Norwegian
University of
Life Sciences

Master's thesis 2024 45 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Spatial aspects of resting site selection by red foxes (*Vulpes vulpes)* in a cultural landscape

Kristin Hågland Hagen

Acknowledgement

This thesis was written as my final submission in my masters' degree in Natural Resource Management at The Norwegian University of Life Sciences (NMBU), under the Faculty of Environmental Sciences and Natural Resource Management (MINA).

First and foremost, I would like to give the biggest thanks to my supervisor, Richard Bischof for the great guidance, cooperation, and patience throughout my master's project. He has given me valuable experience with field work, data processing and analysis, and the writing process.

I would also like to my friends for all the help, support and motivation throughout my master thesis, and making my time at NMBU full of good memories. A special thanks to Mona, Solvei and Synne for making my last years in Ås extra special.

And last, but not least, I want to thank my family for cheering me on and giving me great support.

Abstract

The red fox (*Vulpes vulpes*) is a middle-sized mesopredator, widespread over all of Norway. With its omnivorous diet and ability to adapt and survive in various landscapes, climates, and human-made environments, the species can be found in most parts of the world. Most of the fox's activity occurs during the nighttime, and in the daytime it mostly rests. The landscape features and habitat characteristics of where the red fox rests are not as broadly studied as its foraging habits, although resting sites are also an important part of its ecological needs. This thesis explores the spatial aspects of resting site selection by foxes within a cultural landscape, by comparing resting to other activities. Through a combination of GPS tracking, field observations, and spatial analysis, the study aims to understand the factors influencing resting site selection by red foxes in human-altered environments.

The results showed that landscape features such as cover, distance to development, and distance to roads and area used for transport had a significant effect on the choice of resting sites, indicating that red foxes prefer resting in cover and is more likely to rest further away from infrastructure. There was also a trend for resting further away from forest edges. The habitat type that was most preferred for resting was forest. The probability of resting closer to infrastructure was higher in areas with cover and in forests, highlighting the importance of cover and forests for wild animals in anthropogenically influenced landscapes.

Using similar methods of GPS–tracking free-ranging animals can improve the fundamental knowledge of the ecological needs and dispersal of wild animals, which can be used to improve the management of essential habitats, such as forests. For future research, resting sites have the potential to be used in establishing home ranges of carnivores such as foxes, as resting is an important part of their biology.

Sammendrag

Rødrev (*Vulpes vulpes*) er en mellomstor mesopredator, utbredt over hele Norge. Med sitt altetende kosthold og evne til å tilpasse seg og overleve i ulike landskap, klima og menneskeskapte miljøer, er arten å finne i de fleste deler av verden. Reven er hovedsakelig aktiv om natten og bruker mesteparten av dagen til å hvile. Hva som er karakteristisk for habitatene rødreven velger som hvilested er ikke studert like inngående som revens furasjering, selv om hvilested også er en viktig del av det som utgjør artens økologiske behov. Denne studien utforsker de romlige aspektene ved rødrevens valg av hvilested i et kulturlandskap, ved å sammenligne hvile med andre aktiviteter. Gjennom en kombinasjon av GPS-sporing, feltobservasjoner og romlig analyse, tar denne studien sikte på å forstå faktorene som påvirker rødrevens valg av hvilested i landskap preget av menneskelig aktivitet.

Resultatene fra studien viste at landskapstrekk som dekkende vegetasjon, avstand til utbygging, avstand til veier og områder brukt til transport, hadde en betydelig effekt på revens valg av hvilesteder. Dette indikerer at rødrev foretrekker å hvile i skjul og vil mest sannsynlig velge hvilesteder som har avstand fra infrastruktur. Det var også en tydelig trend for å velge hvilesteder lenger unna skogkantene. Naturtypen som var mest foretrukket for hvile var skog. Sannsynligheten for å hvile nærmere infrastruktur var større i områder med dekke og i skog, noe som understreker viktigheten av skjul og skog som habitat for ville dyr i områder preget av menneskelig aktivitet.

Bruk av lignende metoder for GPS-sporing av viltlevende pattedyr kan forbedre den grunnleggende kunnskapen om de økologiske behovene og spredningen til ville dyr, som kan brukes til å forbedre forvaltningen av essensielle habitater, som skog. For fremtidig forskning har hvilesteder potensial til å bli brukt til å etablere hjemmeområder for rovdyr som rev, ettersom hvile er en viktig del av deres biologi.

Table of Contents

Introduction

According to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Service (IPBES), the main direct cause of the loss of biodiversity and ecosystem services is land-use change (IPBES, 2018). Habitat destruction endangers more species than the following threats combined: overexploitation, invasive species, pollution, and climate change (Hogue & Breon, 2022). Habitat destruction and land-use change are direct results of anthropogenic influences, such as expansion of infrastructure, increased urbanisation, habitat fragmentation, forestry, and both intensified agriculture and land abandonment (Hogue & Breon, 2022; IPBES, 2019; Schaal-Lagodzinski et al., 2024). In increasingly human-altered environments, it is important to research the impacts our actions have on wildlife to adjust our management of nature in a more sustainable way. Cultural landscapes are substantially influenced and shaped by land use, creating fragmented patches of habitats, and affecting all the species living there. In this study, spatial aspects of resting site selection by red foxes in a cultural landscape are examined, considering the behaviour of the red fox in a human-altered environment.

The red fox can live in a wide range of habitats and is a generalist with a broad ecological niche, meaning that their habitat requirements are less strict. A big obstacle to defining the suitable red fox habitat is that it is hunted by humans, and consequently, the density of foxes in an area may simply indicate the species' capability to endure human impacts rather than accurately representing the area's true habitat suitability (Lloyd, 1980). As the fox can survive despite, at times, substantial human efforts to remove it, Loyd (1980) points out that this needs to be considered particularly in "the middle range of human activity" since it is more common throughout the fox's distribution. The cultural landscape in this study can be classified as within this middle range. Accordingly, resting sites are not compared to available habitats in this study. Considering that the foxes might have adapted their behaviour to survive, not necessarily to thrive, the study instead focuses on the spatial use by foxes in cultural landscapes based on their activities and compares resting to other activities. In other words, by examining the areas already in use by the foxes, one can determine how the resting behaviour differs from the behaviour in other activities.

In Norway, the red fox is widespread over most of the country, from the coast to above the treeline, except for some islands. The home range size for a fox varies a lot, depending on habitat and food availability. In Norway, it is normally about 3-6 square kilometres (Frafjord, 2022). The home range size of red foxes in heterogeneous environments is greatly influenced by habitat richness and might be directly related to the distance between resting sites and food patches (Lucherini & Lovari, 1996). The location of resting sites seems to be more important in the establishment of the home range than previously thought (Meia & Weber, 1993). The red fox is a night-active predator, meaning that most of their activity takes place during the night, hunting and scavenging for food. During the day they are mostly resting and sleeping, using dens or resting places. Dens are more studied than resting sites in general (Hewson, 1986) because dens are not only used for resting and shelter but are an essential part of their reproduction, as foxes are so-called underground denning species (Walton & Mattisson, 2021). Dens are often dug by the fox itself, preferably in sand or gravel, but it can also be in a scree or under the root of a tree (Frafjord, 2022). The nocturnal resting sites are often found in proximity to or in the same area where they do their nightly activities, such as foraging, and are mostly above ground (Meia & Weber, 1993). The diurnal resting sites are more studied because this is the time they are most stationary, with resting as the main "activity." In this study, the resting sites are not identified as nocturnal or diurnal resting sites.

There are not many studies on resting sites, both above ground and in dens, in cultural landscapes and their distance to infrastructure. However, a study on fox den distribution predicted den occurrence using resource selection functions (RSFs) at different habitat scales, including agricultural land. The study found that distance to roads negatively influenced fox den occurrence, and that den occurrence was negatively related to forest cover and positively correlated with shrub cover (Zaman et al., 2020). Fox resting sites have been shown to not be evenly distributed within their home range, but in the periphery and away from the most travelled areas, showing that foxes use different areas for resting compared to other activities (Meia & Weber, 1993).

In more rural areas the foxes do not rest close to buildings (Meia & Weber, 1993). However, in urban areas, it has been found that back gardens and allotment gardens were the most favoured habitats for diurnal rest sites (Saunders et al., 1997) as they may represent the quiet habitats in the area. In areas somewhere between rural and urban, their diurnal resting sites are mostly in forests, some in habitats with cover/dense vegetation (reedbeds), and just a few foxes rest inside settlements (in gardens).This indicates that natural habitats such as forests are preferred resting places where this is available and that cover or dense vegetation is a very important requirement for being selected as a safe resting site (Janko et al., 2012).

When it comes to resting site types, dens are usually in places where there is little to no cover (Carter et al., 2012), whereas resting sites above ground are in places with abundant cover. There can be individual differences in the choice between these resting site types (Meia & Weber, 1993). In this study, the individual differences are included in the analysis to see if there is a variation among individuals, but the concrete differences, like individual preferences, are not being studied.

Other variables that may influence the choice of a resting site are season and weather. However, in Meia and Weber's research (1993), weather did not have an influence except in extreme conditions. While dens were more frequently used during the winter season, there were some individuals who preferred dens over resting places above ground regardless of the season. Still, there are not many studies indicating that season and weather influence the choice of resting site, and it is not included in this study.

This study uses GPS collars that create high-frequency position data. This provides detailed position information, making it easier to locate resting sites. Tracks and traces after the fox are easier to find shortly after the fox's activity, making it simpler to examine what type of activity the fox was doing at the site. A downside of using GPS to find resting sites is that dens are more difficult to locate because of the loss of signal underground. Here, all the resting sites, both above and below ground, are included, but there is no statistical analysis on whether there is selection of specific resting site types.

In this study, red foxes are captured and GPS collared, tracking their activity. This is followed by field observations at the sites where foxes have been, to determine the type of activity. The collected data is used in spatial analyses in RStudio, using generalised linear mixed models (GLMM), comparing resting sites to other activities. In the analysis, the effects of these variables are measured: habitat type, cover, distance to forest edge, distance to development, and distance to roads.

Research question:

What are the landscape features and characteristics associated with the resting sites of red foxes?

Predictions:

1. Red foxes in cultural landscapes prefer resting sites in forests and places with coverage.
2. Red foxes in cultural landscapes choose to rest in places far away from infrastructure, in this case meaning areas used for transport and development.

Materials and methods

Study area

The study area is, for the most part, stretching across Ås (59°39.6′–59°42.7′N, 10°43.8′–10°47.7′E) and Vestby (59°34.0′–59°38.3′N, 10°38.8′–10°43.5′E), at elevations 0–152 m.a.s.l., in southern Norway (Bischof et al., 2019). The total area of Ås and Vestby combined is 236.65 km² (Statistics Norway, 2024). The population density is on average 182 inhabitants per km² (Statistics Norway, 2024). The population is mostly concentrated around towns and residential areas, with the rest at farms and single houses scattered across the area. The whole landscape is impacted by human activities and land use, with a high road density and 31% cultivated land (Bischof et al., 2019). This cultural landscape consists of very fragmented forest patches, which is also a subject for forestry, as approximately 42 km² of 45.67 km² is defined as productive forest area (Statistics Norway, 2024). January and February are the coldest months of the year, with average temperatures at −1.0°C and 0.3°C, while July and August are the warmest, with average of 16.7 °C and 15.7 °C. The average total yearly precipitation is ca. 896 mm (Wolff, 2024). Hunting red foxes is permitted in the whole country, from the 15th of July to the 15th of April, which is outside the period when vixens give birth to and raise puppies (Miljødirektoratet, 2022).

Map of the study area

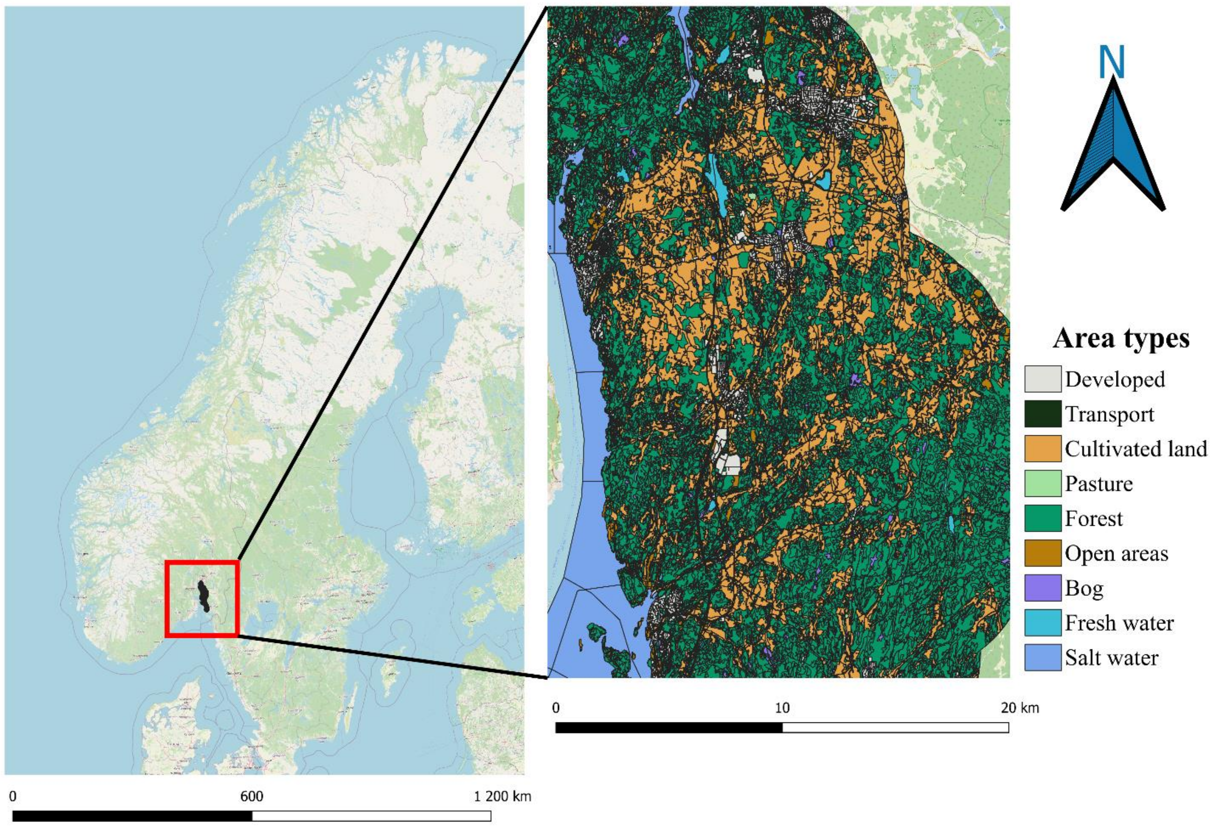

Figure 1. Maps of the study area, situated in southern Norway (left map), mostly in Ås and Vestby (right map). The map on the right shows the area types found in the study area. The background map is OpenStreetMap (from https://tile.openstreetmap.org/{z}/{x}/{y}.png), and map layer with area types is from NIBIO.

Collecting spatial data about fox activity using GPS collars

All the data used in this study is provided by the Fox Project at the Norwegian University of Life Sciences (NMBU) in Ås. For further details regarding the methods, GPS collars, and data collection, I refer to Bischof et. al. (2019). The study is approved by the Norwegian Animal Research Authority (FOTS 8415/17790/24392/30326) with the endorsement of the Norwegian

Food Safety Authority. The capturing and handling of the foxes followed the rules and regulations in Norway.

Foxes were captured using big box traps of wood (size about 200 cm × 80 cm × 80 cm), with two trapdoors. Meat, mostly chicken (*Gallus gallus domesticus*), was used as bait in the traps. The traps were monitored daily. The traps are standard traps permitted by Norwegian regulations for capturing small and medium-sized carnivores (Miljødirektoratet, 2024a). Upon finding a fox captured in a trap, a team of two to four people was gathered. No anaesthesia was used in the process of handling the foxes. Instead, while attaching a GPS collar and collecting additional data about the fox, the handlers used thick gloves, a catch pole, and/or neck tongues, as well as a dark cloth to cover the eyes of the fox to mitigate their stress. Information about the fox, such as gender, weight, age, and general health condition, was measured and documented. Hair and scat samples were collected for DNA analysis. The entire handling process took about 10-20 minutes per fox. It was performed with care and caution to avoid afflicting the fox with unnecessary stress.

Small and lightweight GPS devices were built by the Fox project, with off-the-shelf components on a customised printed circuit board and a standard (8-bit ATmega 328p) microcontroller. The device contained a SIM808 GSM/GPRS module from SimCom™, including GPS, General Packet Radio Service (GPRS), and Bluetooth functions. The module has specialised software adapted to endure harsh environments. An active GPS collar could be controlled using any type of basic mobile. Raw data were sent through GPRS to a server and stored. The GPS unit and lithium polymer batteries (3000mAh) were contained inside a 3D-printed plastic case (7cm × 4cm × 4cm) and attached to a 2cm wide and 1mm thick collar. The collar had a cotton string to it so that the collar would naturally fall off after a while of wearing and tearing. The total weight of a GPS collar was 123 g, less than 2.3% of the average body weight of the foxes in the study. By 2023, a smaller (6.5 × 4 × 2 cm) and lighter (76 g) GPS was in use, with a collar design like the previous model (Iversen, 2024).

The GPS collars produced 20 position fixes in bursts with inter-fixed intervals of 15 seconds and 10 to 60 minutes between each burst. The positions collected within 24 hours after foxes were released were removed to diminish possible primary effects of capture and handling on their movement and behaviour. KML files were generated from the data, including position points and tracks, and uploaded to Google Earth. A cluster was defined as a minimum of 5 successive position points gathered in an area of circa 20 meters, meaning that the fox spent some more time there to interact with or inspect any specific feature (Toverud, 2019). The clusters produced as foxes had been at a location were visited within a week after the fox activity but not too soon to interfere with their behaviour. The cluster visitation followed a protocol and gathered information to find the likely activity of the fox at the site. For further details about cluster visits, I refer to Toverud (2019).

Resting site definitions

In this analysis, these definitions are used on the sites used by foxes for resting or sleeping (resting site types): “bedsite near tree,” “bedsite root fallen tree,” “covered bedsite,” “open bedsite,” “burrow den,” “rock den,” “root den.”. A ‘bedsite’ is here defined as a resting place above ground, either without any coverage in an open bedsite, with cover in a general term (covered bedsite), or next to or under covering structures such as a tree or the roots of a fallen tree. While ‘den’ is defined as an “enclosed structure” (Carter et al., 2012), here underground as a burrow, under a rock, or under roots. In this analysis, both bedsites and dens are considered resting sites, as the activity at the site is ‘resting,’ and since the fox activity in this project is outside the period when vixens give birth to and rear puppies in springtime, the dens are not used as natal dens at the time.

Habitat types

The habitat types used in the analysis are based on the land resource map AR5 from NIBIO, fitted to scale 1:1000 and up. This map is a comprehensive nationwide dataset, where land area is divided by area type, forest quality, tree species, and soil conditions (NIBIO). The habitat types are selected from the area types, with the codes: 11, 12, 21, 23, 30, and 50. Although there are more habitat types in the map, these are the only ones included in the analysis, based on the fox activity. They have the following definitions from NIBIO BOK 5 (5) 2019 (Ahlstrøm et al., 2019) in table 1. Note that the term 'transport' is used from here on instead of area used for transport.

Table 1. Code and definition of area types used in the analysis (Ahlstrøm et al., 2019).

Code	Area type	Definition
11	Developed land	Area that is developed or significantly developed, as well as adjacent areas that are functionally closely related to the developed area.
12	Transport	Area used for transport (mainly roads and railways).
21	Fully cultivated land	Agricultural area that is cultivated to normal ploughing depth, and can be used for field crops or meadows, and that can be renewed by ploughing.
23	Pasture	Agricultural area that can be used as pasture, but that cannot be harvested mechanically. At least 50% of the area must be covered by approved grass species or grazing-tolerant herbs.
30	Forest	Area with at least 6 trees per hectare that are or can grow to 5 metres tall, and these should be evenly distributed over the area.
50	Open land	Land that is not agricultural land, forest, developed land or area used for transportation.

Data analysis and statistical tests

RStudio (version 2024.09.1) with all the necessary associated packages was used for all the statistical analyses.

The field data from cluster visits was the main dataset with coordinates for each cluster, including type of activity and other information about the cluster sites. This included all previous data from the fox project, with a total of 490 observations. After intersecting the dataset with AR5, using st_intersection from the sf package to extract the habitat/area type for each cluster, and removing data with unknown activity, the dataset had 252 observations left. The “cover” variable with the values TRUE and FALSE was made by using the ifelse function with the two habitat types, 23 (pasture) and 30 (forest). The distance from each cluster to development, transport, and forest edge was calculated using st_distance from the sf package, as well as the habitat types 11 (development), 12 (transport), and 30 (forest). This created the three variables: distance to developed, distance to transport, and distance to forest edge, which was measured in meters. The response variable “resting” with the values TRUE and FALSE was created by taking the clusters with the activity “resting” under “possible.activity1” or “possible.activity2” and making them “TRUE.” All other activities: drinking, foraging, herbivory, hunting, patrolling territory, scavenging, scent marking, and wandering through the area became labelled “FALSE.”.

The statistical analyses were performed using generalised linear mixed models (GLMM) using glmer from the lme4 package. This was done to assess whether the resting sites are associated with different habitat types and landscape features, such as distance to development, transport, and forest edge, compared to the location of clusters with other activities. The GLMMs included the difference between individual foxes, using fox ID as a random effect.

To check for correlation between variables, Pearson's product-moment correlation analysis was performed (using cor.test()), with all the combinations of the numeric variables distance to developed, distance to transport, and distance to forest edge. Scaled versions of these variables were used in the GLMMs.

Two models were made, one with habitat type as the ‘main variable’ (Model 1) and the other with cover (Model 2). For both the GLMM analyses, the model with the lowest AIC value was chosen. P-value 0.05 was automatically put as the significance threshold. The cover model that was chosen included cover (FALSE/TRUE), distance to developed areas, and distance to forest edges as predictors (fixed effects). The reference (intercept) of this model was cover = FALSE. The habitat type model included habitat type (the types are described in Table 1), distance to transport, and distance to forest edge as predictors (fixed effects). The habitat type used for reference (intercept) in the GLMM analysis was automatically habitat type 11 (developed land).

Predictions were made for the GLMM results using the average value of the distance variable that had the least effect, which was distance to forest edge in both cases. 96% confidence intervals were made of the predictions. Then ggplots of the predicted probabilities were made, using the variable that had the strongest effect together with cover type or habitat type, displaying the predicted probabilities of foxes resting under those conditions.

Results

Data summary

Identified clusters from GPS data from 21 red foxes, captured between 2018 and 2024, were used in the analysis. Fox numbers 1 to 5 were excluded from the analysis because they were not tracked using high-frequency GPS bursts and thereby did not provide adequate data for fine-scale studies. Fox 28 and 40 were also excluded from the analysis due to lack of data. In summary, the GPS data used for the analysis came from 21 foxes, 12 males and 8 females. The average monitoring period for these foxes was 17.26 days (SD ± 9.63), with an average of 3952.55 (SD ± 1386) position bursts and position fixes with an average of 241.1 (SD ± 91). Extended information on the individual foxes in the study is shown in table 2.

Table 2: Table of summary for all the foxes used in the analysis.

ID	Sex	Age	Body weight (kg)	Date collared	Data days	Number of bursts	Number of position fixes
Fox 6	Male	Adult	7.9	18.01.2018	15.2	2079	106
Fox 7	Male	Adult	6.2	10.02.2018	11.5	3365	173
Fox 8	Male	Adult	6.4	21.02.2018	5.2	3042	177
Fox 9	Male	Adult	5.9	22.02.2019	9.7	3565	189
Fox 11	Female	Juvenile	4.1	21.09.2018	11.4	4725	251
Fox 12	Male	Adult	6.5	12.11.2018	13.7	2314	188
Fox 13	Female	Adult	6.4	08.12.2018	11.5	3191	241
Fox 14	Male	Adult	5.5	09.12.2019	15.0	3569	255
Fox 15	Female	Adult	5.5	13.12.2018	13.6	4908	270
Fox 16	Male	Adult	5.5	17.10.2019	11.6	4850	265
Fox 17	Female	Adult	4.6	10.03.2019	10.1	5697	292
Fox 18	Female	Adult	4.3	24.03.2019	14.8	3851	236
Fox 19	Female	Adult	6.4	07.12.2018	26.0	4714	245
Fox 20	Male	Juvenile	5.5	09.12.2018	17.7	2822	190
Fox 21	Female	Juvenile	*NA*	13.12.2018	28.0	3693	230
Fox 22	Male	Juvenile	5.5	17.01.2019	21.3	4455	242

Fox 30	Female	Adult	6.6	24.01.2023	25.1	3153	226
Fox 31	Male	Adult	6.7	08.02.2023	4.9	1505	102
Fox 32	Male	Adult	7.6	21.02.2023	36.2	6918	463
Fox 33	Male	Juvenile	5.7	02.02.2023	42.7	6635	481

In total, 74 resting sites were used for the analysis, and most of the resting sites were in forests (57 of 74). Developed land and open areas had only one resting site each, and two resting sites were found on roads (transport). The dominating resting site type was 'open bedsite,' followed by 'covered bedsite,' and 'bedsite near tree.' Further details on resting site types are shown in Table 3.

Table 3: The number of resting site types in each habitat type and resting sites in total.

Resting site type	Developed land	Transport	Fully cultivated land	Pasture	Forest	Open areas	Total
Bedsite near tree	0	1	1	0	12	0	14
Bedsite root fallen tree	0	0	0	0	2	0	2
Covered bedsite	0	0	3	0	12	0	15
Open bedsite	1	1	3	1	22	1	29
Burrow den	0	0	1	0	3	0	4
Rock den	0	0	1	1	2	0	4
Root den	0	0	0	2	1	0	3
Total rest sites	1	2	9	4	57	1	**74**

As shown in table 4, most of the cluster observations were from fox activities other than resting (resting = FALSE), and they had a lower average of distance to transport and to development (except for distance to transport in habitat type 23) than the resting sites. For distance to forest edge, there were mixed results between resting and non-resting sites, depending on the habitat type.

Table 4: Summary of cluster observations (n), with mean and standard deviation (SD) of the distance between cluster locations and transport, developed and forest edge, based on habitat type (11 = developed, 12 = transport, 21 = fully cultivated land, 23 = pasture, 30 = forest, 50 = open land) and separating between resting sites (TRUE) and clusters with other activities (FALSE).

Habitat type	Resting	n	Mean dist. transport (SD)	Mean dist. developed (SD)	Mean dist. Forest edge (SD)
11	FALSE	25	31 (33.1)	0 (0)	49.3 (56.7)
11	TRUE	1	29.7	0	172
12	FALSE	1	0	163	22.1
12	TRUE	2	0 (0)	143 (191)	2.1 (1.32)
21	FALSE	35	76.2 (73.7)	119 (89.5)	56.5 (67.8)
21	TRUE	9	119 (76.2)	160 (94.3)	74.8 (85.5)
23	FALSE	11	153 (71.6)	114 (79.6)	87.4 (62.2)
23	TRUE	4	194 (83.4)	48.3 (15.4)	54.5 (44.5)
30	FALSE	98	106 (82.8)	130 (112)	31.5 (39.6)
30	TRUE	57	142 (106)	171 (139)	43.6 (39.5)
50	FALSE	8	91.4 (66.3)	107 (72.5)	66.6 (72)
50	TRUE	1	29.5	154	27.3

Correlations

The results from Pearson's product-moment correlation analysis are shown in Table 5. The correlation test for distance to transport and distance to developed gave an extremely low p-value (< 2.2e-16), strongly suggesting that the null hypothesis is rejected and that there is a relationship between these two variables. The Pearson correlation coefficient (≈ 0.6) indicates a moderate positive correlation between distance to transport and distance to developed. The correlation test for distance to transport and distance to forest edge gave a low p-value (0.001228), suggesting that there is a relationship between these two variables as well. The Pearson correlation coefficient (≈ 0.20), however, indicates a weak positive correlation between distance to transport and distance to developed. The same conclusion can be drawn about the correlation test for distance to developed and distance to forest edge, with a low p-value (0.002607) and a low positive Pearson correlation coefficient (≈ 0.19).

Table 5. Results from the correlation test between the variables distance to transport, distance to developed, and distance to forest edge, including the values of test statistic (t), degrees of freedom (df), P-value, confidence interval (95%), and Pearson correlation coefficient (cor).

	Test Statistic (t)	Degrees of Freedom (df)	P-value	Confidence Interval (95%)	Pearson correlation coefficient (cor)
Distance transport +distance developed	11.865	250	< 2.2e-16	0.5148224 - 0.6738077	0.600211
Distance transport +distance forest edge	3.2698	250	0.001228	0.08096594 - 0.31812438	0.2025126
Distance developed +distance forest edge	3.0413	250	0.002607	0.06687208 - 0.30533022	0.1888841

Model 1: Habitat types and distance to transport and forest edge

The results from the generalised linear mixed model analysis (Table 6) proved statistically significant positive effects at conventional levels ($p < 0.05$) for forest, transport, and distance to transport. Fully cultivated land and distance to forest edge were close to statistically significant ($0.05 < p < 0.1$) and can therefore be considered trends. All these variables had positive estimates/coefficients, implying that they increase the likelihood of resting compared to non-resting sites. Forest had the strongest positive effect (coef. = 3.0411, SE = 1.0892, z = 2.792, p = 0.005238), transport second strongest (coef. = 4.2582, SE = 1.6816, z = 2.532, p = 0.011335), and distance to transport third (coef. = 0.4248, SE = 0.1849, z = 2.298, p = 0.021584).

The intercept showed a highly significant negative effect (coef. = -3.7022, SE = 1.0979, z = -3.372, p = 0.000746), meaning that it is very unlikely that foxes are resting in developed areas when distance to transport and forest edge is set to zero.

The random effect indicates that there are variations in resting behaviour among different individual foxes (fox.id). The variance associated with this random effect is 1.201 (SD = 1.096), suggesting considerable variability between individuals.

Table 6. Statistical results from GLMM model 1, with habitat types and scaled versions of distance to transport and distance to forest edge. The intercept included developed (habitat type 11).

	Estimate/coef.	**Std. Error**	**z-value**	**p-value**
Intercept	-3.7022	1.0979	-3.372	0.000746
Transport (type 12)	4.2582	1.6816	2.532	0.011335
Fully cultivated land (type 21)	2.1251	1.1240	1.891	0.058671
Pasture (type 23)	2.0700	1.2943	1.599	0.109757
Forest (type 30)	3.0411	1.0892	2.792	0.005238
Open land (type 50)	1.5563	1.5487	1.005	0.314944
Distance to transport (scaled)	0.4248	0.1849	2.298	0.021584
Distance to forest edge (scaled)	0.3506	0.1925	1.822	0.068526

The probability of resting increased in all the habitat types with the increasing distance to transport, as seen in Figure 2. The probability of resting was very close to zero in developed areas (habitat type 11), with a minimal increase 400 meters away from transport (roads, etc.). In transport (habitat type 12), the probability is high, but with a big variance. This is likely because of the few observations, see Table 4. Forest (habitat type 30) sticks out in Figure 2, with little variation in the confidence interval and highest probability from 0 to 400 meters distance to transport.

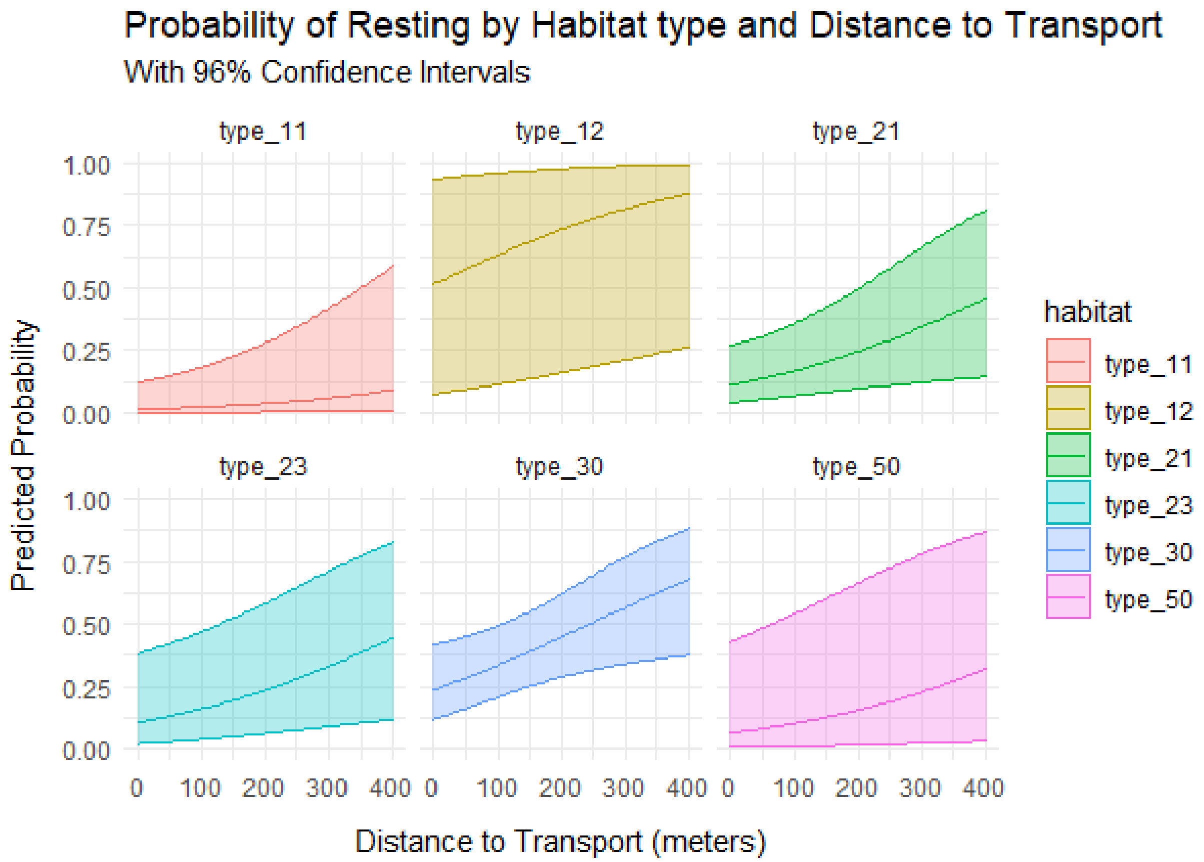

Figure 2. The predicted probabilities of resting in each habitat type and distance to transport (measured in meters), with 96% confidence intervals. Habitat type 11 = developed, habitat type 12 = transport, habitat type 21 = fully cultivated land, habitat type 23 = pasture, habitat type 30 = forest, habitat type 50 = open land.

Model 2: Cover and distance to developed and forest edge

The results of the GLMM analysis, with cover and distance to developed and forest edges as variables, are presented in Table 7. There was a statistically significantly strong positive effect of cover (coef. = 1.4094, SE = 0.4110, z = 3.429, p = 0.000606) on resting sites, indicating that resting in areas with cover is highly favoured over places without cover, compared to non-resting sites. In addition, there was a significantly strong negative effect of the intercept (coef. = -2.1332, SE = 0.4645, z = -4.592, p = 4.39e-06), which is when there is no cover (cover = FALSE) and all the other parameters are set to zero. This implies that foxes are not likely to rest in places with no cover and no distance to developed and forest edge.

There was also a statistically significant positive effect of distance to developed (coef. = 0.4988, SE = 0.1877, z = 2.658, p = 0.007866), meaning that higher distance from development increases the likelihood of resting significantly. Distance to forest edge did not have a statistically significant effect on resting (coef. = 0.2888, SE = 0.1868, z = 1.546, p = 0.122072). It was however included in the model because it had some positive effect together with distance to developed, that gave the lowest AIC value when choosing the GLMM model.

The random effect indicates that there are variations in resting behaviour among different individual foxes (fox.id). The variance associated with this random effect is 1.343 (SD = 1.159), suggesting considerable variability between individuals.

Table 7. Statistical results from GLMM analysis Model 2, with cover, and scaled versions of distance to development and distance to transport. The intercept included cover = FALSE.

	Estimate/coefficient	**Std. Error**	**z-value**	**p-value**
Intercept	-2.1332	0.4645	-4.592	4.39e-06
Cover =TRUE	1.4094	0.4110	3.429	0.000606
Distance to developed (scaled)	0.4988	0.1877	2.658	0.007866
Distance to forest edge (scaled)	0.2888	0.1868	1.546	0.122072

Visualised in Figure 3 are the predicted probabilities of resting with and without cover in relation to distance to development. The figure shows that resting in cover is more likely than resting without cover, no matter the distance to development, and that the probability of resting increases with increasing distance to development, both with and without cover. Especially in the first 200 meters from development, there is little overlap of the confidence intervals, with very low probability of resting without cover, but with cover, the probability of resting is higher. The variability of the probability of resting without cover was higher than with cover, approximately from 400 meters and up.

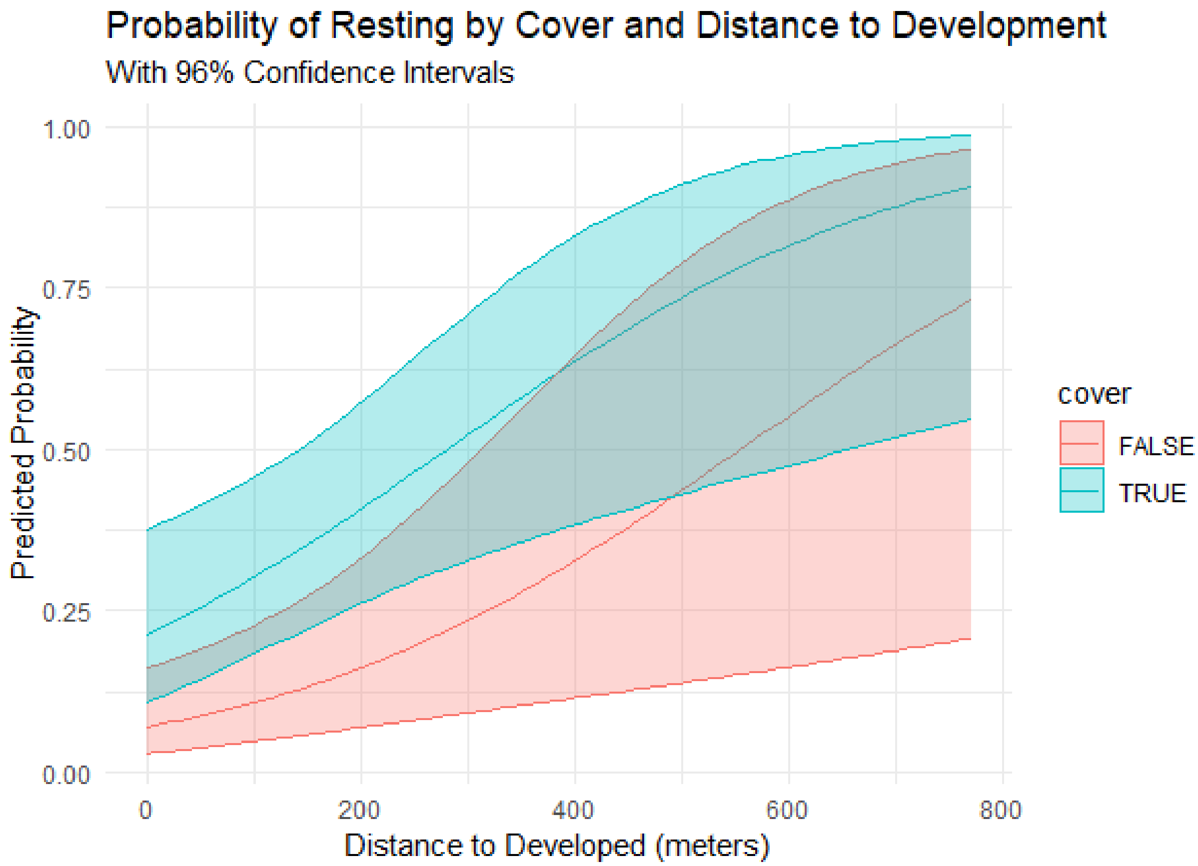

Figure 3. The predicted probabilities of resting with and without cover (cover =TRUE/FALSE) and distance to development (measured in meters), with 96% confidence intervals.

Discussion

The aim of this study was to find out what landscape features and characteristics are associated with resting sites of red foxes. Through a combination of GPS tracking, field observations, and spatial analysis, the characteristics of resting sites were compared to those of the locations of other activities. The results proved that red foxes in cultural landscapes use resting sites further away from infrastructure and preferring areas with cover, favouring forests over the other habitat types.

The habitat type in this cultural landscape that foxes preferred most for resting was forest (Table 6), fulfilling the prediction made in the introduction. There were in total 57 resting sites found in the forest, and most of these were ‘open bedsites’ (Table 3). As approximately 80% of all the resting sites in this study were in forests, and circa 64% of other activities were in forests (Table 4), it might also indicate that forests are the most used habitat type by the foxes in cultural landscapes in general. Regardless, other studies have shown that rural foxes usually prefer forests as a diurnal resting habitat, as this habitat is more available than in urban areas (Gloor, 2002). A study done in a countryside in Germany showed that forests are the most preferred diurnal resting habitat, with about 62% of the resting sites located in the forest (n=826), with 16 of 17 foxes having resting sites in the forest at least once (Janko et al., 2012). Reedbeds were also significantly preferred by the foxes in their study, and some foxes even rested within villages and small towns (Janko et al., 2012). This means that forests are key resting habitats even in places where foxes are comfortable resting near settlements and in cases when there is also selection for other habitats. In this study it was only one instance of resting in developed areas (table 3), and forest was highly favoured as a resting habitat, implying that forests are even more important in this type of landscape.

There was a trend for resting in distance to forest edges (Table 6), indicating that foxes might avoid the forest edges when resting or rest deeper into the forest to some extent. A reason why they might avoid resting around the forest edge could be that the density of the forest or vegetation around forest edges might not have provided enough cover to make it a safe resting site. Considering that most of the forests in this cultural landscape are fragmented and consist of many patches of forests, the smaller size of the forests could draw them deeper into the forest to provide more safety and quiet habitats for resting. The red fox is a highly mobile species and is therefore not isolated or necessarily negatively affected by habitat fragmentation in its simple sense. However, since habitat fragmentation is caused by habitat loss, reducing the size of the patches of natural habitat, this could limit the area utilised by foxes for resting (Fahrig, 2018). Nevertheless, more studies on this would be needed to find out if and why they rest further away from the forest edge, for example, the selection of microhabitats within forests.

The foxes preferred habitat type transport (roads, etc.) second most (Table 6). This, however, does not make sense considering that distance to transport had a positive effect on the selection of resting sites. What may have given this counterintuitive result is that there were only 3 clusters visited on the habitat type transport (table 4), with two of them being resting sites and one non-resting site. This leads to an exceedingly high proportion of resting sites when comparing them to non-resting sites. The roads that were found to have two resting sites could be forest roads or trails with little traffic or sufficient cover (Janko et al., 2012). The predicted probabilities of resting in roads (transport) are increasing with the distance to transport (Figure 2). This is contradictory since the distance to transport in habitat type transport is zero and would become a different habitat type with increased distance. In the case of distance from the centre of the road, it could mean that the resting sites were at the edge of the road, though it would have to be on a small scale of a few meters to still be considered inside habitat type transport.

There was a trend for resting in fully cultivated land (Table 6). This might be because it was the habitat type with the second most observations (Table 4) and is one of the most abundant habitat types in the cultural landscape (Figure 1). Another reason can be that there was enough cover, such as bushes, tall grass, or cereals at the sites where they rested, as diurnal resting sites are usually hidden (Meia & Weber, 1993). In fully cultivated land, most of the resting sites were in dens or in cover of some sort (Table 3), providing security to rest there. However, these resting sites are not defined as diurnal or nocturnal. This means that it is a possibility that resting happened during the night, and in connection with some other activity, which is when they usually do not move from a present habitat to rest but rest where they have been active (Meia & Weber, 1993). Since foxes travel mostly in cover during the daytime, while at night they can cross open fields, it is more likely that the resting sites in cultivated land were used at night (Allan, 1968). In addition, there is less human activity at night, and they are less visible in the dark and therefore not necessarily in need of cover.

The foxes in this study had a strong selection toward areas in cover when resting, and areas without cover were strongly selected against (Table 7). This indicates that cover is a very important part of resting site selection in a cultural landscape and supports the prediction that foxes prefer resting in places with cover. Also, by looking at the number of dens and covered resting sites in open areas compared to forests (Table 3), cover seems to be important, although it was not proven statistically. Especially in daylight, when foxes are more likely to be found by humans or other predators, cover provides shelter and safety in an environment with a lot of human activity. Other studies have shown foxes resting near settlements and in other habitat types than forest, as long as there is sufficient coverage or vegetation. This indicates that cover is a very important factor for the choice of resting sites and where they stay during the day (Allan, 1968; Janko et al., 2012; Meia & Weber, 1993).

As shown in Figure 3, the probability of resting close to development is higher in areas with cover than in areas without cover. It is the same case for distance to transport and forest in Figure 2 when compared to other habitat types that are more open. This type of resting behaviour was observed during a study in Germany, where rural foxes had resting sites concentrated in forests in the vicinity of settlements. The researchers assumed that human proximity did not make the foxes avoid or shy away from areas close to development if they had enough cover and that resting close to settlement could also provide quick access to anthropogenic food resources after resting (Janko et al., 2012). However, there is a considerable increase in the probability of resting with increased distance from development, both with and without cover (Figure 3). This indicates that the foxes prefer resting further away from development. Besides, distance to development had a strong effect on resting site selection (Table 7), supporting the prediction that red foxes in cultural landscapes choose to rest in places far away from infrastructure. This prediction is also supported by the fact that distance to transport had a substantial effect on resting site selection (Table 6), with increased probability of resting further away from transport (Figure 2).

The effect of distance to development was stronger than the effect of distance to transport, but since the variables were in two different models, it is not necessary to compare the two. However, there was a positive correlation between these two variables, with a correlation value of approximately 0.6 (table 5). We can infer from this that the distance to transport increases with the increasing distance to development and vice versa. This is logical, because roads and railways are connected to development. Since these variables were not used in the same GLMM model, there is no issue to discuss about this correlation. The effect of both variables suggests that foxes prefer their resting sites away from human activity, as human activity is centred around infrastructure.

Foxes in cultural landscapes prefer resting sites further away from infrastructure compared to other activities (Table 4, 6, and 7). This resting behaviour is similar to that of foxes in more rural areas, where the foxes have been conditioned by hunting to avoid humans (Meia & Weber, 1993). Urban foxes have adapted to resting in gardens and close to development, but they still choose the most quiet and undisturbed habitats available to avoid human activity. While in rural areas where there are both natural habitats and infrastructure, foxes prefer the natural habitats (Gloor, 2002; Janko et al., 2012; Saunders et al., 1997). This indicates that foxes in general try to avoid people when they rest, no matter the environment. The differences in resting behaviour between populations across different landscape types may be a result of both available habitats and the degree of intolerance for foxes (Janko et al., 2012; Meia & Weber, 1993).

Both models showed that there are substantial individual differences in resting behaviour, which has been the case in other resting site studies as well (Meia & Weber, 1993). This is a factor that needs to be considered more in further research on resting behaviour and is possible to determine by using GPS collars.

There were fewer dens than resting sites above ground (Table 3), which might be a result of the loss of GPS signal as foxes go underground. This was also seen in a study that identified parturition dates and denning activity based on missing GPS positions (Walton & Mattisson, 2021). This fault could potentially undermine the number of dens and their importance as a resting site. In addition, dens are more used by foxes in the period of giving birth to and rearing puppies. This behaviour is not included in this study as the foxes were wearing the collars outside this season.

Forest is an important natural habitat. It provides cover, shelter, and food resources, not only for foxes but for many other species as well. 60% of all species registered in Norway exist in the forest, and close to half of all the threatened species on the Norwegian Red List from 2021 live in the forest (Miljødirektoratet, 2024b). In forest and natural resource management, it is therefore especially important to consider the negative impacts of anthropogenic influences in a cultural landscape, like habitat destruction, fragmentation, and land use change, if the goal is to preserve biodiversity and minimise the negative effects on wildlife. Although the red fox is not a threatened species in Norway (Eide, n.d.-b), it would be advantageous to perform similar studies on closely related carnivores, such as the arctic fox (*Vulpes lagopus*). This fox species is endangered in Norway and is also an underground denning species (Eide, n.d.-a) Thus, this type of study can advance the understanding of the behaviour and ecological needs of the arctic fox, laying the foundation to improve management of the species.

Knowing more about foxes' rest sites helps identify and understand their home ranges and not basing habitat suitability or preference only on available food resources, for example, but also resting (Lucherini & Lovari, 1996). Although the home ranges of the foxes were not a part of this study, home ranges are one of the most researched ecological attributes of wild mammals and are elementary to portray their dispersion and ecological needs (Walton et al., 2017). More studies that include resting behaviour while identifying home ranges would be beneficial and important to assess the whole spectrum of fox behaviour. Most studies on dens concern natal dens, which of course is an important part of foxes' reproduction and their life history traits. There is, however, a lack of studies merely on the resting aspect of dens. This is also important to consider given that foxes rest more frequently than they give birth and rear pups.

Other aspects that also would need more research are temporal aspects of resting, differences between sexes, and intraspecific competition or territoriality regarding resting sites, where the use of high-frequency GPS position fixes, such as in this study, would be advantageous. Considering that distance to infrastructure influences the selection of resting sites, more research is needed to find out whether this is associated with noise pollution.

Conclusion

The red foxes in this cultural landscape choose natural habitats for resting, favouring forest and areas with cover. Compared to other activities, resting composes a significantly different spatial use, with higher distance to areas used for transport and development. This behaviour is similar to other foxes in rural areas, where they avoid open areas and infrastructure, and mostly rest in forest because this is the habitat available that provides most cover and security. Foxes have a higher probability of resting closer to infrastructure in cover and forests compared to open areas, showing how important cover and forests are to mitigate the effects of an increasingly human-altered environment. The distance to the forest edge had some effect on the selection of resting sites, but this is a feature that needs to be researched further to be able to make a conclusion.

Using GPS collars to track the foxes' activity using high-frequency position data was an effective way of locating resting sites and sites with other activities. Most of the resting sites located were above ground, as the signal can get lost when the fox enters a den. This might have been hindering finding more dens in the study area. Determining whether the resting sites were used at daytime or nighttime might have helped explain unexpected results more, for example in the case of resting in fully cultivated areas that are more open. Anyway, similar methodology has potential to be used for further research on resting site selection and include more variables such as temporal aspects, individual differences and noise pollution. Including resting sites to establish home ranges could also be beneficial for future studies.

Enriching the knowledge about the dispersal and ecological needs of wild animals is fundamental for the management of nature resources and wildlife. As this study showed how important forests are for foxes, representing only one of the many species associated with forests, the negative effects of fragmentation and habitat loss should be considered when managing these natural habitats in a highly human-altered landscape.

References

Ahlstrøm, A. P., Bjørkelo, K. & Fadnes, K. (2019). *AR5 Klassifikasjonssystem*. NIBIO BOK 5(5)2019, vol. 5: NIBIO. Available at: http://hdl.handle.net/11250/2596511.

Allan, R. A. (1968). Movements and Daily Activities of Fox as Determined by Visual Observations and Radio Tracking. *Proceedings of the Iowa Academy of Science*, 75 (1): 147-151.

Bischof, R., Gjevestad, J. G. O., Ordiz, A., Eldegard, K. & Milleret, C. (2019). High frequency GPS bursts and path-level analysis reveal linear feature tracking by red foxes. *Scientific Reports*, 9 (1): 8849. doi: 10.1038/s41598-019-45150-x.

Carter, A., Luck, G. W. & Wilson, B. P. (2012). Ecology of the red fox (Vulpes vulpes) in an agricultural landscape. 1. Den-site selection. *Australian Mammalogy*, 34 (2): 145-154.

Eide, N. (n.d.-a). *Fjellrev Vulpes lagopus (Linnaeus, 1758)*. Available at: http://www.artsdatabanken.no/Pages/180944 (accessed: 10.12.2024).

Eide, N. (n.d.-b). *Rødrev Vulpes vulpes (Linnaeus, 1758)*. Available at: http://www.artsdatabanken.no/Pages/180936.

Fahrig, L. (2018). Habitat fragmentation: A long and tangled tale. *Global Ecology and Biogeography*, 28 (1): 33-41. doi: https://doi.org/10.1111/geb.12839.

Frafjord, K. (2022). *Rødrev*. SNL. Available at: https://snl.no/r%C3%B8drev.

Gloor, S. (2002). *The Rise of Urban Foxes (Vulpes vulpes) in Switzerland and Ecological and Parasitological Aspects of a Fox Population in the Recently Colonised City of Zurich*. Dissertation. Zürich: Faculty of Mathematics and Natural Sciences

of the University of Zürich. (accessed: 04.12.2024).

Hewson, R. (1986). Distribution and Density of Fox Breeding Dens and the Effects of Management. *Journal of Applied Ecology*, 23 (2): 531-538. doi: 10.2307/2404034.

Hogue, A. S. & Breon, K. (2022). The greatest threats to species. *Conservation Science and Practice*, 4 (5): e12670. doi: https://doi.org/10.1111/csp2.12670.

IPBES. (2018). *Summary for policymakers of the regional assessment report on biodiversity and ecosystem services for Europe and Central Asia of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*: Zenodo.

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services*. IPBES Plenary at its seventh session (IPBES 7, Paris, 2019): Zenodo.

Iversen, T. (2024). *Space use of red foxes in relation to*

farms within the cultural landscape. Master's theses (MINA) [778]: Norwegian University of Life Sciences. Available at: https://hdl.handle.net/11250/3148343.

Janko, C., Schröder, W., Linke, S. & König, A. (2012). Space use and resting site selection of red foxes (Vulpes vulpes) living near villages and small towns in Southern Germany. *Acta Theriologica*, 57: 245 - 250.

Lloyd, H. G. (1980). Habitat Requirements of the Red Fox. In Zimen, E. (ed.) *The Red Fox: Symposium on Behaviour and Ecology*, pp. 7-25. Dordrecht: Springer Netherlands.

Lucherini, M. & Lovari, S. (1996). Habitat richness affects home range size in the red fox Vulpes vulpes. *Behavioural Processes*, 36 (1): 103-105. doi: https://doi.org/10.1016/0376-6357(95)00018-6.

Meia, J. S. & Weber, J. M. (1993). CHOICE OF RESTING SITES BY FEMALE FOXES VULPES-VULPES IN A MOUNTAINOUS HABITAT. *Acta Theriologica*, 38 (1): 81-91. doi: 10.4098/AT.arch.93-7.

Miljødirektoratet. (2022). *Forskrift om jakt- og fangsttider samt sanking av egg og dun for jaktsesongene fra og med 1. april 2022 til og med 31. mars 2028*: lovdata. Available at: https://lovdata.no/dokument/SF/forskrift/2022-01-21-128.

Miljødirektoratet. (2024a). *Forskrift om utøvelse av jakt, felling og fangst med kommentarer, instrukser og avtaler*. In Miljødirektoratet (ed.). Available at: https://www.miljodirektoratet.no/publikasjoner/2016/mars-2016/forskrift-om-utovelse-av-jakt-felling-og-fangst-med-kommentarer-instrukser-og-avtaler/.

Miljødirektoratet. (2024b). *Miljøindikator 1.2.4*

Antall nær truede og truede arter og naturtyper i skog: Miljøstatus. Available at: https://miljostatus.miljodirektoratet.no/miljomal/naturmangfold/miljomal-1.2/miljoindikator-1.2.4.

Norway, S. (2024). *Kommuneareal Ås*. Available at: https://www.ssb.no/kommuneareal/as (accessed: 27.11.2024).

Saunders, G., White, P. C. L. & Harris, S. (1997). Habitat utilisation by urban foxes (Vulpes vulpes) and the implications for rabies control. *Mammalia*, 61 (4): 497-510.

Schaal-Lagodzinski, T., König, B., Riechers, M., Heitepriem, N. & Leventon, J. (2024). Exploring cultural landscape narratives to understand challenges for collaboration and their implications for governance. *Ecosystems and People*, 20 (1): 2320886. doi: 10.1080/26395916.2024.2320886.

Toverud, F. S. K. (2019). *Linking high frequency GPS data with multiscale habitat selection : a study of an adaptable carnivore in a fragmented landscape*. Master's theses (MINA) [778]: Norwegian University of Life Sciences. Available at: http://hdl.handle.net/11250/2609100.

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

Walton, Z. & Mattisson, J. (2021). Down a hole: missing GPS positions reveal birth dates of an underground denning species, the red fox. *Mammalian Biology*, 101 (3): 357-362. doi: 10.1007/s42991-020-00089-9.

Wolff, M. A. (2024). *Været i Ås 2023*. nmbu.no: NMBU. Available at: https://www.nmbu.no/fakulteter/fakultet-realfag-og-teknologi/vaeret-i-2023 (accessed: 28.11.2024).

Zaman, M., Tolhurst, B. A., Zhu, M. & Jiang, G. (2020). Den-site selection at multiple scales by the red fox (Vulpes vulpes subsp. montana) in a patchy human-dominated landscape. doi: https://doi.org/10.1016/j.gecco.2020.e01136.

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway