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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 (km²)	95% MCP (km²)
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 km² ± 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 km²) was 171.1 ± 7.5 SD positions per km² (range = 148–198). The minimum density simulated (148.9 per km²) 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).

	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)

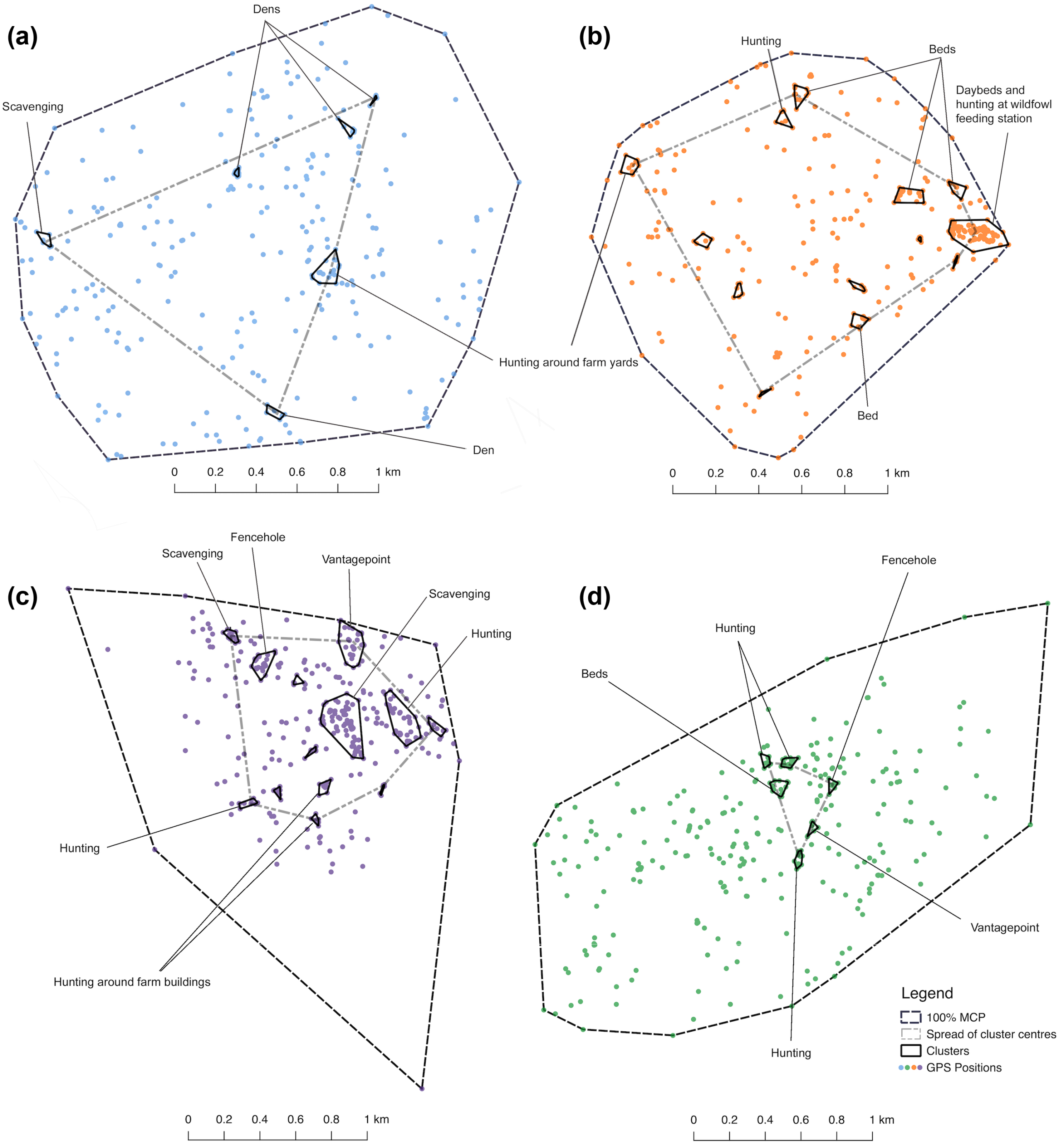

Figure 1. Illustration of the spatial dispersion and proportional area of clustered GPS positions within the 100% MCPs of two female and two male foxes: (a) F3 over 89 days in the winter, (b) F7 over 66 days in the summer, (c) M5 over 75 days in the winter and (d) M3 over 52 days in the summer.

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

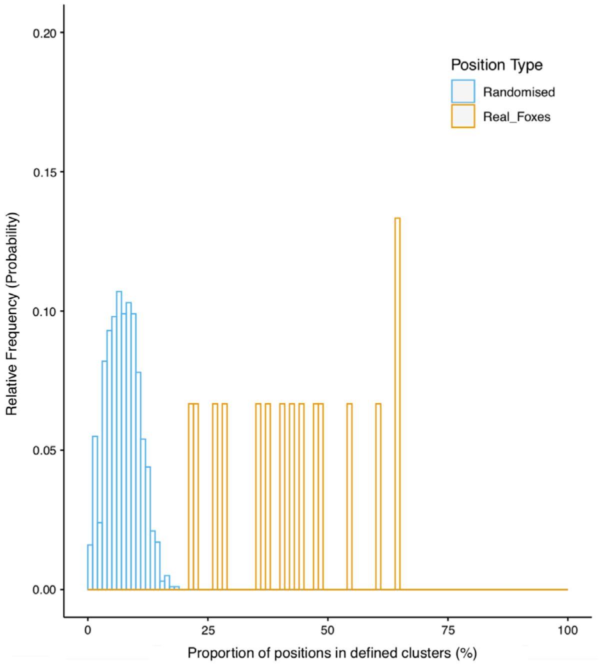

Figure 2. Results of randomisation test where the histogram shows the proportion of positions in defined clusters from real fox position data within their 100% MCP, compared to clustering of 1000 simulations of 402 randomly distributed points within the smallest sized 100% MCP (2.4 km^2).

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-

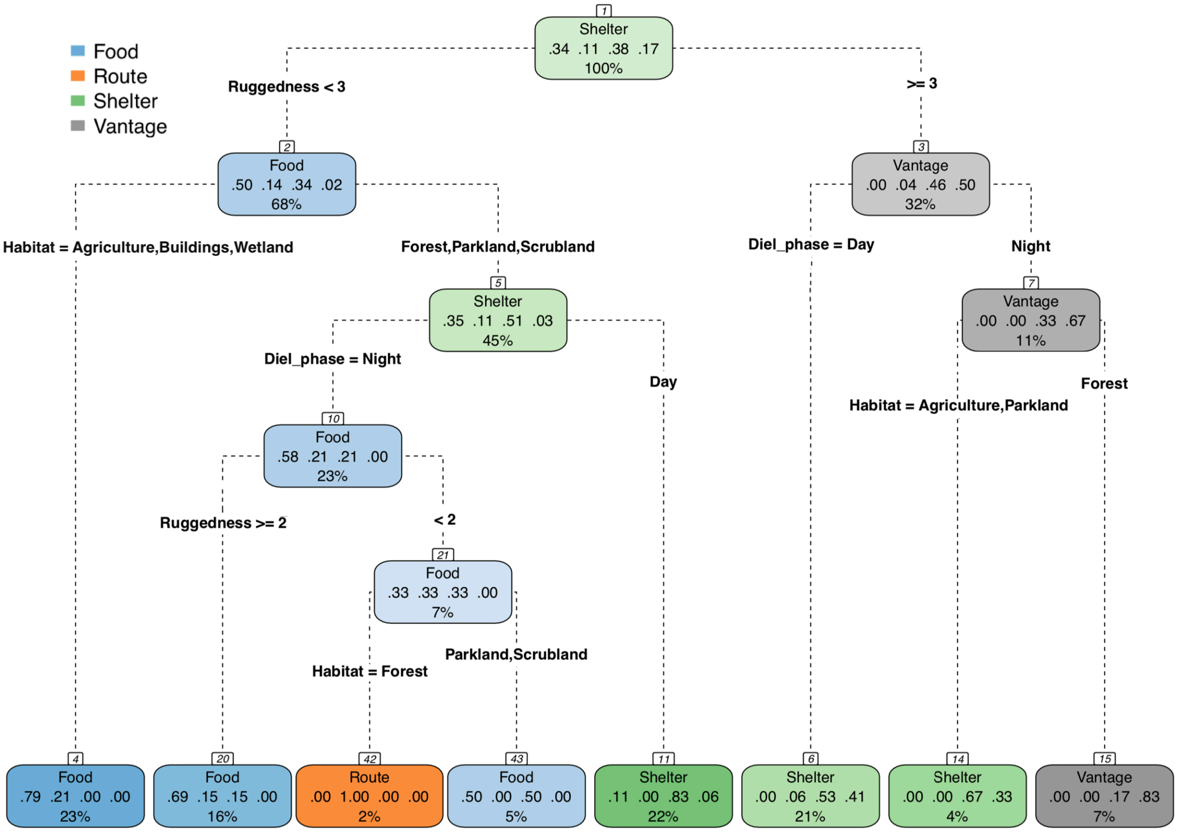

Figure 3. Classification tree predicting cluster utility of 82 red fox clusters identified as food, shelter, route or vantage, by habitat type, site ruggedness and diel phase. Each node details the classification probability of each utility at that node in order: Food, Route, Shelter and Vantage.

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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