.14
Null Model	3	815.7	3.14

Table 5: Model averaged coefficients and standard errors of the variables included in the four best models (Δ AIC <2) explaining number of visits to cluster locations. RI is the relative importance of the variables.

# Visits ~	β .	SE	Adj. SE	z	RI	P
Intercept *	-1.5	0.26	0.26	5.82	-	<0.001
Ruggedness	-0.21	0.09	0.09	2.31	1	0.02
Season=Winter	0.29	0.20	0.26	1.40	0.26	0.16
Sex=Male	-0.27	0.21	0.21	1.30	0.24	0.19
Diel=Night	0.16	0.15	0.15	1.11	0.19	0.27

*Female fox on flat terrain (ruggedness =1) in diurnal phase during summer season.

Terrain ruggedness, season, diel phase and sex of the fox were identified as the most influential factors affecting recursive use of cluster locations as indicated by model selection (Table 4). The coefficients of model averaging from the four best models are listed in Table 5. The most important variable was the ruggedness of cluster locations, suggesting that clusters locations in flat terrain received more recursive visits. The models also suggest that recursive site use was greatest at night and during the winter. Female foxes also tended to visit cluster locations more often than males; although apart from ruggedness, these relationships were not statistically significant.

3.5.2 Residence Time

According to AICc model selection, variation in number of consecutive positions at cluster locations was most influenced by both diel phase and sightability (Table 6).

Table 6: Evaluation of GLMMs to assess the relationship between habitat characteristics and Diel phase on the number of consecutive positions following the initial visit to a cluster. Lists the five best and null model for comparison. All models are Poisson distributed and include Fox ID as a random effect. Candidate models included Sex, Season, Diel Phase Sightability, Canopy openness, Distance to human habitation, site ruggedness, habitat type and cluster utility as fixed factors.

# Consecutive positions ~	df	R ² m	AICc	ΔAIC
Diel Phase + Sightability	4	0.13	525.6	0.00
Utility + Diel Phase + Sightability	8	0.14	527.8	2.15
Utility + Diel Phase + Sex	8	0.14	529.1	3.46
Utility + Diel Phase	9	0.16	530.4	4.73
Utility + Diel Phase + Ruggedness	8	0.14	530.6	4.92
Null Model	2	0.00	562.5	36.83

Table 7: Coefficients of the best model (ΔAIC <2) explaining consecutive positions at cluster locations. Response is offset by the total number of positions in each cluster. Fixed effects include Diel phase and horizontal sightability at each site. Individual fox id is included as a random effect.

Variable	β	SE	z	P
Intercept*	-1.08	0.09	-12.26	<0.0001
Diel Phase=Night	-0.67	0.12	-5.49	<0.0001
Scale(Sightability)	-0.16	0.05	-2.93	0.003

*Diurnal phase, lowest sightability.

The coefficients of the model suggest that nocturnal clusters are occupied for less consecutive positions than diurnal clusters, and that sites with greater horizontal sightability also receive significantly less consecutive positions (Table 7). 13% of the variance was

accounted for by these variables ($R^2_m = 0.13$). These trends are evident in the data plotted in Fig. 8.

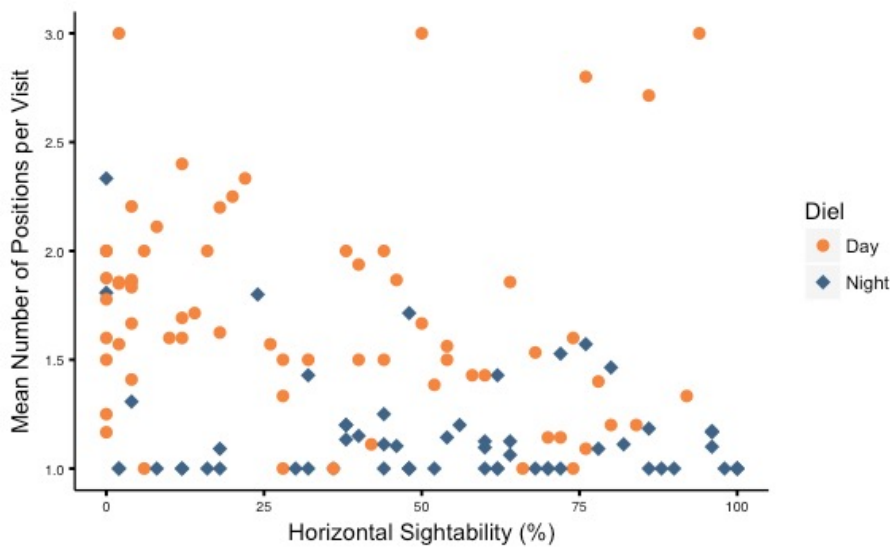


Figure 8: The relationship between sightability and diel phase and the mean number of recorded positions in clusters per visit.

3.6 Intervals

At the four hourly fix schedule, the mean interval between cluster positions was 10.1 hours (IQR = 4 - 12, Fig. 9). This equates to an average rate of 2.38 (out of six total) positions at any cluster per day. This supports that visits to these locations were routine, but a significant proportion of time was also spent elsewhere.

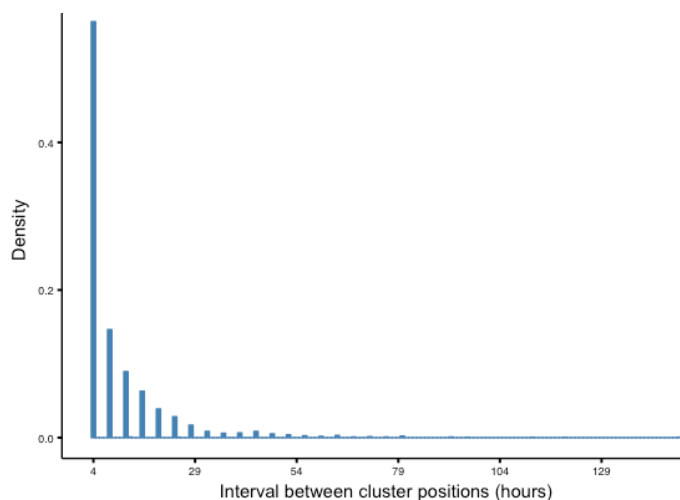


Figure 9: Histogram shows the frequency density of interval periods between all clustered positions. Does not distinguish between consecutive and non-consecutive cluster positions. Minimum fix interval is four hours due to collar schedule.

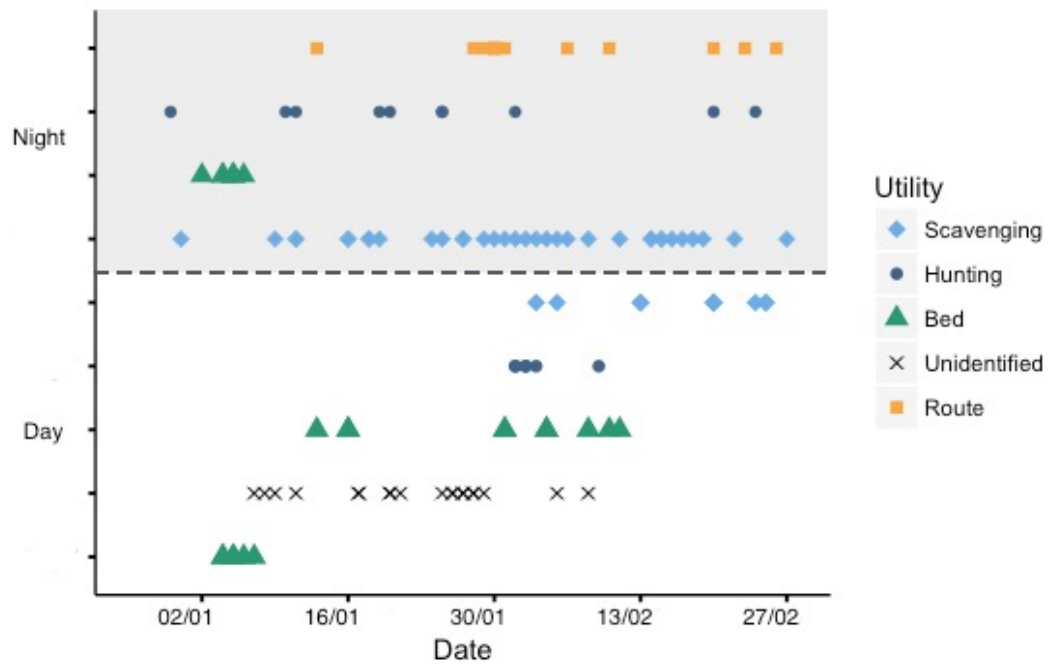


Figure 10: The recorded positions in clusters over time for one male fox (Mattias) during the winter study period. Y-axis separates the nine individual cluster timelines. These are divided into nocturnal clusters above, and diurnal clusters below. Based on habitat, site ruggedness, and diel phase the classification tree predicts the utility at the unidentified cluster to that of Shelter.

4. Discussion

I found significant clustering in recorded positions, providing evidence that red foxes use space highly disproportionately. On average 43% of total recorded positions were clustered within relatively small proportions (1.1%) of their maximum range extent (100% MCP, Table 1). These aggregations of positions were significantly greater than would happen by random occurrence (Fig. 4), and non-homogenous space use is in line with previous observations that the red fox's home range is made up of distinct zones that are occupied more intensively than others (Ables 1969, Macdonald 1983, Lucherini and Lovari 1996, Pandolfi et al. 1997).

The activity sensors integrated in the GPS collars confirmed that foxes follow a well-defined circadian rhythm, as observed in previous studies (Díaz-Ruiz et al. 2016). Motion was on average less during the daylight hours, suggesting that red foxes are making greater or more frequent movements at night, and are resting during the day. There were a number of outlying recordings during the day that did not fit this trend (Fig. 2). However, these could be attributed to any manner of movement during the time taken to fix position, such as scratching, grooming, shaking or disturbance. They may also serve as precursory reminder that red fox behaviour can be highly variable given their adaptive nature.

During the winter foxes ranged outwards considerably further at night than during the day. This was not due to greater outward excursions in winter, as might be expected due to prolonged darkness or reduced prey densities, but rather the generally more confined daytime movements in comparison to summer. This pattern is illustrated by the example of two female foxes (Fig. 5). Red foxes are widely considered to be facultative nocturnal. A degree of crepuscular behaviour is not uncommon however (Ables 1969, Servin et al. 1991, Doncaster and Macdonald 1997), and has been attributed to synchrony with prey activity patterns (Díaz-Ruiz et al. 2016). A good spatial and temporal memory may allow predators to adjust their movement strategy according to the behaviour of their prey (Lima 2002). Increased prey availability in summer, in concert with shorter nights, may necessitate an increase in crepuscular behaviour. However, for red foxes in anthropogenic habitats where prey densities may indeed be higher (Moreno et al. 1996), crepuscular activity may carry the increased risk of human persecution. Fox activity still peaked around the darkest hours in summer (Fig. 2), but activity patterns were less clearcut early in the mornings when I would expect prey activity to be greatest (Díaz-Ruiz et al. 2016).

Whilst visiting clustered positions, I attributed site utility to a broad range of probable events. From chicken coop raids to rearing cubs, these were broadly classified as Food, Shelter, Vantage points or Routes. There was no general difference in habitat classification between clustered and non-clustered positions, which confirms that clustering was a result of more than habitat heterogeneity. Indeed, utility at cluster locations were quite distinguishable in comparison to that of non-clustered positions (Table 3). Specifically, at clusters I discovered more beds, dens, and clumped food sources. Construction of classification trees (Fig. 7) revealed that clusters around buildings or in agricultural or wetland habitats, were most likely to be related to food sources. Diurnal clusters in most habitats were most likely attributed to shelter, or in the most rugged terrain, to distinct highpoints and outcrops, presumably used as vantage points for surveillance (Wam et al. 2012). Nocturnal clusters in forests, parkland and shrub were also related to food. Clumped food sources, at farms or baiting stations for wild boar, highlight how human activity may subsidise red fox numbers, particularly over periods of decreased prey.

It was not possible to identify utility at all locations and 7% of clusters and 45% of non-clustered positions remained unclassified. This was not surprising as visits were carried out following a delay of up to three months from the start of the sampling period. 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 example, carcass remains may be the result of hunting, scavenging or may have been relocated to a cache. Distinguishing between the three is difficult, hence all clusters of this nature were classified broadly as 'food'. A proportion of clusters could also have simply occurred by random occurrence (Fig. 4). I used the classification tree to predict the utility of the unclassified clusters to be shelter, food or routes. The cluster of unclassified utility in Fig. 10, for example, was predicted to be shelter. The fact that this cluster fits the period of time when the other identified shelter locations were not visited, reaffirms the validity of this prediction. However, predictive accuracy was 67%, suggesting that the sample size was too small for training of more accurate models. On the other hand, it is probable that red fox behaviour doesn't always follow general rules relating to habitat characteristics, or time of day.

As distinguished by the classification trees, I found notable differences in attributed utility of clusters between diel phases. Indeed, the timing and geographic location of these focal points was significantly related. Terrain ruggedness, horizontal vegetation density (sightability) and

distance to human habitation were, on the whole, greater during the day than at night (Fig. 6). These predictions confirm that red foxes do indeed demonstrate an aversion to flat, open habitats in proximity to humans during the day. They also signify that the contrary is true; foxes capitalise on anthropogenic habitats and resources at night.

Memory provides many advantages to animals at several landscape scales. At large scales, spatial memory aids in landscape navigation and is vital to the creation of a cognitive map. Locally, benefits may include the informed choice of safe resting spots, den sites or proven foraging patches. Indeed, habitat selection is a form of memory, and will strongly effect how animals move through the landscape. In habitat mosaics of intermediate complexity such as rural landscapes, remembering these locations and attributes will accrue fitness benefits (Fagan et al. 2013) through efficient and safe navigation or optimal foraging strategies. Where renewable resources are patchily distributed in space or time, a good spatial and temporal memory allows for systematic returns to foraging sites, which allows foragers to capitalise on resource recovery rates, a concept termed ‘trap-lining’ (Berger-Tal and Bar-David 2015). Red foxes are also known to cache surplus food that they return to for consumption at a later date. In short, recursive clustering patterns infer memory and memory maintenance (Fagan et al. 2013). The clustering I identified in this study was a combination of both recursion and extended residence times.

Recursions to cluster locations were most influenced by site ruggedness, season, sex and diel phase. Cluster locations on flatter ground received significantly more revisits than those in rugged terrain. In the study area flatter terrain is more likely to be bog and wetland, or more productive ground used for agriculture and human settlement. As identified previously (Fig. 7), clusters in these habitats were probably related to food. Model averaging also implied that foxes are more recursive at night or in winter, and that female foxes demonstrate greater recursion than males (Table 5). However, these relationships were not statistically significant. This, and the fact that cluster utility was not included in the best models to predict cluster visits, confirms initial preconceptions that red fox behaviour is highly variable. Red foxes are intelligent and adaptive organisms living in a dynamic landscape, and this lack of predictability only emphasizes their individual and adaptive behaviour that is integral to their success. The number of visits to any return location may be limited by any number of confounding interactions. As illustrated by the cluster timeline (Fig. 10), clusters are dynamic and either evolve or cease with time. Resources such as carrion, prey density and other food resources may be temporally pulsed (Gomo et al. 2017) and visits to visited

reliable food sources may be intermittent or sporadic in response to foraging strategies or fear of disturbance (see following sections). In addition, this study does not take into account the interactions and competition with other resident foxes. The resource dispersion hypothesis (RDH) asserts that if resources patches are heterogeneous in space or time, and their quality is sufficient for maintenance of multiple individuals, group living is possible and may in fact confer fitness advantages (Macdonald 1983, Johnson et al. 2002). Where foxes share space there is likely to be a dominance hierarchy around patches of higher quality; foxes of lower status might have to move about more, and visit less predictable patches (Dorning and Harris 2017). Female foxes, especially those rearing offspring, will require efficient foraging at predictable food patches to meet the energetic demands of breeding (Gittleman and Thompson 1988). Breeding females may therefore demonstrate more frequent visits to food or den locations, which may explain the marginal trend for greater recursive behaviour in females.

The proportion of clusters that were positioned along tracks and necessary movement paths, such as fence holes or culverts, demonstrate route fidelity, indicative of a cognitive map, that has been observed in other studies of red foxes (Fabrigoule and Maurel 1982, Carter et al. 2012). These aggregations also highlight the risk of making false inferences regarding resource selection from GPS positions alone. Discrete clusters of recursive visits are not necessarily indicative of important resource locations; they may merely be product of physical landscape constraints, or the most efficient route between the memorised resource patches. With this in mind, residence time at clusters may better infer resource value.

Residence time at attractant points was most associated with diel phase and vegetation density (sightability). Extended residence times at these locations suggest that they are either resting locations, or resources that the foxes could exploit intensively whilst securely hidden by dense vegetation. The exceptions to this trend were the extended residence times during the day, at locations with high sightability (see outliers in Fig. 8). These were identified as subterranean dens in relatively open forest, or activity in arable crops that were harvested recently prior to field visits. The utility of food resources usually decreases with residence time as a consequence of resource depletion (Charnov 1976), satiation, or increased predation risk (Mitchell and Lima 2002). The fix schedule of every four hours, used in this study, is too coarse for accurate measurements of residence time in this regard. Four hours may indeed be a long time for a fox to spend in any one place. However, assuming that foxes

were still resident between consecutive positions, residence times of up to 12 hours were not uncommon especially at established shelter or dens (Fig. 8).

That fact that foxes showed fidelity to very specific shelter locations indicates resource selection decisions influenced by memory and previous experiences. For instance, a resting location that has to be proven sheltered and safe in the past may be favoured over unproven options nearby. Shelter locations have been recognised as an integral component in home range requirements and their subsequent size in a number of studies relating to RDH. Lucherini et al. (1995) suggest that the location of shelters, in relation to that of the main food patches determines the size and shape of the red fox's home range. Pandolfi (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.

Non-clustered movements:

Although foxes spent a significant proportion of time at discrete locations, they also spent an average of 57% of their time elsewhere. Absence from cluster locations was relatively short however, as recursions were relatively routine. Activity away from core areas could be attributed to patrolling, marking, hunting, or general exploratory behaviour. The extent of these movements, and seasonal differences, is illustrated by the two examples shown in Fig. 5. Of particular note is the bounded distance (or time) that these single positions appear to be dispersed around the core areas. Suggesting, perhaps, that movement away from cluster locations may be limited by strategic decisions that maintain regular returns. These might include daily visits to proven shelter locations, or returns to exploit and defend predictable foraging sites (Stewart et al. 1997).

Unless reinforced or maintained, memory will decay (Fagan et al. 2013). Movement in dynamic environments allows updates of a memorised landscape to current environmental conditions. Whilst navigating between one core area to another, foxes may take detours or exploratory routes to patrol their surroundings, perhaps seeking new foraging or mating opportunities whilst simultaneously updating their cognitive map. Absence may also be a ploy associated with 'trap-lining' strategies. Predators have been observed to improve chances of catching prey by moving away from a patch when prey reach a certain vigilance level (Brown et al. 1999, Mitchell 2009). They may then move between patches in a systematic way that allows sufficient interval periods for prey vigilance to decrease, or they

might adopt more random movements between patches that make their visits more unpredictable (Laundré 2010).

Exploratory movements also beg the question: How do foxes then find their way back home? Do they utilise visual and sensory cues or a cognitive map and ‘compass’ perhaps (Mackintosh 2002, Begall et al. 2013)? To investigate these outward movements and returns in sufficient detail, a more intensive fix schedule would be required.

Conclusions:

In this study, I reaffirm preconceptions that; unless emboldened by hunger and the cover of darkness, red foxes generally seek to avoid exposure to humans, shaping both their movement patterns and home range requirements. The degree of recursive clustering at specific daytime shelter locations highlights the importance of safe resting sites in rural landscapes. The number of recursive nocturnal visits to anthropogenic food sources, on the other hand also demonstrate how humans can subsidise red fox populations. A good spatial-temporal memory is a prerequisite for deliberate recursive movement to take place, and in concert with the red fox’s adaptable and opportunistic nature, intelligent movement strategies based on learning and memory, may maximise their fitness in heterogeneous landscapes. Route fidelity along distinct movement pathways or strategic points also infer memory, but they also serve as a reminder that high densities of recursive positions do not necessarily infer core areas or resource selection. On this basis, I advocate the importance of ground-truthing any presumed activity or behaviour that has been identified remotely.

Recursive patch use, to both shelter and clumped food sources, played a significant role in constraining red fox movements between distinct core areas, especially as intervals between cluster visits were generally short. I therefore conclude that these patterns support the concept that memory based return events lead to emergence of bounded ‘home ranges’, rather than a continuous drifting across the landscape. It would be pertinent, however, to test this across landscape gradients, in areas where resources may be more or less dispersed, and both human and fox populations vary in density.

5. Acknowledgements

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A pat on the head for Orchy, my trusted field assistant, and last but not least, a special thanks to the foxes, for getting up to all kinds of cunning mischief and dragging us to all the interesting places hidden away in the Swedish countryside. On behalf of the foxes I’d like to thank the local community of Kolmården: Tack för kyckilingarna!

6. Appendices

Appendix 1: The duration and season of the sampling period (following removal of dispersal events) for each fox individual included in this study. Table details the sex and age class of each fox. The number of successful GPS fixes is listed, as is the spatial extent of those positions in the landscape (measured by both 95 and 100% MCPs). F= Female, M = Male; SA= Sub Adult, AD = Adult; W = Winter, S = Summer

Fox ID	Sex	Age	Season	Telemetry Days	Start (D/M/Y)	End (D/M/Y)	Successful fixes	100% MCP (km ²)	95% MCP (km ²)
Charlotte	F	SA	W	41.0	15/01/17	28/02/17	246	98.5	14.9
Felix	M	AD	W	46.3	12/01/17	28/02/17	278	5.4	3.0
Artur	M	SA	W	52.5	05/12/16	30/01/17	313	4.9	2.1
Mattias*	M	AD	W	63.0	27/12/16	27/02/17	362	11.5	7.1
Jakob	M	AD	W	71.3	01/12/16	12/02/17	409	18.3	5.7
Ludde	M	SA	W	74.7	01/12/16	13/02/17	390	3.6	1.5
Inger	F	AD	W	77.0	01/12/16	15/02/17	391	4.5	1.6
Daniella	F	SA	W	89.0	01/12/16	27/02/17	324	4.1	3.7
Hen	F	SA	W	89.3	01/12/16	28/02/17	258	3.8	2.2
Maja	F	AD	S	36.0	01/05/17	06/06/17	215	5.1	3.9
Bettan	F	AD	S	38.5	01/05/17	08/06/17	221	4.3	3.3
Mattias*	M	AD	S	52.0	01/05/17	22/06/17	302	4.3	3.3
Lisa	F	AD	S	65.7	25/06/17	29/08/17	375	2.4	2.1
Josephine	F	AD	S	80.8	01/06/17	30/08/17	459	5.4	4.6
Frans	M	AD	S	121.7	01/05/17	30/08/17	710	6.5	5.7

* Fox monitored over both winter and summer study periods.

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