Norwegian University
of Life Sciences

Master's Thesis 2024 60 ECTS
Faculty of Environmental Science and Natural Resource Management

Space use of red foxes in relation to farms within the cultural landscape

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Acknowledgements

This thesis was written as my final submission in my master's degree at The Norwegian University of Life Science (NMBU).

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

I would also like to thank my family who have been giving support and motivation throughout my master thesis work. A special thanks to Trygve for all the help and conversations regarding my project, and the great support given.

At last, I want to thank my friends for making my four years in Ås truly memorable.

Norwegian University of Life Science
Ås, May 15, 2024

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Abstract

Previous studies have demonstrated the profound impact of cultural landscape and human activities on wildlife. Red foxes (*Vulpes vulpes*), known for their adaptability and opportunistic feeding habits, exhibit highly versatile behavior in fragmented environments. By living in human-dominated habitats, foxes are able to exploit a variety of anthropogenic resources. Due to their predominant nocturnal activity pattern and elusive behavior, studying how foxes move in the landscape presents significant challenges. This study aims to explore the intricate relationship between farms in the cultural landscape and the spatiotemporal behavior of the red fox using GPS technology. Data from 34 GPS-collared foxes were analyzed. The GPS device recorded periodic bursts of positional data with intervals of 10 to 15 seconds between each location, providing detailed insight into the foxes' movements. To investigate how foxes select for or against proximity to farms within their home range depending on different environmental covariates, a resource select function was applied. The results revealed significant variation in selection towards farms, influenced by diel period and cover. When cover, such as trees or dense vegetation, is present, foxes exhibit a higher probability of coming into close proximity to farms. This selection is likely driven by the dual benefit of cover and exploitation of anthropogenic resources provided by farms. The availability of cover close to farms may increase their willingness to approach and interact with such features as it reduces the risk of coming into direct contact with humans. By strategically adjusting their behavior both temporally and spatially near farms, red foxes optimize their foraging strategy while also assessing the risk posed by human presence. These finding highlight the remarkable adaptability of red foxes' navigation through a highly fragmented landscape.

Sammendrag

Tidligere studier har vist hvordan kulturlandskapets og menneskelig aktivitet påvirker dyrelivet. Rødreven, kjent for sin tilpasningsdyktighet og opportunistiske natur, viser en svært allsidig adferd i et fragmenterte miljøer. Fordi reven klarer å utnytte en rekke antropogene ressurser, trives den i et menneskedominert landskap. Reven er nattaktive og svært unnvikende, dette kan by på utfordringer knyttet til å undersøke hvordan reven beveger seg i og bruker landskapet. Formålet med denne studien er å utforske det komplekse forholdet mellom gårder og rødrev i kulturlandskapet, og hvordan det påvirker den romlige og tidsmessige adferden ved hjelp av GPS-teknologi. Data fra 34 GPS-merkede rever ble benyttet i analysen. GPS-enhetene registrerte periodiske posisjoner med intervaller på 10–15 sekunder mellom hver lokasjon, for å få detaljer informasjon om revens bevegelsesmønster. For å undersøke i hvilken grad revene selekterte for nærhet til gårdsbruk, ble det benyttet en resource select funksjon. Resultatene viste betydelig variasjons i hvor nære revene oppholdt seg gårder, basert på tid på døgnet og dekke. Når dekke er til stede, som trær og tett vegetasjon er til stede, viser resultatene en høyere seleksjon for å være nærmere gårdsbruk. Tilgjengeligheten av dekning kan redusere risikoen for direkte kontakt med mennesker. Disse funnene understreker de strategiene revene brukes for å tilpasse seg i et menneskedominert landskap. Ved å benytte både tidsmessig og romlig adferdsendringer, i forbindelse med å være i nærheten av gårdsbruk, optimaliserer rødreven utnyttelse av ressurser samtidig som de vurderer risikoen knyttet til menneskelig aktivitet.

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1. Introduction

One of the biggest threats to biodiversity is habitat loss and fragmentation of the landscape (Reshamwala et al., 2022). Anthropogenic activities create divers environments by altering landscape compositions and connectivity (Ruas et al., 2022). The replacement of natural habitat withing a human-modified landscapes result in long-term changes, spatial arrangements, and connectivity (Fischer & Lindenmayer, 2007). While some species suffer negative consequences from these alterations, others display remarkable adaptivity and resilience, utilizing the resources and opportunities provided by human-modified environment, not only survive but also thrive (Alberti, 2024). These resilient species may exhibit behaviors such as adjusting foraging strategies, expanded habitat utilization, or increased tolerance to human presence(Carter & Linnell, 2023).

Human-altered environments is becoming increasingly more important for wildlife, as natural habitats no longer provides a suitable environment for a lot of species (Hunter, 2007). The decrease in natural vegetation and a reduction in natural food abundance, is counterbalanced by an increase in anthropogenic food sources (Alberti, 2024). Certain organisms demonstrate a great capacity to thrive in urban environments compared to others (Plumer et al., 2014). The capacity of species that exploit and florish in urban settings is linked to a combintion of life history, morphological, physiological, behavior and cognitive attributes (Charmantier et al., 2017; Schell et al., 2021). It is commonly observed that mammals thriving in highly-dominated human environments often are mid-size species with a flexible diet, high annual reproductive capacity, and highly adaptable behavior(Güthlin et al., 2013; Jahren et al., 2020a). Red foxes serve as a great example of a generalist predator, thriving across a wide spectrum of environments, from densely populated areas to farmland (Bateman & Fleming, 2012). The key to their success lies in their opportunistic and generalistic behavior, allowing them to exploit a diverse range of diets and movement patterns (Reshamwala et al., 2022). This makes them an ideal model species for studying ecological adaptations to human-altered environments (Alexandre et al., 2020).

A highly fragmented and human-altered landscape, can both offer benefits and high risk. Human-dominated landscapes often provide available food sources and great scavenger opportunities (Alberti, 2024). The secondary effects arising from human land use practices, such as forestry and agriculture, may exert indirectly influence. Specifically, cultivation of agricultural fields provides habitats for preferred prey, thereby enhancing predation success due to the increased in habitat edges, creation by the heterogeneity in the landscape (Kujala et al., 2024). The secondary effects are consistent throughout the year and may affect the overall carrying capacity (Jahren et al., 2020b). However, alongside these benefits come significant risks, including increased hunting pressure, threats from domestic dogs and pets, habitat disturbance, and collisions from roads (Schell et al., 2021).

Conflicts between humans and wildlife can arise when living in close proximity to each other, and may pose a threat to humans, domestic animals, or livestock (Mekonen, 2020). While they may not directly threaten humans, foxes can compete over game species, which they have the ability to actively control in some cases (Fehlmann et al., 2020). Predation on threatened or endangered species is a significant concern (Fehlmann et al., 2020) . Overall, conservation and management goals can pose challenges in relation to controlling a big population together with conservation (Kehoe et al., 2021). Other concernes in relation to living in close proximity to red foxes, includes their ability to transmit diseases to people and pets, seed dispersal and predation on livestock and animals (Cancio et al., 2017). In general, conservation and management present challenges when it comes to effectively managing red fox populations while also promoting conservation efforts (Otieno, 2023).

Given the significant implications for management and conservation, particularly in relation to the increasing fragmentations of habitats, it is important to comprehend how animals engage with elements, such as farms, in their environemnt (Schell et al., 2021). One interesting aspect is how covariates, such as diel period and cover, influences the selection foxes make to stay in close proximity to farms. Highly opportunistic species may exhibit temporal and spatial behavior, in relation to efficiently exploit resources and the foraging opportunities farms provides, while avoiding potential risks associted with human activity (Reshamwala et al., 2022).

Foxes are nocturnal animals, meaning they are more active during the night and twilight hours, which can makes observation studies difficult (Wooster et al., 2019). Because of this, GPS technology is particularly useful for studying detailed behavior and movement (Bouten et al., 2013). The use of telemetry technology, such as GPS tracking, has greatly improved the ability to observe and quantify detailed behavior in animals (Fehlmann et al., 2020). Researchers can now identify distinctive patterns in animals behavior and collect spatio-temporal data due to the development of new tracking technology (Recio et al., 2011). Which has enormous potential and value for management and conservation of species (Acácio et al., 2022). Typically, a common strategy involves using a low fix frequency over extended periods of time (Recio et al., 2011). However, this approach may not always capture rare events, such as animals interacting with specific infrastructures like farms.

In this study, GPS information from 34 red foxes was used to quantify spatio-temporal changes in relation to the distance from farms, influenced by the covariates diel period and cover, for foxes living in a highly fragmented landscape. By using periodic bursts of high-frequency GPS position fixes made it possible to detect behavior at a finer scale (Bischof et al., 2019).

Specifically, I aimed to determine:

Main question: How does farms within a fragmented landscape influence space use in red foxes.

i) Do foxes select for proximity to farms within their home range depending on diel period? If so, how strong is the effect?

ii) Does cover influence the selection for proximity to farms.

Prediction: When cover is present, the preference for interacting with farms will be most pronounced during night and twilight, while it will be least pronounced in the absence of cover during daylight.

To answer the questions, I used GPS information provided by the red fox project by The Norwegian University of Life Science.

2. Methods

2.1 Study area

The data used in this study is provided by the red fox project at the University of Life Science in Ås, Norway.

The study was conducted in southern Norway, in the municipalities of Ås and Vestby, falling within the coordinates of 59.47 - 59.77 N latitude and 10.62 - 10.89 E longitude (Decimal degrees, WGS84) (geonorge.no, 2019). The elevations ranging from 0 to179 meters above sea level (NIBIO, 2023). The total area spans 235 km^2 (Statistics Norway, 2024). Vestby and Ås have an average human population densities of about 182 people/km^2 (Statistics Norway, 2023). January and February are typically the coldest months of the year, with average temperatures ranging from -4.8 °C to -3.5 °C, while July is typically the warmest month, with average temperatures ranging from 16.1 °C to 17.6 °C, From early December to late March, the ground is sporadically covered with snow. (Norwegian Metrological Institute, 2024).

Fox hunting is permissible throughout the year in the study area, except during the period when female foxes have dependent young (April 15 – July 15) (Lovdata, 2022).

Overview map of the study area

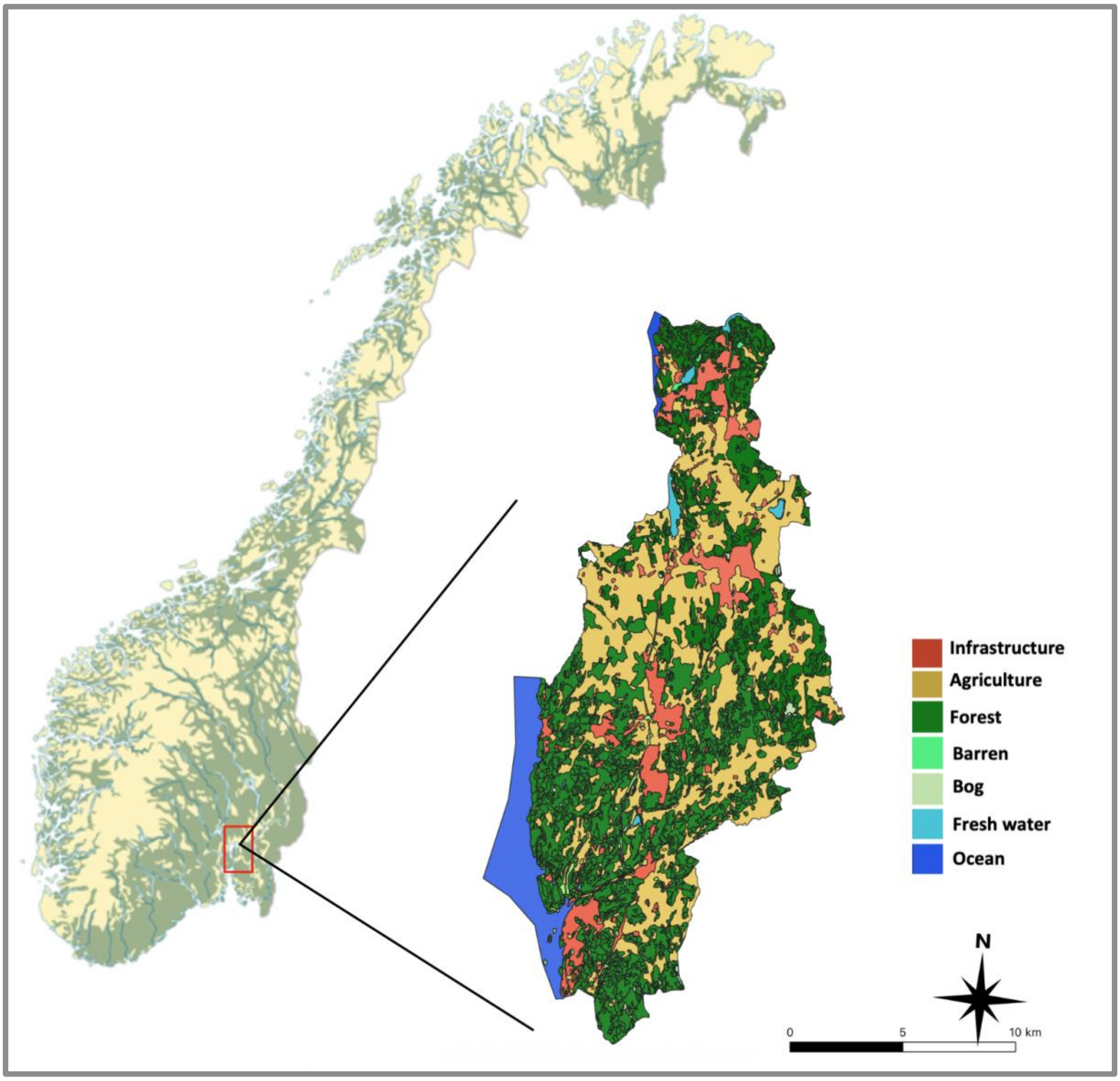

Figure 1: Map showing the study area in Norway. The study was conducted in the south of Norway, specifically in the municipality of Ås and Vestby. Map layers were obtained from kartnorge.no and NIBIO.no.

2.2 Fox capturing and handling.

The foxes were captured using large wooden box traps, measuring approximately 200 cm x 80 cm x 80 cm, featuring two trapdoors positioned at the front and back (Bischof et al., 2019). These box traps adhere to Norwegian legal standards and are commonly used for capturing small to medium-sized carnivores (Miljødirektoratet, 2024).
The traps were lured with meat, primarily consisting of dead chicken (*Gallus gallus domesticus*) or portions of venison sourced from roe deer and moose. Monitoring of the traps was conducted on a daily basis. Trap alarms have been installed in the majority of the traps, although they are not intended to replace daily inspections.

Figure 2: One of the traps used in the study. Photo: T. Iversen

When a fox was captured, a team (2 to 4 people) were gathered within the following hours. Foxes captured were initially managed using a catch pole, followed by neck tongs and by hand. To reduce stress, a dark cloth was used to cover the fox´s eyes during handling, as handling was performed without anesthesia. By doing so, the animals could be released without experiencing the negative effects of anesthesia. Through the process, priority was given to ensure the care and cautious handling of the animals to minimize unnecessary stress. Once the fox was under control, a GPS-unit attached to a collar was fitted to allow 2-3 fingers between the collar and the neck off the fox. Information such as weight, sex, and general health status was assembled. Hair and feces samples were collected for DNA analysis. The entire handling process, from trap removal to release, typically lasted between 10 to 20 minutes.

The study is granted approval from the Norwegian Animal Research Authority (FOTS 8415/17790/24392/30326), by direction from Norwegian Food Safety Authority. Capturing and handling procedures complies with the current laws and regulation in Norway.

2.3 GPS collar tracking

The GPS collars were developed by members of The Norwegian University of Life Science Red fox project. For additional and more detailed information regarding the GPS collars and data collection I refer to Bischof et al. (2019).

The GPS units are small and lightweight, constructed from readily off-the-shelf parts integrated into a custom printed circuit board, along with an 8-bit ATmega 328p microcontroller. The core electronics includes a SIM808 GSM/GPRS module from SimCom™, providing integrated GPS, GPRS and Bluetooth capabilities. The system is designed to withstand harsh environments and ensure reliability while running specialized software. Raw data is automatically transmitted via GPRS to a server for storage. The GPS units were powered by 3000mAh lithium-polymer batteries and were embedded in a 3D printed plastic case of 7 x 4 x 3.5 cm. The cases were attached to a collar (2 cm by 1mm). Equipped with a cotton string causing the collar to fall off after time. The combined weight of the GPS collar was 123g, compromising less than 2.3% of the average body weight of the foxes in the study. Starting in 2023, a smaller (6.5 x 4 x 2 cm) and lighter (76 g) GPS was used, but with a collar configuration similar to the previous model.

The foxes were monitored by using bursts of 20 positions, with inter-fix intervals of 10-15 seconds with 20 to 60 minutes between bursts. The average monitoring duration was 16.4 days (SD ± 10.8). The units decreased their sampling rate to 1-20 positions (depending on GPS model and setting) every 6 hours when the battery capacity fell below 37%, increasing the likelihood of collar retrieval. The GPS data was cleaned to ensure data accuracy and minimize potential biases. Data collected within the first 24 hours post-release were excluded to mitigate short-term effects on relocation patterns caused by capturing and handling. Any obvious errors or false points were identified and removed from the dataset to improve data quality and reliability.

2.4 Data analysis and statistical test

R studio (version 2023.09.01) was used to perform all the statistical analysis, with all the associated packages needed.

2.4.1 Home range estimation

Estimating the home range of each fox allows to gain insight into their spatial behavior and preferences within their environment (Kobryn et al., 2023). To achieve this, a kernel density estimation was employed, by using the kernelUD () function available in the adehabitatHR package in R (Calenge, n.d.). The kernelUD () function computes a utilization distribution based on the spatial coordinates of the animal's locations. In this analysis a 95% utilization distribution were used, representing the area the fox is predicted to spend 95% of its time. This vertex provides a robust estimate of the core area used by the animal, offering valuable information on its primary habitat. Furthermore, to account for potential variability and uncertainties in the estimated home range, a buffer of 1 km^2 around the 95% utilization distribution was applied. This buffer serves as a precautionary measure, ensuring that the estimated home range encompasses a sufficient area to capture the animal's movement and potential encounters with farms.

Home-range estimation

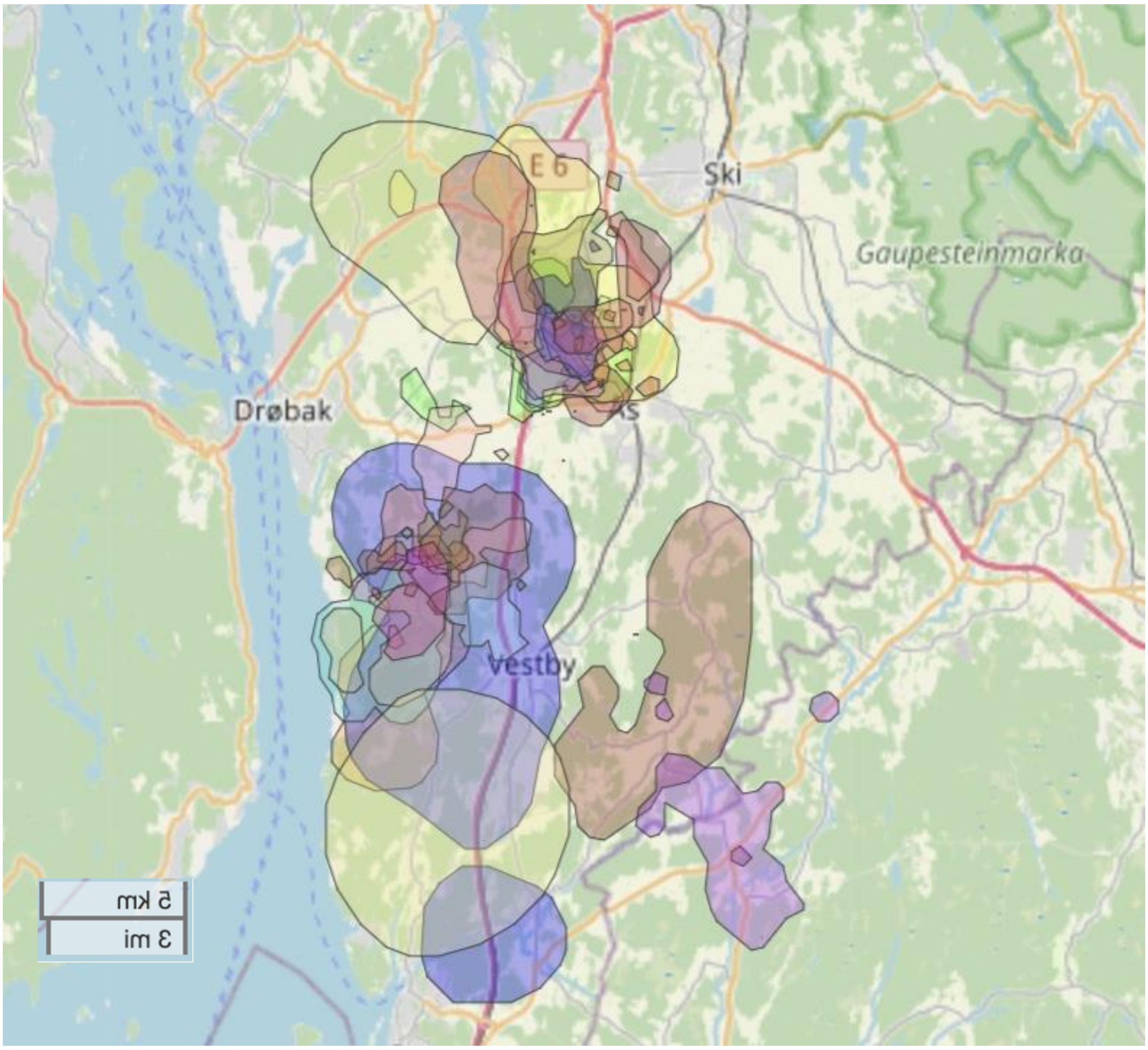

Figure 3: Showing the 95% calculated home range together with a buffer zone of 1km². One additional fox (ID_11) was excluded from the map as it dispersed south out of the study area.

2.4.2 Calculating diel period

In order to determine whether foxes exhibit a preference for proximity to farms depending on diel period, the suncalc package in R was employed to gather detailed information about the various phases of daylight (Thieurmel & Elmarhraoui, 2022). Each GPS position recorded comes with a date-time stamp from the POSIX format in R. By using the getSunlightPositions() function to collect data in radians, providing information about the elevation of the sun above and under the horizon. This process allows to categorize different time periods based on the positions of the sun relative to the horizon. When the sun is below the horizon, representing night, it is indicated by negative values. Twilight ranging from 0 to –0.314 radians. Conversely, positive values indicate daylight, signifying that the sun is above the horizon. By integrating this solar elevation data with the foxes` GPS positions, it is possible to explore potential correlations between movement and diel period, shedding light on whether they demonstrate a tendency to utilize farm areas during specific daylight phases.

2.4.3 Calculating Cover

Cover was identified using land cover information from a comprehensive national AR5 map, adapted for scales of 1:1000 and larger (NIBIO, 2023). The dataset is based on the AR5 classification system, which describes land resources based on the production basis for agriculture and forestry. The classifications divide the land area into polygons described by a set of attributes for the properties of land types, forest site quality, tree species, and substrate. The main division is land types based on criteria for vegetation and cultural influence. In the analysis, both the real GPS positions together with positions generated from a null model were integrated with the highly detailed AR5 map. This integration enabled the detection whether the GPS points corresponded to locations within forest cover or open areas. With this spatial information it was possible to investigate the influence of cover on the movement and habitat selection, contributing to a more nuanced understanding of their spatial ecology.

2.4.4 Calculating distance to nearest farm

The st_distance function in the sf package in R was utilized to calculate the distance between each GPS point and the nearest farm related infrastructure (Pebesma, 2024). This function calculates the shortest distance between two spatial objects. By using a map layer that containing detailed information about farm infrastructure within the study area was overlaid onto the GPS position data. The farm infrastructure data is collected from Geonorge.no (2023). Each feature is represented as a spatial object, allowing for precise distance calculations. The calculated distances are used to create new variables, such as “distance to nearest farm”, and provides quantitative measures of the proximity of each GPS point to nearby farms.

2.4.5 Resource select function.

A step selection analysis was conducted to elucidate the movement decisions of foxes in response to environmental cues and resource availability (Thurfjell et al., 2014). In this analysis a “step” refers to a discrete unit of movement taken by individual animals between successive GPS fixes. Each step was calculated from the inter-fix intervals of the bursts, with each burst consisting of a series of 20 positions recorded within 10-15 seconds.

To analyze the steps, a set of alternative steps was generated randomly within the animal’s available habitat. For each real step (case), five corresponding random steps (control) were calculated. Each random step was rotated and placed randomly within the home range of the individual. This approach enables the assessment of the relative likelihood of an animal choosing a particular movement path based on the present environmental conditions (Thurfjell et al., 2014).

Next, a conditional logistic regression was employed to quantify the extent to which foxes exhibit a preference for proximity to farms, considering both the diel period and cover. This analysis was fitted using a cox proportional hazard model, which allowed for the examination of interaction among key variables (Sheng & Ghosh, 2020). The model includes the interaction between the distance to nearest building used as explanatory variable, representing a measure of proximity to human infrastructure, together with time of day and cover as response variables. These variables help capture the multifaceted nature of fox habitat selection and movement behavior in relation to the anthropogenic features and environmental conditions (Hill et al., 2022). Furthermore, to address the potential clustering effect in the data, it was accounted for any spatial dependencies or autocorrelations that may arise due to the proximity of individual observations, as suggested by F. Dormann et al. (2007)

3. Results

3.1 Data summary

The analysis utilized GPS data collected from 34 red foxes trapped between 2018 to 2024. The first foxes that were trapped in this study, number 1 to 5, were excluded from the analysis because they were tracked using longer frequency GPS fixes and did not provide enough data for fine-scale information. Fox 28 and 40 were also removed from the analysis because they did not provide enough data. The GPS data from 34 foxes, 19 males and 15 females, were therefore used in the following analysis. The average monitoring period for these foxes was 16.4 days (SD ± 10.8). The average captured position bursts used in the analysis was 3233 (SD ± 1772), and position fixes with an average of 202 (SD ± 109). More detailed information about the foxes in the study are shown in table 1.

Table 1: 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 10	Male	Juvenile	4.0	07.09.2018	0.8	190	12
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 23	Female	Juvenile	4.6	10.03.2019	27.4	4453	245
Fox 24	Female	Juvenile	4.3	24.03.2019	35.1	1479	140
Fox 25	Male	Adult	7.5	03.09.2019	23.8	3991	234
Fox 26	Female	Juvenile	4.6	15.11.2019	32.0	2184	161
Fox 27	Male	Adult	6.4	21.11.2019	30.6	2864	179
Fox 29	Female	Adult	5.5	21.01.2023	7.5	2060	170

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
Fox 34	Male	Adult	7.1	05.03.2023	0.06	79	4
Fox 35	Female	Adult	8.0	17.03.2023	12.8	127	10
Fox 36	Female	Juvenile	5.4	30.03.2023	2.9	1010	68
Fox 37	Male	Adult	6.7	11.04.2023	12.4	4573	303
Fox 38	Male	Adult	6.8	16.10.2023	5.8	1604	105
Fox 39	Male	Adult	6.6	07.02.2023	15.0	1023	72
Fox 41	Female	Adult	4.4	09.02.2023	5.0	5236	357

3.2 Resource select function (RSF)

The analysis reveals intriguing insight into the dynamics of the fox's behavior in relation to farms. Notably, during nighttime, there is a pronounced increase in the likelihood for foxes to remain in close proximity to farms, as seen in figure 4. Furthermore, when considering the variable of cover alongside this, the probability of foxes exhibiting this behavior is significantly amplified, indicating a strong preference for covered areas near farms during the night. During the daylight hours, the foxes display a tendency to avoid infrastructure. However, when cover is present there is a small shift in this trend, suggesting a moderation of their avoidance behavior in the presence of cover. During twilight hours presents a more complex picture, with the foxes exhibiting variability depending on the presence or absence of cover. In the absence of cover, the trend during twilight is relatively mild, indicating a less defined pattern of behavior. When cover is present there is a notable strengthening of the trend, suggesting that foxes are more likely to approach farms during twilight when it is provided by cover.

Conditional logistic regression: diel periode and cover

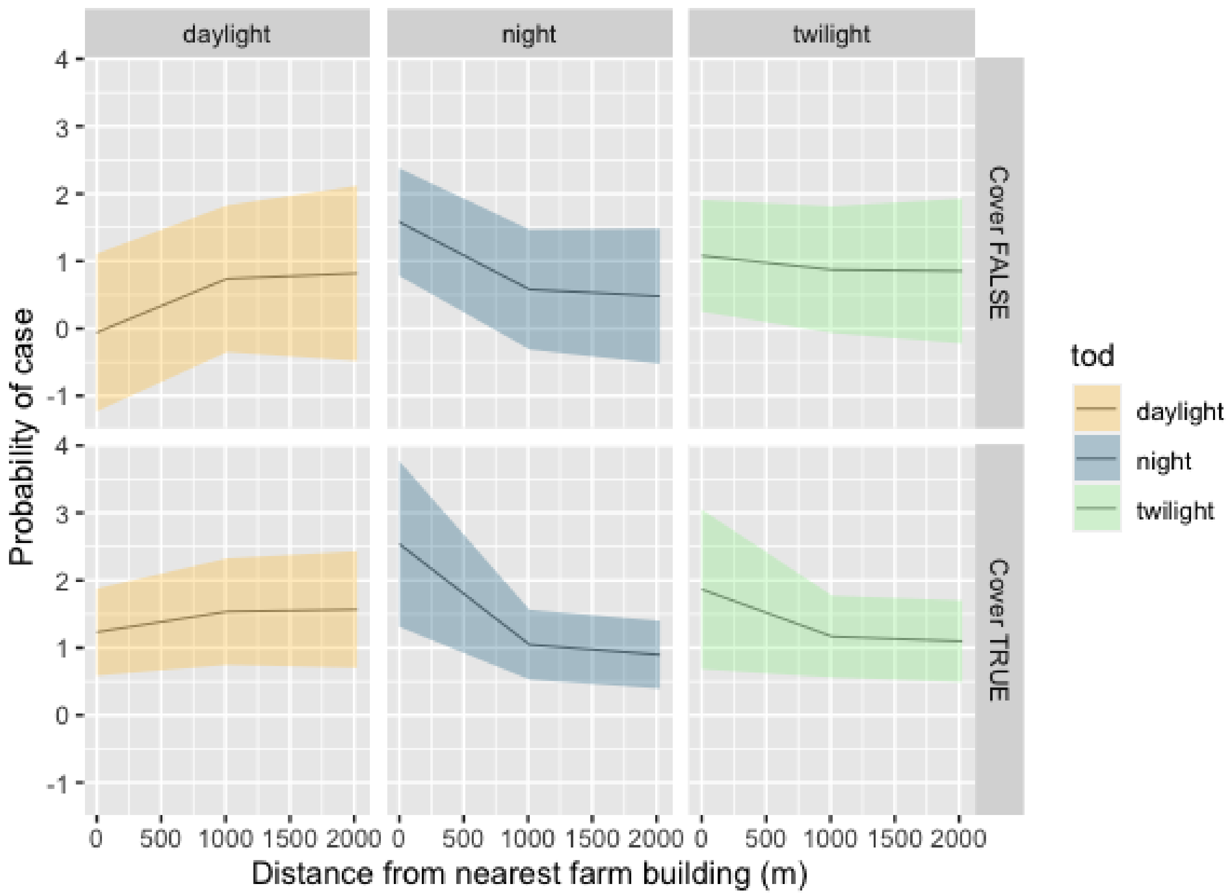

Figure 4: Result from the conditional logistic regression using a 95% confident interval. Showing selection strength for distance from nearest farm building, with the response variables diel period and cover.

The results from the conditional regression analysis indicate that distance from farm buildings during night was associated with a significant positive selection (coef = 1.63964, z = 3.465 and p = 0.000531), as well as twilight (coef = 1.13821, z = 2.782 and p = 0.005402). Conversely, a negative selection, suggesting that selection to stay close to farms was avoided, emerged during daylight (coef = 0.11535, z = 0.715 and p = 0.474599).

When considering diel period under the influence of cover, it was observed that distance from farms in all diel periods was significantly affected by positive selection. Daylight exhibited a slight increase in selection (coef = - 0.07132, z = - 0.466 and p = 0.640986), but still suggests that foxes in general tend to avoid farms during this period. Positive selection was reinforced during the night (coef = -0.33026, z = - 2.619 and p = 0.008814), as well as twilight (coef = -0.50268, z = -3.160 and p = 0.001576)

Table 2: Estimates from performing a conditional regression model, with diel period and cover as covariates in relation to distance from farms.
Divided into 9 effects, looking at daylight (log (distance. nearest. farm + 1)) in relation to night and twilight. Cover, without the effect from covariates, during day (cover) as well as night (log (distance. nearest. farm + 1): night) and twilight (log (distance.nearest.farm + 1): twilight. Covariate, diel period and cover, together during daylight (log (distance. nearest. farm) + 1): cover), night (Night: cover) and twilight (Twilight: cover)

Conditional regression model: diel period and cover.

	Coef	Exp(coef)	Se(coef)	Robust se	z	Pr(>│Z│)
Log (distance. nearest. farm + 1)	0.11535	1.12227	0.04680	0.16133	0.715	0.474599
Night	1.63964	5.15332	0.25242	0.47322	3.465	0.000531
Twilight	1.13821	3.12119	0.27661	0.40913	2.782	0.005402
Cover	1.29055	3.6348	0.24451	0.81367	1.586	0.112717
Log (distance. nearest. farm + 1): Night	-0.26008	1.77099	0.04741	0.08542	-3.045	0.002330
Log (distance. nearest. farm + 1): Twilight	-0.14523	0.86482	0.05235	0.07471	-1.944	0.051908
Log (distance. nearest. farm + 1): cover	-0.07132	0.93116	0.04365	0.15294	-0.466	0.640986
Night: cover	-0.33026	0.71874	0.07537	0.12609	-2.619	0.008814
Twilight: Cover	-0.50268	0.60491	0.08261	0.15906	-3.160	0.001576

4. Discussion

This study revealed temporal and spatial changes in relation to distance from farm buildings, influenced by the covariates, diel period and cover, for foxes living in a highly fragmented landscape. The utilization of high-frequency GPS bursts and a resource select function enabled the detection of fine-scale behavior that would otherwise go unnoticed with a lower fixed frequency. By using GPS units to capture rapid bursts of locations allows for an average monitoring duration of 16.4 days (SD ± 10.8). This approach ensured sufficient amount of data collected, that allows to draw conclusions regarding habitat selection within the home range, as well as to observe fine scale, short-lived behavioral events (Hebblewhite & Haydon, 2010). The strength and direction of selection varied throughout the diel periods, with daylight showing the most significant effect of keeping foxes further away from farms. Selection towards farm buildings was strongest during the night, followed by twilight. Additionally, the presence of cover had a significantly positive effect on all diel periods, suggesting that foxes tend to select closer to farms when cover is present.

I found strong evidence of the effect diel period has on red foxes' selection towards farm buildings, confirming the first question (i). Diel periods, as in this study, daylight, night, and twilight, can have contrasting effects on the selection towards farms on a temporal scale. Individuals may display behaviors aimed towards avoiding areas with high human activity, such as farm lots. As a result, maintaining greater distance indicating avoidance of the potential risk associated with human presence. Conversely, during the night, as human activity tends to decrease, reducing the risk of encountering humans, foxes may feel more secure approaching farms. Based on the result from the RSF (table 4), the coefficients show that foxes were 14.2 times more likely to stay closer to infrastructure during the night than during the day. During twilight, fox behavior may display traits from both daytime and nighttime behavior, resulting in intermediate levels of proximity to farms during this period. Consequently, their selection is 1.4 times lower compared to night, but 9.8 times higher than during the day. Overall, this study suggests that diel period strongly influence of how close foxes choose for proximity to farms, in a highly fragmented landscape, as foxes demonstrate varying degree of selection based on time of day.

A study done by Gallo et al. (2022), showing similar results on how carnivores tend to become more nocturnal in areas experiencing higher levels of human disturbance. The parallels drawn between the findings presented and the results from this study are interesting, as these studies were performed in different continents and ecosystems. Despite these differences, the results suggesting that species living in human-dominating environments, will exhibit some degree of avoidance behavior to navigate the landscape safely (Gallo et al., 2022). As a result, changes in temporal behavior to avoid potentially dangerous interactions may serve as an alternative strategy (K. Smith et al., 2023). Considering the results from the mentioned study together with my findings suggests that human presence significantly affects the temporal utilization of the landscape by red foxes.

Natural landscapes are under threat from anthropogenic development factors, including increased human population density, land conversions, and transportation infrastructure (Hill et al., 2022). In fragmented ecosystems, the availability of habitat patches for animals that seeks spatial refuge from human disturbance or negative interactions with other species is limited (Mullu, 2016). A species` ability to adapt to human-altered ecosystems likely reflects on the variety in their capacity to survive in a highly fragmented landscape (Woodroffe, 2000).
As human population density rises, animals may become more inclined to engage in conflict with humans as a consequence (Hill et al., 2022). Repeated exposure to human activity may cause wildlife to become bolder, potentially leading to increased interactions between humans and foxes (Gil-Fernández et al., 2020; Morton et al., 2023; Padovani et al., 2021). However, a study done by Kobryn et al. (2022) showing that foxes living in a highly urban area in Australia showed a significant avoidance of residential areas, and strongly selected for urban parkland. By this it is important to notice, as Larm et al. (2021) mentions, that certain individual and situational factors, such as sex, age, breeding status, group composition, time of year, food availability, prior experience with humans, and personality traits, can influence an animal's tolerance and the risk-foraging trade-off.

I found compelling evidence that cover has a profound effect on foxes' selection towards farms, confirming the second question (ii). As seen in the results, cover strongly influenced the foxes' tendency to select for close proximity to farms (figure 4). Trees and dense vegetation, can provide foxes with a sense of security and protection from potential threats (Gil-Fernández et al., 2020). The presence of cover may reduce the perceived risk associated with human activity or other potential dangers, encouraging foxes to utilize the resources provided by farms while minimizing their exposure to perceived threats. Results showing, based on the coefficients (table 4), that the selection towards farms during daylight when cover is present is 1.2 times greater. This suggests that cover continues to exert a significant effect even during daylight hours. Although the results show that foxes still actively avoid farms, the effect is less pronounced. During night the effect is 4.9 times stronger, and 2.3 times stronger during twilight. Overall, this study demonstrates that there seems to be a trend that cover significantly influences foxes` proximity to farms in a highly fragmented landscape.

This behavior aligns with observations done by Gil-Fernández et al. (2020), where urban red foxes exhibited significantly greater confidence, compared to peri-urban individuals, when they were sheltered by dense vegetation cover. Given that human-activity is more pronounced in urban environments, the selection for cover in densely populated areas pose a possible explanation (Gil-Fernández et al., 2020). Other urban-adapted carnivore, as the spotted hyena (*Crocuta Crocuta)* have also been observed with similar behavior (Boydston et al., 2003). By the results from my analysis and the mentioned studies, highlighting how adaptable species adjust their activity pattern and behavior across diverse habitats.

The remarkable adaptability of the red fox and its utilization of human resources in anthropogenic environments significantly influence wildlife management and human-wildlife interactions (Jahren et al., 2020 ; Schell et al., 2021). Human subsidies can dramatically alter the ecology of predators and their prey species (Reshamwala et al., 2018). Exploiting a variety of habitats, red foxes exhibit both positive and negative ecological impacts (Hradsky et al., 2017). While they help manage rodent populations, their predation on small mammals, birds, and insects can disrupt local ecosystems, raising concerns for biodiversity conservation (Saunders et al., 2010). By this, red foxes can contribute to the declining numbers of endangered species and can play a significant role in altering the surrounding ecosystems as humans develop the landscape (Khattak et al., 2023). Changes in local abundance, as foxes increasingly rely on human-altered food sources, can result in disrupted predator-prey dynamics, leading to the emergent of an urban predation paradox (Leighton et al., 2023). The paradox arises from conflicting predictions regarding the effects of top-down control in highly fragmented ecosystems, caused by a decline in predation rates alongside an increase in predator numbers (Fischer et al., 2012).

As urbanization and fragmentation of the environment increases, the challenges in managing wildlife population are becoming bigger (Bradley & Altizer, 2007; Hanski, 2011). If the management goal is to reduce red fox population, identifying how foxes may utilize farms in their environment, by providing extensive resources, can help raise awareness and potential management measures. Because foxes can benefit from resources associated with farms, both in a direct and indirect ways, predation pressure experienced from foxes may be heightened in these regions (Andrén & Andren, 1994; Khattak et al., 2023). By restricting access to resources regarding farms can lead to significant impacts on population dynamics and highlighting the importance of implementing such measures in the management strategies for red foxes and other generalist predators (Jahren et al., 2020c). Because carnivore species increasingly inhabiting human altered landscapes in recent decades, suggests a future of coexistence between carnivores and humans (Gallo et al., 2022). Consequently, gaining a deeper understanding of the biology of these animals will be increasingly crucial for leveraging these circumstances towards carnivore conservation and minimizing their potential impact on humans (Bateman & Fleming, 2012).

The use of GPS telemetry has revolutionized the understanding of the ecology for a variety of species (Recio et al., 2011; Tomkiewicz et al., 2010). This allows for the observation of animals without being affected by the bias of human presence (Trappes, 2023). However, challenges associated with using GPS telemetry in studying animal behavior often stem from limitations in the telemetry data or other covariates (Hebblewhite & Haydon, 2010). A typical strategy, exemplified by Gravel et al. (2023), involves using a low fix frequency over a longer period of time, which is effective for tracking long-distance dispersal (Walton et al., 2018). However, by using this method, it would not be able to detect rare events, such as short-term interactions with farm infrastructure (Bischof et al., 2019). Thus, by using high-frequency GPS position fixes in conjunction with a highly detailed landcover map, I was able to study specific behavior. This made it possible to detect how foxes utilize farms, based on the covariates diel period and cover, and allows for the detection of why foxes choose to be in a specific spot at a particular time.

Modifications of the techniques present here could be advantageous for any investigations into the temporal and geographical dynamics between GPS-monitored animals and particular ecosystem characteristics (Bouten et al., 2013; Rutter, 2007). The trade-off between resolution and battery life might not be as significant in the future due to technological advances (Hebblewhite & Haydon, 2010). Until then, using high-frequency GPS bursts provides a limited means to mitigate this compromise. Given that GPS monitoring can be invasive, it`s essential for researchers to prioritize minimizing animal stress and discomfort throughout the monitoring process (B. J. Smith et al., 2018). This includes maximizing the usefulness of each deployment to reduce the number required.

Topics for further research that would be interesting to investigate is how age and sex influence spatial and temporal behavior in relation to farms. Within a species, it is possible that different age groups could react differently to farm infrastructure (Woodruff, 2001). Juveniles may exhibit less anxiety towards unfamiliar structures and engage in more adventurous behavior compared to adults (Morton et al., 2023). Furthermore, the use of GPS technology, as demonstrated in this study, presents opportunities to explore additional human-wildlife interactions (Rutter, 2007). Human infrastructure and activities intersect with the habitats of larger carnivores like wolves, bears, and lynx, human-wildlife conflict has been a recurrent problem throughout Scandinavia (May et al., 2008). Carnivores frequently prey on livestock, endanger human safety, and cause property damage (Lazzeri et al., 2024). These activities contribute to conflict between conservation efforts and community needs (Ghosal et al., 2015). However, there are promising approaches to mitigating these conflicts using GPS technology (Recio et al., 2011). Carnivores equipped with GPS collars allow researchers to precisely map how they use their habitat and travel in the landscape (Bouten et al., 2013). With the aid of this data, wildlife managers may pinpoint conflict hotspots and build buffer zones or wildlife corridors around human settlements (Hebblewhite & Haydon, 2010).

Further exploration of advancements and additional testing using the methods outlined in this study would be valuable. This approach can help researchers obtain more accurate information, especially when examining scenarios similar to those discussed earlier. Moreover, the application of these methodologies has the potential to improve data quality in diverse situations requiring a comprehensive understanding of wildlife behavior in response to specific habitat features.

5. Conclusion

Advancements in telemetry technology, combined with adaptable analytical approaches, provides insight into short-term behavior that are still biologically significant. Together with GPS bursts and a step selection analysis revealed how red foxes' proximity to farms is modulated by diel period and the availability of cover, in a highly fragmented landscape. The results are suggesting that farms play an important role in shaping spatio-temporal behavior of red foxes living in a highly fragmented area. Foxes exploit a variety of both direct and indirect resources associated with farms. If the management goal is to reduce the impacts foxes have on the environment, resources provided by human activity should be removed or constricted for wildlife.

The use of high-frequency GPS telemetry presents new opportunities for advancing our understanding of wildlife behavior and habitat use, applicable not only to red foxes but also to other wildlife species. This methodology has potential to benefit future investigations of the relationships between humans and wildlife as well as to guide conservation initiatives in areas with high human activity.

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