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Linking high frequency GPS data with multiscale habitat selection; A study of an adaptable carnivore in a fragmented landscape.

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Preface

This thesis was written as my final work in my master's degree at the Norwegian University of Life Sciences (NMBU), and is part of the Red fox project at the University.

Working on this project has been truly fun and challenging, and has taught me a lot about the ways of science. For teaching me this, and for providing invaluable guidance, I would like to thank my supervisor Richard Bischof at NMBU. Working with him has been a pleasure. I would also like to thank my fellow colleage Benedicte Beddari for helping me in finding out what the foxes were up to.

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Abstract

BACKGROUND: The expansion of human activity has had a significant impact on wildlife. Some of these effects are challenging to observe, especially in the case of illusive and nocturnal carnivores. GPS technology offers solutions to these challenges, yet previous telemetry studies have failed to capture fine-scale behaviors and movements, mainly due to long intervals between captured positions. The aim of this study was to investigate how new ways of using GPS technology can be used to reveal some of these effects, through studying fine-scale patterns of red fox *(Vulpes vulpes)* selection towards infrastructure in a human-dominated landscape. I examined 16 wild red foxes living in fragmented, human-dominated landscapes. The foxes were captured in box traps and fitted with lightweight GPS collars, collecting periodic bursts of positions at 10 to 15 second intervals between relocations. Three hundred and seventy-eight relocation clusters were inspected to determine likely activity at the sites. RESULTS: Collected data were analyzed using a step selection function to determine selection towards infrastructure within the home range over fine changes in distance to infrastructure, and at different times of day. Activity at relocation clusters was analyzed using a general linear mixed effects regression model, to determine how proximity to infrastructure influences the likelihood of resting and foraging behavior. In the step selection analysis, the foxes showed significant differences in selection at specific distances to infrastructure, depending on time of day and presence of cover. The foxes avoided proximity to infrastructure in open areas during the day, and selected for proximity to infrastructure at night. Foraging behavior at relocation clusters was more likely to occur near infrastructure than resting, which was more likely to occur in remote areas. Dung piles, bird feeders, carcass remains and compost bins were repeatedly visited by foxes when foraging. CONCLUSIONS: The findings imply that red foxes are drawn close to human infrastructure at night to exploit available food subsidies, while avoiding direct confrontation. Using high frequency GPS bursts provided information about short-lived events in activity that would have remained hidden if using conventional approaches, and offers a reduction in the tradeoff between battery life and monitoring resolution.

Sammendrag

BAKGRUNN: Menneskelig utvikling har medført dramatiske effekter for viltlevende dyr. Enkelte av disse effektene er vanskelige å observere, særling hos sky og nattaktive rovdyr. GPS teknologi kan brukes til å avdekke disse effektene, men tidligere telemetristudier har i liten grad lykkes i å belyse fin-skala atferd og bevegelser, hovedsaklig grunnet for lange intervaller mellom registrerte posisjoner. Målet med denne studien var å undersøke hvordan denne teknologien kan brukes på nye måter for å avdekke slik atferd, ved å studere fin-skala mønstre i rødrevens (*Vulpes vulpes*) seleksjon mot infrastruktur i et menneskedominert landskap. Jeg undersøkte adferden til 16 ville rødrev som ble fanget i fragmenterte, menneskedominerte landskap. Revene ble fanges i båsfeller, og utstyrt med lette GPS halsbånd som registrerte periodevise, hurtige sekvenser av posisjoner, med 10-15 sekunder mellom hver posisjon. Tre hundre og syttiåtte ansamlinger av registrerte posisjoner ble inspisert for å bestemme sannsynlig aktivitet på punktet. RESULTATER: Innsamlet data ble analysert ved hjelp av en steg-seleksjonsmodell for å bestemme graden av seleksjon for infrastruktur innen hjemmeområdet, til ulike tider av døgnet. Ansamlinger av posisjoner ble analysert ved hjelp av en generell lineær blandet effekt regresjonsmodell, for å avgjøre hvordan nærhet til infrastruktur påvirker sannsynligheten for matsøk og hvile. I steg-seleksjonsanalysen viste revene signifikante forskjeller i seleksjon ved spesifikke avstander til infrastruktur, avhengig av tid på døgnet, og tilgjengelighet av dekning. Revene unngikk nærhet til infrastruktur i åpne områder på dagtid, og selekterte for nærhet til infrastruktur på nattestid. Adferd knyttet til matsøk ved ansamlinger av posisjoner, var mer sannsynlig nærme infrastruktur enn hvile, som var mer sannsynlig i mer ødeliggende områder. Besøk ved hauger bestående av husdyrgjødsel og høy, diverse kompost og frukt, fuglematere og åtselrester ble registrert ved gjentatte tilfeller. KONKLUSJONER: Disse resultatene indikerer at rødrev tiltrekkes infrastruktur på nattestid for å utnytte tilgjengelige matsubsidier. Samtidig søker de å unngå direkte konfrontasjon med mennesker. Periodevise, høyfrekvente sekvenser av posisjoner, gav informasjon om kortvarige hendelser i aktivitet som ville ha forblitt skjulte ved å benytte mere konvensjonelle metoder. Dette bidrar til å redusere avveiningen mellom batterilevetid og overvåkningsoppløsning.

Contents

Acronyms and definitions

Cluster: Locations where a foxes has stopped to spend time, resulting in multiple GPS-fixes within a small area. Also referred to as “relocation clusters”.

Temporal resolution (high/low): High temporal resolution refers to GPS data collected using short fix-intervals.

Real position: An actual position from the movements of a fox.

Control position: A position generated in the “null”-model used in A-RQ1, not used by a fox.

Null-model: The area defined as available to an animal during the study. In this study, this is in the form of available points in the landscape, defined by the step-selection model.

Mesopredator: “Mid-ranking predator in a food web, regardless of its size or taxonomy” (Prugh et al. 2009)

(Human-derived) food subsidies: Food resources procured directly or indirectly from humans.

Spatio-temporal: Referring to aspects of space and time simultaneously.

GPS: Global positioning system.

VHF: Very high frequency: Remote sensing method using radio-transmitters.

A-RQ1: Analysis for research question 1.

A-RQ2: Analysis for research question 2.

Fix/GPS-fix: Location estimate recorded by a GPS unit (Tomkiewicz et al. 2010)

FI: Fix interval: The time interval between consecutive recorded locations.

GLMM: General linear mixed model: Regression model.

GPRS: General packet radio services

Figure 1: Acronyms and definitions.

1. Introduction

The process of habitat loss and fragmentation is currently one of the greatest threats to biodiversity (Butchart et al. 2010; Pereira et al. 2010), including mammalian species (Haddad et al. 2015; Schipper et al. 2008). The degree of this development can be viewed as a gradient of change in ecological systems (Bateman & Fleming 2012). Each point along this gradient presents novel and complex challenges to the species inhabiting them. These must be met for the animals to thrive (Birnie-Gauvin et al. 2016; Kowarik 2011). Only a few species succeed in adapting to their altered habitats (Lowry et al. 2013; McKinney & Lockwood 1999). Human-dominated landscapes can be rich in food subsidies, with increased fitness and population density often observed in populations of so-called “urban exploiters” in comparison to their rural relatives (Luniak 2004; McKinney 2006). However, the overall result of human development is biotic homogenization and species richness decline (McKinney & Lockwood 1999; McKinney 2006; McKinney 2008).

Within the gradient ranging from pristine nature to fully urbanized environments are mosaics of suburban, agricultural and forested areas. These are often inhabited by a range of species such as early successional plants, mesopredator mammals and omnivorous or frugivorous birds (McKinney 2006). Humans and wildlife may therefore live in close proximity to one another, potentially bringing consequences for one or both (Bateman & Fleming 2012; Conover 2001). For wildlife, the outcome is not always obvious and may result in either an increase or decrease in fitness, depending on the specific scenario. For example, increased food supply may come hand in hand with an increased risk of collision with transportation (Birnie-Gauvin et al. 2016; Coffin 2007).

Interactions involving carnivores, some of which are dangerous to livestock, pets, or even humans, have caused numerous conflicts (Treves & Karanth 2003). Although they are not often a direct threat to humans or large livestock, medium sized carnivores may compete with humans over game species (Panzacchi et al. 2008; Reynolds & Tapper 1996), which these animals in some cases effectively control (Jahren et al. 2016; Lindstrom et al. 1994). Additionally, predation on endangered species is a problem (Aarvak et al. 2017). Management goals for these medium-sized carnivores can be challenging and diverse, ranging from conservation (Angerbjörn et al. 2013), to controlling numbers of highly abundant species

(Macdonald & Reynolds 2004). Other concerns regarding medium-sized carnivores, are risk of disease transfer of various zoonosis to humans or pets (Lempp et al. 2017), their role as seed dispersers (Grunewald et al. 2010), and predation of small domestic animals such as domestic chickens (*Gallus gallus domesticus*) (Baker & Macdonald 2000; Bateman & Fleming 2012). For these reasons, a solid knowledge basis is required for making informed decisions regarding these species.

Due to their often nocturnal and crepuscular activity patterns and elusive behavior towards humans (Sillero-Zubiri et al. 2004), direct observation of behavior and movement can be difficult. Advances in technology over previous decades have led to substantial advancements in methods for studying animal behavior (Tomkiewicz et al. 2010). Remote sensing applications, such as GPS technology with units attached to the animal, are currently among the more popular methods for studying the animals' movements (Cagnacci et al. 2010). A unique strength of this method – in comparison with methods like very high frequency (VHF) – is to provide the researcher with accurate and precise time stamped location data of animal movements regardless of weather and light conditions (Coelho et al. 2007; Frair et al. 2010; Tomkiewicz et al. 2010)

As with other tracking methods, there are limitations to remote sensing applications (Cagnacci et al. 2010). The number of positions obtained from a single deployed unit is constrained by battery capacity, although technological advances have reduced this issue (Brown et al. 2012; Frair et al. 2010; Tomkiewicz et al. 2010). This necessitates a tradeoff between battery longevity, the temporal rate at which the GPS units capture positions, and the weight of the units (Johnson & Ganskopp 2008; Mills et al. 2006; Recio et al. 2010; Tomkiewicz et al. 2010). With the exception of the largest animals, the total weight of the collar needs to be low to avoid affecting the animal (Wilson & McMahon 2006). The battery capacity must therefore be limited for small to medium sized animals (Ryan et al. 2004). In order to make inferences about movements and behavior occurring over longer time frames such as seasons, and at larger spatial scales such as home ranges, long monitoring durations are favored (Johnson & Ganskopp 2008). To reach these durations without rapidly draining battery capacity, fix intervals (hereby FIs) are often in the range of hours as a consequence (Johnson & Ganskopp 2008). The resulting data gives an incomplete account of the animals' movement path, and is not suitable for documenting detailed behavior (Brown et al. 2012; Mills et al. 2006; Zeller et al. 2016)

Research questions regarding large scale behavior have been studied in a range of species (Beckmann et al. 2012; DeCesare et al. 2012; Forester et al. 2009; Salek et al. 2015). In contrast, movement and behavior of animals at very fine temporal and spatial scales have received less attention in the field of GPS monitoring, although there are some examples using FIs in the range of 2-15 minutes (Bonnell et al. 2013; Brown et al. 2012; Hradsky et al. 2017; Palacios & Mech 2011; Postlethwaite & Dennis 2013; Stillfried et al. 2015; Zeller et al. 2016). To my knowledge, the only studies using FIs in the order of seconds are studies of birds (Humphries et al. 2012; Ryan et al. 2004; Sabarros et al. 2014; Weimerskirch et al. 2007), and loggerhead sea turtles (*Caretta caretta*) (Schofield et al. 2007). The reasons for this might be attributed to the previously mentioned tradeoff between battery capacity and FI, and the fact that GPS locations inherently have some degree of spatial inaccuracy. On a very fine scale, this can substantially affect the inferences derived from the data. A measurement of this error is therefore important for evaluating the degree to which the results are valid (Frair et al. 2010).

I propose that by combining GPS location data of very high temporal grain (FI <1 min), with both a step-level null model and subsequent field inspections at relocation clusters (hereby clusters) of recorded locations, new insights about the behavior of carnivores can be gained. As a case in point, this study investigates how infrastructure in the home range drives spatio-temporal patterns in red fox activity at multiple scales. This is studied both at the larger home range scale, and at the very fine scale of specific, often short-lived behavior events. To maximize monitoring duration without sacrificing temporal detail, GPS units are programmed to capture rapid bursts of locations, separated by longer intervals. To my knowledge, this scheduling of relocations has not been used prior to deployment by the Red fox project at NMBU (Bischof et al. 2018), which this study is a part of.

Red foxes are an interesting species to study in this context, because they thrive along the gradient from undisturbed natural areas to urban environments, including city centers

(Bateman & Fleming 2012). They are able to exploit human food subsidies in urban environments (Bino et al. 2010; Contesse et al. 2004). Highly mobile, they manage to exploit a wide variety of niches when available, due to their lack of specialization in both food items and habitat requirements (Lloyd 2013; Macdonald & Reynolds 2004; Soulsbury et al. 2010).

1.1 Research questions and predictions

Main Question: How does infrastructure in a human-dominated landscape drive spatio-temporal patterns in red fox activity at multiple scales?

RQ1: Do foxes select for areas with infrastructure within their home range during periods of activity? - The purpose of this question is to investigate how these animals relate to infrastructure in their environment, depending on time of day, presence/absence of cover, and how far from it these features matter to foxes.

- P1.1: Selection for proximity to roads and buildings. - Due to (likely) available food subsidies close to humans, and the ability of red foxes to adapt to, and exploit these (Bino et al. 2010; Lombardi et al. 2017; Lowry et al. 2013; Macdonald & Reynolds 2004).

- P1.2: Selection for proximity to infrastructure is strongest during the night and in the presence of cover, and weakest during daylight and in the absence of cover. – Red fox activity patterns has been seen to shift spatially and temporally in order to exploit available resources, and avoid interaction with humans (Boitani et al. 1984; Diaz-Ruiz et al. 2016; Doncaster & Macdonald 1997). Also, other studies indicate the patterns in selection suspected by P1.2 (Hradsky et al. 2017; McKeown 2018).

- P1.3: Effects of factors influencing selection for or against proximity to infrastructure will become less pronounced with increasing distance (buffer size) due to scale dependence. - Selection for specific habitat features tends to occur at local scales and becomes less important as scale increases (Wiens 1989) (DeCesare et al. 2012; Zeller et al. 2016).

RQ2: What brings foxes into proximity to infrastructure? – The purpose of this question is to determine where foxes prefer to perform different activities (foraging/resting), in relation to infrastructure, and what specific features likely attract these animals towards infrastructure.

- P2.1. Relocation clusters in close proximity to infrastructure are more likely to be associated with foraging and less likely with resting, than relocation clusters in more remote forested areas. – Based on the rationale and literature provided for P1.2, foxes should be more likely to use areas near humans for foraging, and areas further away for resting. (McKeown 2018) showed this pattern, using data of far lower temporal resolution.

2. Materials and methods

2.1 Study area

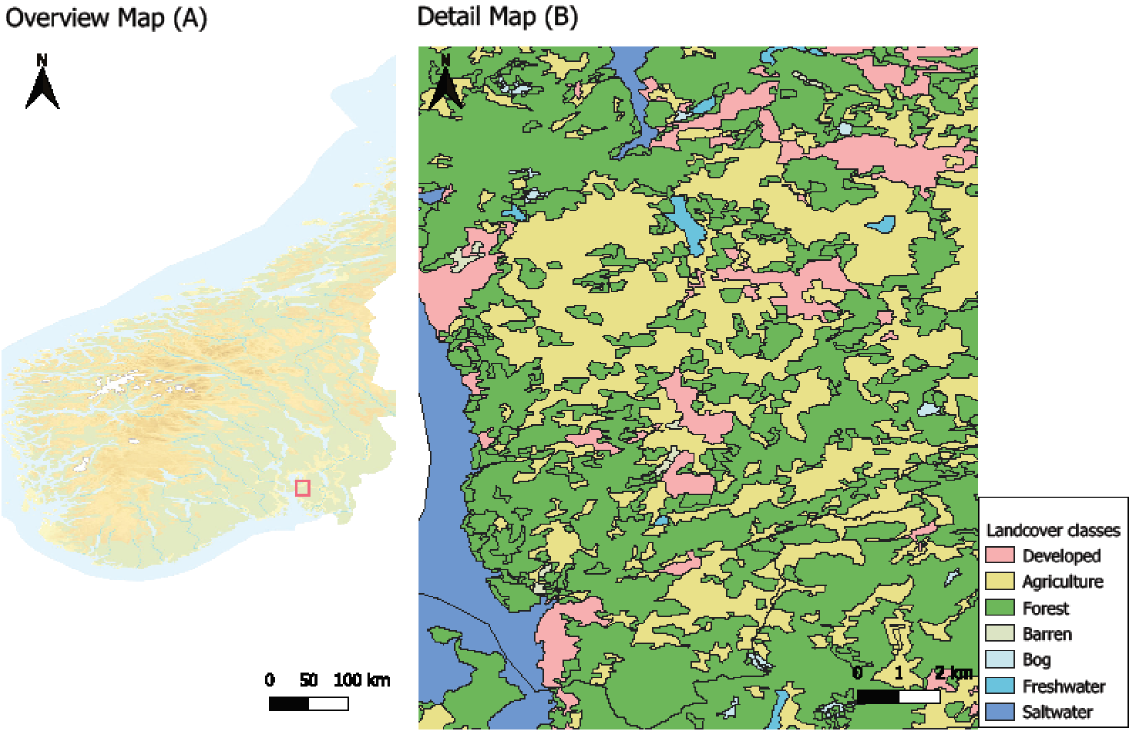

Figure 2: Study area with location in southeastern Norway (map A), and an approximate overview of Vestby and Ås municipalities, where most of the data were collected (map B). Note the amount of various land cover classes in map B.

The study is based on data provided by the Red fox project, with a base of operations at the University of Life Sciences in Ås, Norway.

The study area is situated in southeastern Norway, in municipalities Vestby and Ås. These are encompassed in the rectangle drawn by coordinates: 59.47 - 59.77 N, 10.62 - 10.89 E (Decimal degrees, WGS84) (Kartverket 2017). Elevations for the area is 0 – 179 m a.s.l (Kartverket 2012). One fox dispersed further south during data collection, and reached Fredrikstad municipality (approx. 59.05 – 59.32N, 10.61 – 11.13E) (Kartverket 2017). The following description will cover Vestby and Ås municipalities (235 km² combined (SSB 2016)), as most of the data were collected here. The area is situated in the boreonemoral vegetation zone, and in the vegetation section “slightly oceanic” (Moen & Odland 1998). The coldest months of the year are equally January and February at average temperatures of -4.8

°C (1961-1990), and -3.5 °C (2014-2018) for whichever month was the coldest that year. The warmest month is July, at an average temperature of 16.1 °C (1961-1990), and 17.6 °C (2010-2018). Snow covers the ground irregularly from approximately early December until late March (NMBU 2019).

Average human population densities for Vestby and Ås municipalities are approximately 162 inhabitants/km² (SSB 2019d), where the majority of these (~84%) live in densely populated areas, of which there are two main towns; Vestby and Ås (SSB 2018). These are surrounded by suburban areas. The remaining population live more scattered across the landscape, in rural farmland, as defined by (Bateman & Fleming 2012). The landscape is heavily affected by human land use, resulting in a fragmented mosaic of forest (53.4 %), cropland (30.4 %), developed and transportation (9.3 %), barren areas (4.7 %), freshwater (1.1 %), pasture (0.6 %) and bog (0.5%). The forests consist of conifer forests (84.6%), deciduous (4.1%), mixed conifer and deciduous (3%) (NIBIO 2017). However, much of the conifer forest also contains some percentage of deciduous species. The conifer forests are dominated by Norway spruce *(Picea abies),* Scots pine *(Pinus sylvestris)* and birch *(Betula spp.).* Other common species include rowan *(Sorbus aucuparia), Salix spp*. and European aspen *(Populus tremula).* About 92% of the forested area is considered “productive” (SSB 2019a), and very little of the total area is under any form of legal protection (~1%) (SSB 2019b), which means most of the forested areas are likely logged on a regular basis.

It is permitted to hunt and trap foxes across the whole study area between July 15th and April 15th (Lovdata 2017), which means these animals are protected by law the during the pup-rearing part of the breeding season. The average number of foxes shot for the time period 2010-2018 for both municipalities combined, were 0.47 foxes/km²/year (SSB 2019c).

2.2 GPS units and data collection

The GPS units were developed and built by members of the NMBU Red fox project. A brief description will be provided here. I refer to Bischof et al. (2018) for more detailed technical descriptions. The units are small and lightweight, -approximately 125 grams, and are composed of various off-the-shelf components, built onto a customized printed circuit board and a standard micro controller (ATmega 328p). The most important component would be the SIM808 GSM/GPRS Simcom™ module, which has GPS, GPRS and Bluetooth capabilities built in. The GPRS functions enable the collar to be controlled via SMS messages from any type of basic cellphone. The location data collected by the units is sent to a dedicated server via GPRS, available for download. External dimensions of the 3D-printed plastic cases used to house the components and batteries are 70mm x 40mm x 40mm. The collars are made of 20mm x 1mm plastic coated strap material (BioThane ®). These are fit to size using metal rivets, and secured to the foxes using a thin plastic zip-tie, with a weak point consisting of a ~ 3mm cotton string as a wear-and-tear drop off mechanism. Sharp edges were not in contact with the fox. The units reduce their sample rate to only 1 position every 6 hours after reaching 37% of battery capacity to increase chances of collar recovery.

A measure of the true location error of the GPS units during movement, as recommended by (Cagnacci et al. 2010; Frair et al. 2010), was performed by Bischof et al. (2018). A highly accurate reference unit (APX-15 GNS/IMU), and two of the custom GPS units were mounted on the roof of a car, and then driven at slow speeds of 1-5 m/s through narrow forest roads, where tree canopies vary. The reference unit is highly accurate (down to a few centimeters), even during times when the GPS signal is temporarily reduced. This is due to its inertial measurement unit (IMU). Post processing of the raw data from the reference unit yielded an overall precision of about 10 cm. Compared to this, our GPS units had a median true error of 2.4m (95% CI: 0.6m- 10.1m). This is based on the 300 positions captured during the test drive.

Foxes were tracked using rapid burst of 20 positions (10-15 seconds inter-fix time), separated by 10 minute intervals. KML-files were generated from the data, using package “plotKML” (Hengl et al. 2015) in R (R Core Team 2013).

2.3 Fox capture/handling

Red foxes were captured by using baited wooden box traps of the type "Värmlandsk tunnelfelle", with dimensions approximately 3.5m x 1m x 1m. The project operates four of these traps. Additionally, landowners were given an economic reward when trapping foxes for the project. All traps deployed and tended by the project satisfy current rules and legislations (Miljødirektoratet 2016), and have been inspected daily. Trap alarms have also been utilized for most traps, though not as a substitute for daily inspection. Traps were baited, usually with dead chickens (*Gallus gallus domesticus)*.

Following a fox capture, a team of typically two to four people has been assembled within about 2 hours. Captured foxes were handled with a catch pole, before using neck tongues and gloves. Care and caution to avoid unnecessary stress of the animals was prioritized during the whole process. For example, by blindfolding them with a black cloth, and avoiding high noise. Sex, weight, broad age category and general health status were determined, as well as hair and fecal samples for future DNA analysis. Two collars with GPS units were prepared for each capture, to ensure a working unit. A collar with a verified working GPS unit was fitted (not tightly) around the neck of the fox. The entire process lasted 10-20 minutes**.** By not tranquilizing the animals, they can be released without being impacted by anesthetics. None of the captured foxes showed apparent injury such as lacerations, fractures or signs of apparent disease. Had we caught such a fox, it would not be collared, and depending on the severity, euthanasia could be an option. Juveniles (<1yr) were identified by body weight, tooth wear and general appearance. All capture and handling done by the Red fox project conformed to the current laws and regulations in Norway and the study was approved (case ID 2016/4769) by the Norwegian Animal Research Authority (FOTS) under the auspices of the Norwegian Food Safety Authority.

2.4 Cluster visits

Clusters were defined by loading kml files containing positions and tracks of a given fox into Google earth (Google 2019), and creating numbered “pins” for each cluster. In order to be defined as a cluster, the following criteria must be met: Minimum 5 consecutive positions grouped together in a minimum area of approximately 20 meters, indicating the fox has stopped to interact with/inspect some specific feature for approximately 1 minute. As many clusters as possible were inspected within one week of the fox visiting the site. Clusters where the fox had visited very recently, or were likely still present at, were avoided in order to not interfere with behavior. The protocol for identifying, visiting and recording data from the clusters can be viewed in Appendix 1.

The identification of clusters was done by visually inspecting the data. Cluster visits were not randomized due to practical limitations, but clusters of all sizes and in different habitats were identified and visited, resulting in something close to a representative sample with a total of 378 clusters. Later in the project, from fox 19 and onwards, the process of identifying clusters was automated in R. To check if the manual identification/visitation-process resulted in any major bias towards clusters in certain habitats, a comparison between the two was conducted. Clusters identified using both methods were overlayed with highly detailed 1:5000 AR5 land cover maps (NIBIO 2017), to extract habitat information for each visited cluster by using the function “over” in the package “sp” (Bivand R.S. et al. 2005). The proportions of visited clusters in the various habitat categories were calculated for both manually identified clusters and automatically identified clusters, and compared to each other.

If signs of likely hunting behavior, prey remains, scavenging or herbivory was observed at a cluster, the prey type/species or food item was recorded. A summary of these observations was made. Additionally, the likely source of this food was determined. To check for recurring patterns of specific behaviors at clusters in association with specific habitat features, a summary of the relationship between these were made.

2.5 Data analysis and statistical tests.

All analyses and statistical tests were performed using R v.3.5.1 (R Core Team 2013), and its associated packages.

Two primary analyses were performed. The first (A-RQ1), analyzed to what degree foxes selected for proximity to infrastructure within the home range, by using GPS data in combination with a step-level null model, and highly detailed land cover maps (NIBIO 2017). The effect of fine changes in spatial scale (distance to the nearest infrastructure), was looked at in this model. Temporal and spatial aspects were analyzed jointly, to uncover how selection for these areas changed depending on the time of day. This analysis referred approximately to the third order of selection ("usage of the various habitat components within the home range"), as described by (Johnson 1980). When determining how an animal selects one area or resource over another, it is essential to determine the appropriate area available to the animal (Johnson 1980). Determining this by using a step-selection null model can help to solve this challenge (Thurfjell et al. 2014).

Next, information gathered by inspecting clusters were used to determine the differences in activities of foxes at these sites, in relation to human infrastructure, and the specific habitat features they visited (A-RQ2). The behavior studied in this analysis also referred to the third order of selection, but the actual field observations "dived deeper", and looked at "the procurement of specific food items", termed the "fourth order of selection" (Johnson 1980). This analysis used a general linear mixed effects model (hereby GLMM) to determine where foxes preferred to rest, and where they preferred to forage in relation to infrastructure.

The following parts of data processing were done for both analyses: The variable "cover", was created using the function "over" in the package "sp" (Bivand R.S. et al. 2005), by overlaying both real and null-model locations (in A-RQ1), and cluster positions (in A-RQ2), with detailed AR-5 land cover maps (NIBIO 2017) to determine whether foxes experienced cover in the form of forest or not at each location. The distance from each point (real and control/ or clusters) to the nearest road and building, was calculated by overlaying map layers containing information about roads and buildings in the area to real/control and cluster locations. The function “st_distance” in the package “sf” by Pebesma (2018) was used for this. The variable “distance to nearest infrastructure”, was created by choosing the shortest distance to any of these types of infrastructure for each point. The functions “sunriset” and “crepuscule” in the R package “maptools” by Bivand and Lewin-Koh (2019) were used to assign both real and null model locations (A-RQ1), or cluster locations (A-RQ2), to their respective light period. Locations used in A-RQ1 were separated into categories “dark”/ “twilight”/“daylight”. Locations used in A-RQ2 were separated into categories “dark”/ “daylight”.

Because results are reported for combinations of several of these variables, abbreviations were created and used in all figures, see Table 1 below.

Table 1: Abbreviations of variables, and the meanings of these under certain conditions.

Variable abbreviation	Full name	Meaning
inf.T	Infrastructure = True	Within buffer surrounding infrastructure
inf.F	Infrastructure = False	Outside buffer surrounding infrastructure
dark	Lightperiod = dark	Dark hours of the day
twil	Lightperiod = twilight	Twilight hours of the day
dayl	Lightperiod = daylight	Daylight hours of the day
cov.T	Cover = True	Cover is present
cov.F	Cover = False	Cover is absent

2.5.1 Selection for infrastructure within the home range (A-RQ1)

A step-selection function inspired by Thurfjell et al. (2014) and (Fortin et al. 2005a) was used, combined with a conditional logistic regression (Therneau 2015). This method is based on the assumption that the straight line segments connecting two consecutive locations can be viewed as “steps” (Fortin et al. 2005a; Turchin 1998). The model compares a set of habitat variables for real fox locations to the same variables at n control “steps”, based on the previous movements of the individual animal. In this way, the movements of the animal itself help make up the available/control area.

First, the GPS data were cleaned by removing data from the first 24 hours after release in order to minimize the short-term impacts of capture and handling on patterns in the relocation data. Positions featuring inactive behavior were removed, because the interest of the analyses were on active behavior. Obvious errors/false points were also removed. A buffer was generated around all infrastructure. Relocation data for all foxes were combined, retaining fox IDs. The data were divided into sections, separated by temporal gaps in data larger than 60 minutes. Within these sections, steps between mainly 10, but up to 60 minute intervals were chosen to avoid autocorrelation of the data. Based on the step lengths and turn angles of that individual fox, a null-model of control steps was generated for each real step in a section, at a ratio of 10 to 1 control/real. The real locations are connected to the control via the use of a strata variable of fox ID.

Two versions of the model were used. In the simplest version (hereby A-RQ1.1) of the conditional logistic regression model, the chance of drawing a “real/case” point was used as a response variable. Proximity to infrastructure (inside or outside buffer), and strata of fox ID were used as explanatory variables. The buffer size was varied in distance to the nearest infrastructure. The model was repeated for 30 buffer distances along a logarithmic scale from 8 to 98m. Distances outside this range were also investigated. The model call is showed in Figure 3. This analysis was as simple as possible, therefore no model selection using AIC or similar was performed.

```
coxph(formula = Surv(rep(1, 8492L), real) ~
near.infrastructure + strata(id), data =
this.step.data, model = TRUE, method =
"breslow")
```

Figure 3: Model call for A-RQ1.1

Additionally, a more complex version of the model was used (hereby A-RQ1.2). Here, light period and cover were added as explanatory variables. A step-AIC function (Venables & Ripley 2002) was included in the model, which selected the optimal variables and interactions between these, using a 35m buffer size. Again, the model was repeated for 30 buffer distances along a logarithmic scale from 8 to 98m. Distances outside this range were also investigated. The model call is shown in Figure 4. Log-odds predictions, at the scale of the linear predictor, were calculated based on the model estimated coefficients.

```
coxph(formula = Surv(rep(1, 8492L), real) ~ near.infrastructure +
lightperiod + cover + strata(id) + near.infrastructure:lightperiod +
near.infrastructure:cover, data = this.step.data, model = TRUE, method =
```

Figure 4: Model call for A-RQ1.2

2.5.2 Location and characterization of activity clusters (A-RQ2)

Only observations related to foraging or resting were relevant to this model, therefore some observations were removed from the data. Categories of relevant registered activity at the clusters were simplified. More specifically, activities “hunting”, “scavenging”, “herbivory” were simplified to “foraging”. The two activity categories “resting” and “foraging” were used further in the model. Only clusters where the activity had sufficient proof of activity in the form of visual fox signs, prey sign/remains and bed sites were included. For each of these clusters, the duration of the foxes visits to the clusters, and the light period present, were extracted from the GPS locations.

A general linear mixed effects model “glmer”, in the package “lme4” (Bates et al. 2015) was used. Recorded activity at clusters (foraging/resting) was used as the response variable. Category for distance to nearest infrastructure, light period, cover and duration spent in the cluster (by the fox) were included as fixed effects explanatory variables in the initial model. Fox ID was also included, and treated as a random effect. Distance to nearest infrastructure for each observation was divided into five distance categories, “Very close” (0-20m), “Close” (20-60m), “Medium” (60-140m), “Far” (140-220m) and “Very far” =(220-290m).

Model selection consisted of comparing AIC-values when varying explanatory variables within models of the same response variable “resting” or “foraging”. In addition, a test to see whether a nonlinear fit of the variable “duration” would improve the model, cubic splines were added by using the “ns” function in the “splines” package (R Core Team 2018). The number of splines yielding the lowest AIC-values were selected. An interaction link between cover and light period was also attempted. The final model selected, excluded the variable “cover”, and used three splines for the variable “duration”. One regression analysis was performed for each distance to nearest infrastructure and foraging/resting. Therefore, a total of five models were performed. An example model call for one of these is shown in Figure 5

```
resting ~ very.close +
dominant.lightperiod +
ns(durationscaled,3) + (1 | fox.id)
```

Figure 5: One of the model calls for A-RQ2. The response variable was either foraging or resting. This was combined with all distance categories.

3. Results

3.1 Fox capture and GPS data

22 red foxes were trapped over the course of the study period. The first five foxes were not tracked using high frequency bursts, and were excluded from analysis. One unit failed to provide data. GPS telemetry data from 16 foxes were therefore used in the analyses. The monitoring of these lasted an average of 12.3 days (SD ± 5.6), captured an average of 3348 positions (SD ± 746), and an average of 1808 moving positions (SD ± 454). Further details regarding these individual foxes is shown in Table 3.

Table 3: Information summary for all foxes included in analysis.

Fox.ID	Sex	Age category	Body weight (kg)	Date collared	Data days	Number of positions	Number of moving positions
fox_6	male	adult	7.9	18.01.2018	6.2	1,994	965
fox_7	male	adult	6.2	10.02.2018	10.9	3,267	1,864
fox_8	male	adult	6.4	21.02.2018	4.6	2,939	1,734
fox_9	male	adult	5.9	22.02.2018	8.9	3,737	1,507
fox_11	female	adult	5	14.04.2018	10.8	3,899	2,724
fox_12	male	juvenile	4.6	27.07.2018	13.1	2,154	1,215
fox_13	female	juvenile	3.5	27.07.2018	11	2,906	1,646
fox_14	male	juvenile	4.9	03.08.2018	11.5	3,331	1,671
fox_15	male	juvenile	4.6	05.09.2018	12.9	4,319	1,523
fox_16	male	juvenile	4	07.09.2018	11	3,712	1,815
fox_17	female	juvenile	4.1	21.09.2018	9.2	4,617	2,344
fox_18	male	adult	6.5	12.11.2018	14.2	3,298	2,038
fox_19	female	adult	6.4	08.12.2018	7.9	3,041	1,428
fox_20	male	adult	5.5	09.12.2018	16.4	2,519	2,002
fox_21	female	adult	5.5	13.12.2018	27.8	3,643	2,448
fox_22	male	adult	5.5	17.01.2019	20.5	4,195	2,014

3.2 Selection for infrastructure within the home range (A-RQ1).

The aim of this analysis was to determine whether foxes select for infrastructure within their home range when they are active, in addition to investigating how the time of day, presence/ absence of cover and small changes in scale influences this selection. The number of positions used in this analysis, both real and control, is shown in Table 4. In A-RQ1.1, conditional logistic regression combined with a step selection null model resulted in significant differences in relative selection towards infrastructure within the range of 13 to 17 meters from infrastructure, see Table 5. When adding variables “cover” and “light period” in A-RQ1.2, more detailed patterns of selection appeared.

Table 4: The total number of positions used in the model for A-RQ1, divided into combinations of light period and real/control.

Light period	Control/null positions	Real/case positions
Dark	6,640	664
Daylight	590	59
Twilight	490	49

In A-RQ1.1, foxes show significant selection for areas close to infrastructure when they are active, at distances 13, 15, 16 and 17 meters from said infrastructure, shown in Figure 6. Selection for infrastructure is strongest at 15m. With the exception of this short interval however, foxes did not select for proximity to infrastructure overall.

Table 5: Conditional logistic regression coefficient estimates, for areas near infrastructure, using a buffer size of 15m.

A-RQ1.1 – Condition logistic Regression: Calculated using a 15m buffer size

	Dependent variable:
	Selection estimate (Real fox location)
Near infrastructure	0.25**
	(0.04, 0.47)
Note:	*p**p***p<0.01

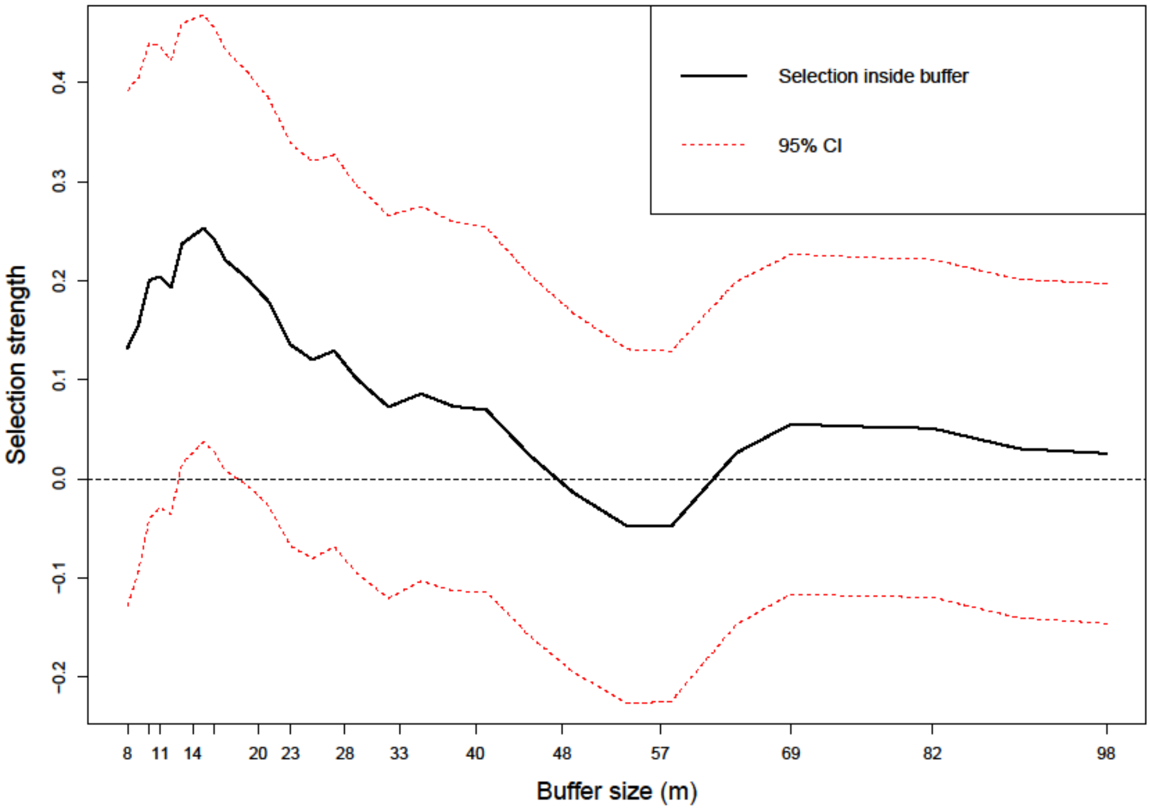

Figure 6: A-RQ1.1; Conditional logistic regression coefficient estimates, showing selection strength for areas near infrastructure, along buffer sizes ranging from 8 to 98m. Strongest positive selection occurs at 15m. Model estimates in black, 95%CI intervals in dashed red lines.

In A-RQ1.2, a buffer size of 27m, showed the most pronounced effects in selection. Regression model output with estimated coefficients is provided in Table 6. At this distance the fox did not select for proximity to infrastructure in general. When adding interactions between the variables, it can be interpreted from the model that foxes avoid proximity to infrastructure in daylight without cover, and that the presence of cover inside the buffer provides higher selection/ less avoidance.

Table 6: A-RQ1.2; Conditional logistic regression coefficient estimates, and 95% Confidence intervals at a buffer size of 27m.

A-RQ1.2 – Condition logistic Regression: Calculated using a 27m buffer size

	Dependent variable:
	Selection estimate (Real fox location)
Near infrastructure	0.07
	(-0.18, 0.31)
Dayl	0.17
	(-0.13, 0.46)
Twil	0.05
	(-0.26, 0.37)
Cover	-0.09
	(-0.26, 0.08)
Inf.T:Dayl	-2.33**
	(-4.32, -0.34)
Inf.T:Twil	-0.34
	(-1.38, 0.70)
Inf.T:Cover	0.47**
	(0.09, 0.86)
Note:	*p**p***p<0.01

Based on the regression output at a buffer size of 27m, predictions can be made for all combinations of variables. These combinations form a wide array of “scenarios”. For example, a fox may experience cover and darkness while being inside the buffer. Figure 7 provides a visual display of these scenarios. See Table 1 for explanation of abbreviations used. The prediction values provided can be interpreted as the chance of drawing a “real” fox position in this scenario, from the sample of both real and control locations. The predicted values are provided with 95% confidence intervals. Some of these scenarios were significantly different from each other at this level of confidence, see Table 7. More specifically, foxes showed a significantly higher relative selection close to infrastructure at night with cover present, than further away from infrastructure (both with and w/o cover) (1 and 2). Selection was also significantly lower for infrastructure during the day with no cover present, than at nighttime, regardless of cover (3 and 4).

Table 7: A-RQ1.2; Combinations of variables significantly different from each other, at a buffer distance of 27m. See Table 2 for explanation of variable abbreviations. Values are prediction fits of model coefficients, not the coefficients themselves.

Interaction number	[Scenario A]	[A]> [B]	[Scenario B]	fit[A]	fit[B]	[95%.CI.-.A]	[95%.CI.-.B]
1	[inf.T / dark / cov.T]	>	[inf.F / dark / cov.T]	0.428	-0.113	[0,15 < -> 0,70]	[-0,23 < -> 0,00]
2	[inf.T / dark / cov.T]	>	[inf.F / dark / cov.F]	0.428	-0.022	[0,15 < -> 0,70]	[-0,11 < -> 0,06]
3	[inf.T / dark / cov.T]	>	[inf.T / dayl / cov.F]	0.428	-2.123	[0,15 < -> 0,70]	[-4,09 < -> -0,15]
4	[inf.T / dark / cov.F]	>	[inf.T / dayl / cov.F]	0.044	-2.123	[-0,13 < -> 0,23]	[-4,09 < -> -0,15]
5	[inf.F / dark / cov.F]	>	[inf.T / dayl / cov.F]	-0.022	-2.123	[-0,11 < -> 0,06]	[-4,09 < -> -0,15]

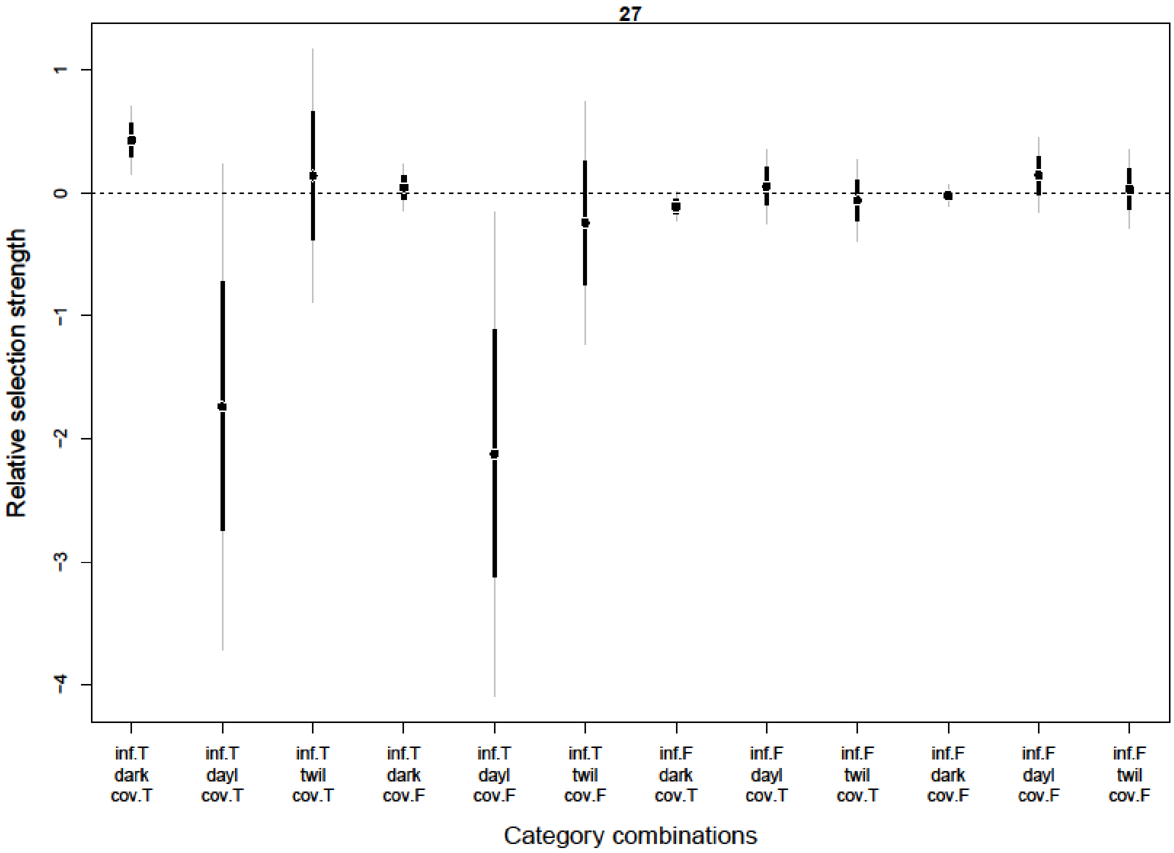

Figure 7: A-RQ1.2; Prediction values of relative selection strength for combinations of variables compared to each other in the step selection analysis, performed using a 27m buffer around all infrastructure. SE bars in black, 95% CIs in grey. All values are at the scale of the linear predictor. Abbreviations explained in Table 1.

Significant differences between these scenarios can be viewed as a measure to describe at what distance the infrastructure matters to foxes, and where the different variables have the most pronounced impacts, shown in Figure 8. All of the five relevant combinations of variables are significant at buffer sizes of 27 and 35m. However, at least two of these are significant in the range of 10-35m. Some significance is seen for buffer sizes up to 98m, but not above. Figure 4 therefore only shows buffer sizes in the most relevant range. Inside buffer sizes < 25m, the data contained no real positions during daylight, and coefficient estimates of this light period was not possible. The same was true for twilight < 4m buffer sizes.

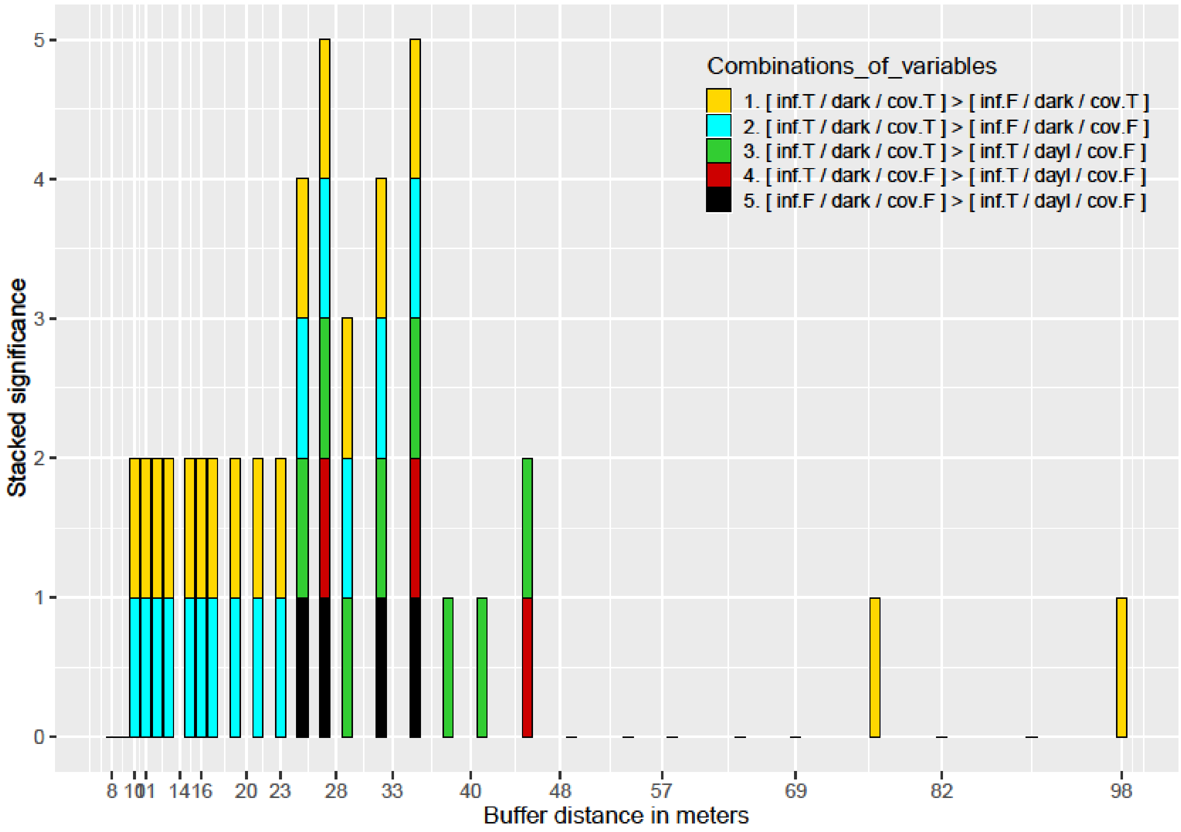

Figure 8: A-RQ1.2; Stacked significant differences between scenarios at various buffer distances. Each combination of scenarios either has value not significant (0), or significant/significantly different from each other (1). The cumulative score on the y-axis indicate how many of the combinations in the legend are different from each other at any given buffer distance. Note that the model was not able to estimate coefficients for daylight below 25m, and for twilight below 4m.

3.4 Location and characterization of activity clusters (A-RQ2)

The aim of this analysis was to determine where foxes prefer to do different activities (foraging/resting), in relation to infrastructure, and what specific features likely attract these animals towards infrastructure. 378 clusters of activity were identified and inspected within a short time of the fox visiting the site. Of these, 140 clusters with sufficient proof of activity were included in analysis A-RQ2. An example of a cluster where the degree of evidence for the activity would be set to "high", is showed below in Figure 9.

Figure 9: An example of a foraging-related cluster. The fox has likely followed a road in search of food, and seems to have been rewarded. Upper right: Associated GPS track-log, viewed in Google earth (Google 2019). Left: Overview image of activity and habitat. Lower right: Close-up image of fox tracks and likely food item.

Sufficient tracking conditions seemed to improve the information and certainties derived from clusters. 114 (72%) of the clusters had sufficient evidence to include in analysis, and these were inspected over either snow or soft, bare ground. In comparison, 224 (58%) of the total 378 clusters visited had the same tracking conditions.

Because clusters were identified non-randomly for the inspections, a comparison of the habitat distribution between these and autogen. clusters are provided in Table 8. The difference between these were within 2% for any given category, although 5 times more clusters were identified by the autogen. clusters. Agricultural fields, forests, and urban areas contained the majority of clusters, at 90% of the manually identified clusters, and 91% of the autogen. clusters. However, this should not be interpreted as habitat selection by foxes in favor of these areas, as these habitat categories also make up the majority of the study area (see Methods chapter).

Table 8: Proportions of habitats among manually identified and autogenerated clusters, based on AR5 1:5000 habitat maps (NIBIO 2017).

Habitat	Agri.fields	Pasture	Infrast.	Forest	Barren	Freshwater	Bog
Visited clusters	166 - (42%)	17 - (4%)	51 - (13%)	137 - (35%)	13 - (3%)	8 - (2%)	0 - (0%)
Autogen. clusters	847 – (42%)	89 – (4%)	234 – (12%)	736 – (37%)	66 – (3%)	25 – (1%)	1 – (0%)

Detailed accounts of foraging activities observed at clusters are provided below in Table 9.

Table 9: Species/group/item hunted for and possibly killed, or scavenged by foxes

Species/group/item	Likely hunted for	Evidence of kill	Likely consumed food item (Scavenged/hunted - unknown)	Of which supplied by humans (verified)
Ants	1	NA	0	NA
Birds	4	0	8	1
Hare *(Lepus timidus)*	1	0	0	0
Small mammals	50	1	0	0
Roe deer (*Capreolus capreolus)*	1	1	15	3
Carcass attributed to hunting	NA	NA	2	2
Carcass/unknown prey remains	NA	0	6	1
Domestic livestock	0	0	1	1
Fish	0	0	1	0
Compost/food scraps	NA	NA	9	9
Fruit	NA	NA	7	6
Bird seed	NA	NA	5	5

A summary of recorded activities at clusters, linked to the specific habitat feature at which they occurred, showed in Table 10. Only recurring combinations of these are included.

Table 10: Fox activities at clusters, related to specific habitat features.

Habitat feature	Hunting	Scavenging/Herbivory	Resting
Bird-feeder	0	5	0
Brush-pile	3	0	2
Compost bin/pile	1	4	0
Dung-silo/pile	3	0	0
Fallen tree	0	2	4
Hilltop	5	2	11
Mound/rock	0	2	8
Shrubs	6	1	3
Swamp/wet area	2	1	1
Under tree	1	4	14
Long/grazed grass	3	4	0

Foxes were significantly more likely to forage in areas very close to, and significantly less likely to forage in areas very far from, infrastructure. Due to the binomial response variable in the GLMM regression model, where all observations are either resting or foraging, only the coefficient estimates for activity "foraging" is shown. The opposite and equally strong pattern is seen for the activity "resting", where foxes were significantly more likely to rest "very far" (220-290m) from, and significantly less likely to rest "very close" (0-20m) to infrastructure. Foraging was significantly more likely to occur during dark hours as opposed to resting, and the opposite is seen during daylight hours, where resting was the more likely activity. If a fox spent longer time at a cluster, it was significantly more likely to be used for resting than foraging, and vice versa. However, this was only significant when assuming a non-linear relationship by using two cubic splines to explain the variation in the variable "duration". See Table 11 below.

Table 11: A-RQ2; Coefficient estimates from GLMM regression model, with foraging vs resting behavior at clusters predicted by distance to infrastructure divided into five categories. light period, duration of fox visits to clusters, and a random effect of the fox ID. Due to binomial response variable (resting/foraging), the coefficients are of equal strength for both activities, but of opposite sign (±). The values shown in this table are for foraging.

There are five models in total, each for one unique distance-to-infrastructure category, see methods for specification of distance categories and explanation of variables. Each element in the upper part of the table contains a coefficient estimate, and (95% CI)-values below.

Values for the row "Std.Dev (Fox ID)", are standard deviation of the variance for the random effect (Fox ID). Duration (1,2,3), refer to the number of cubic splines used.

A-RQ2-GLMM regression model estimated coefficients: Foraging vs resting

	Dependent variable:				
	Selection for foraging				
	1. Very close (n=44)	2. Close (n=36)	3. Medium (n=40)	4. Far (n=26)	5. Very far (n=11)
1.Very close	**1.47****				
	(0.002, 2.95)				
2.Close		-0.03			
		(-1.10, 1.05)			
3.Medium			-0.09		
			(-1.20, 1.03)		
4.Far				-0.17	
				(-1.41, 1.08)	
5.Very far					**-2.06****
					(-4.06, -0.07)
Daylight	**-1.61****	**-1.95*****	**-1.94*****	**-1.90*****	**-2.07*****
	(-2.92, -0.30)	**(-3.24, -0.66)**	**(-3.23, -0.65)**	**(-3.23, -0.56)**	**(-3.41, -0.73)**
Duration 1	-0.18	-0.48	-0.51	-0.47	-0.67
	(-3.10, 2.73)	(-3.31, 2.34)	(-3.33, 2.31)	(-3.28, 2.33)	(-3.59, 2.26)
Duration 2	**-5.87*****	**-6.05*****	**-6.06*****	**-6.03*****	**-6.14*****
	(-8.60, -3.14)	**(-8.71, -3.39)**	**(-8.72, -3.40)**	**(-8.69, -3.37)**	**(-8.85, -3.43)**
Duration 3	-1.00	-0.95	-0.93	-0.90	-0.99
	(-4.71, 2.71)	(-4.58, 2.67)	(-4.54, 2.68)	(-4.50, 2.69)	(-4.65, 2.68)
Constant (Dark)	**3.18*****	**3.59*****	**3.61*****	**3.61*****	**3.79*****
	(1.80, 4.55)	**(2.25, 4.94)**	**(2.24, 4.98)**	**(2.26, 4.96)**	**(2.42, 5.17)**
Variance (Fox ID)	0.44	0.31	0.32	0.33	0.44
Std.Dev (Fox ID)	0.66	0.56	0.57	0.58	0.66
Group size (Fox ID)	17	17	17	17	17
Observations	140	140	140	140	140
Note:					*p**p***p<0.01

4. Discussion

The aim of this study was to investigate how infrastructure drives spatio-temporal patterns in red fox activity at multiple scales. The results revealed significant patterns of selection in relation to infrastructure both within the home range, and at the finer scale of detailed, short-lived behavioral events.

4.1 Selection for infrastructure within the home range scale (RQ1)

When active, foxes did not generally prefer to be close to infrastructure. Although significant positive selection was found at some distances from infrastructure, this is not enough to fully support the prediction that foxes select for proximity to infrastructure (P1.1). When adding other variables to explain the behavior of the foxes, larger differences in selection appeared. Foxes selected for areas close to human infrastructure during dark hours when in cover. Moreover, they showed significant avoidance against open areas close to human infrastructure during daytime, with selection also being significantly lower than for the same areas during dark hours. These results support the prediction that selection for proximity to infrastructure is strongest during the night, in the presence of cover, and weakest during daylight and in the absence of cover (P1.2). Because the model lacked real positions closer than 25m from infrastructure during daylight, selection patterns between 0 and 25m from infrastructure during daylight remains uncertain. This perhaps serves as an indication that foxes do not select strongly for these areas at those times – to say the least.

Similar results are reported in (Hradsky et al. 2017), using GPS-tracking with an FI of 60 minutes. Although considerable variation among individuals were seen, several foxes showed stronger selection for human-modified habitats including infrastructure during the night. The similarities to the results presented here is interesting, considering that these studies were conducted at essentially opposite parts of the globe and in vastly different ecosystems. The similarity of the results, despite the mentioned habitat differences, indicates that presence of human infrastructure in the landscape is a strong shaping force of habitat selection at different times of day within the home range.

4.2 Location and characterization of activity clusters (RQ2)

Foxes preferred to use areas very close to humans for foraging during the night, while preferring more remote areas for resting during the day. When resting, foxes spent longer time at clusters than when they were foraging. These results support the prediction that relocation clusters in close proximity to infrastructure are more likely to be associated with foraging and less likely with resting, than relocation clusters in more remote forested areas (P.2.1). Due to a comparatively smaller sample size in the category "very far", the results at this distance interval is less certain than for other categories. A few older studies using VHF telemetry show similar patterns (Janko et al. 2012; Pandolfi et al. 1997) However, the sample size used by Pandolfi et al. (1997) was less than half (7 vs. 16) of what is presented here, and the use of VHF radio telemetry has substantially lower accuracy compared to my methods, with a self-reported fix-accuracy of 100-200m.

Although McKeown (2018) only looked at clusters associated with recurring use, his results are similar to mine. Nocturnal clusters were significantly closer to farms and houses as opposed to diurnal clusters, and they were in more open areas with "greater sightability". Clusters showed higher frequencies of bed sites, dens, and clumped food resources, as compared to non-clustered locations. Interestingly, variations in terrain seemed to help predict likely activities at clusters. This variable was recorded in my study, but not included in analysis. The FI used was 4 hours, and inspection of clustered locations were done with a delay of up to three months.

Although these mentioned studies share some of my results, none of them collected data at sufficiently high temporal resolution, specifically suited to answer questions at such fine scales. My findings are based on methods with substantially higher precision, accuracy, and temporal resolution, and therefore hold higher validity for the purposes studied, in my opinion. Low temporal resolution leads to a bias towards long-lived behavioral events such as resting or handling of large prey. In order to capture clusters of activity created over very short timeframes, higher temporal resolution is required (Palacios & Mech 2011). This element of fox behavior has to my knowledge not been studied with data of similar temporal grain as presented here.

As a result, I was able to detect these shorter-lived behavior events. For example, many accounts of likely hunting behavior for small mammals were recorded, as well as several accounts of scavenging close to humans for food items such as compost/food scraps, fruit, bird seeds and carcass remains from hunting or domestic livestock. In the cases of presumed herbivory, it is unclear whether the foxes were in fact in pursuit of seeds/fruit/food scraps, or rather aiming to predate upon other animals attracted to the same food (such as small mammals). Red foxes are opportunistic, and have been shown to consume all these food items and prey (Contesse et al. 2004; Macdonald 1977; Macdonald 1976; Macdonald & Reynolds 2004). Regardless, human-derived food subsidies are the primary reason they are drawn to visit these sites.

In their critical review of GPS monitoring methods, Hebblewhite and Haydon (2010) highlighted the combination of "fresh" GPS data with physical field inspections of recorded locations as a potentially valuable and understudied addition to GPS monitoring, also supported by (Coelho et al. 2007). Moreover, Hebblewhite and Haydon (2010) make the point that sampling data at very high temporal resolutions sacrifices inferences at larger scales. However, I would contend that in order to fill the gaps of knowledge as they stand now, the methodical choices made in this study were the most appropriate. Some of the behavior documented in this study would have remained hidden if data of lower detail had been used. I would argue that these temporally fine-scale behaviors must be studied with equally fine-scale location data.

4.3 The element of scale

An important aspect of this study was the inclusion of different scales, as well as fine variations in distance to the nearest infrastructure within these. First of all, the two analyses performed, studied selection and behavior at separate scales. This resulted in different information being derived from each analysis, with general selection patterns for proximity to infrastructure within the home range in the first (A-RQ1), and preferences for detailed behavior and specific activities in the second (A-RQ2). This by itself provides support for selection and activity preference related to infrastructure being scale dependent (P1.3).

This scale dependence can be seen in greater detail by observing how patterns in habitat selection and activity preference changed, as the distance from infrastructure varied. In the first analysis (A-RQ1), buffer sizes around all infrastructure was varied from 8 to 98 meter, allowing a more detailed view of where these features mattered to the foxes. Selection varied across this range, showing the effects in selection were scale dependent. The most pronounced differences in selection appeared within a distinct distance interval, fairly close to the infrastructure, see Figure 8. The effects of factors influencing selection towards infrastructure were less pronounced as the distance to infrastructure increased, thus supporting P1.3. Support for this prediction is also found in the results from the analysis related to location and characterization of activity clusters (A-RQ2). Here, the preferred activity changed significantly as distance from infrastructure at clusters varied.

4.4 Main research question

My results suggest that the foxes included in the study have adapted to exploit the available foraging benefits of human presence while avoiding direct confrontation with humans. To accomplish this, foxes use time of day and presence of cover to remain hidden from sight when they are close to infrastructure (distance from human activity centers). However, other variables not included in my analyses may also be of importance to the foxes.

My results indicate that the “landscape of fear”-concept (Brown et al. 1999) applies to red foxes, in that they generally seek to avoid direct contact with humans. Bino et al. (2010) demonstrates how red foxes can be completely dependent on anthropogenic resources, which is supported by the high presence of anthropogenic food in fox stomachs shown in (Contesse et al. 2004). (Diaz-Ruiz et al. 2016) shows the activity patterns in urban foxes to be determined more by human activity than by prey activity, in that foxes display more nocturnal behavior than expected based on prey activity alone. (Boitani et al. 1984) found foxes to avoid human presence in their habitat only temporally (during the day). The temporal avoidance seems to result in foxes becoming more nocturnal in areas with high human presence, whereas this does not occur in more pristine areas (Servín et al. 1991). My findings, viewed in light of results from these studies, indicate that human presence is an important factor in shaping how foxes use these landscapes.

4.5 High frequency GPS bursts for studying space use at multiple scales

To my knowledge, this is the first study done on red foxes looking at field-verified fine-scale behavioral events in clusters of activity, using high frequency bursts of GPS locations. With a mean monitoring duration of 12 days (± SD 5.62), scheduling the GPS units to capture rapid bursts of locations helped provide sufficient monitoring durations to make inferences regarding habitat selection within the home range, and about fine scale, short-lived events in behavior.

The capture of many such shorter-lived behavior events were crucial in making the detail level in my second analysis (A-RQ2) possible. This underscores the importance of linking GPS data with actual "boots in the field", suggested by (Hebblewhite & Haydon 2010), supported by (Coelho et al. 2007) and demonstrated by (Elbroch et al. 2017). By conducting the cluster inspections shortly following the foxes' activity at the cluster, I was able to detect even the finest clusters, and relate these to activity, prey/food diversity, among other things. This relates to another point made by Elbroch et al. (2017); When the researchers excluded field visits to smaller clusters which would not be captured using longer FIs, the estimates of prey diversity went down. Although their minimum FI was far longer than what is presented here, the same principle likely applies, as red foxes in my study regularly performed very short-lived hunting attempts lasting only seconds. The fleeting nature of such behavior, expressed both in the data as well as my experiences in field inspections, suggests that further research would miss significant amounts of data should it fails to design study methods that captures it. The fleeting nature of such behavior, expressed both in the data as well as my experiences in field inspections, suggests that further research would miss significant amounts of data should it fail to design study methods that captures it.

Some clusters in activity were lost between GPS bursts. This was detected by manual tracking from the end of one burst, to the start of the next, only possible when tracking conditions were near optimal. Among these were scavenging of fish, and cannibalism/scavenging of a dead fox. Palacios and Mech (2011) stated that even at a relatively short FI of ten minutes for grey wolves (*Canis lupus*), short-lived predation events involving small prey were lost. My results effectively demonstrate this.

Through conducting fieldwork, a good sense of the spatial error was achieved. Frair et al. (2010) state that the most influential source of GPS inaccuracy is canopy cover. My observations support this, however this was only noticeable under canopies heavily covered in snow. Luckily, these conditions were isolated to a few events over the course of the study. Frair et al. (2010) also states that one of the largest gaps in knowledge associated with GPS telemetry studies, is how the behavior of individual species affect the accuracy and precision of GPS locations. Based on observation, locations associated with verified resting activity seemed to have lower spatial precision, likely because the GPS unit is hidden underneath the head/neck of the animal. This was also observed by (Coelho et al. 2007) when studying maned wolves *(Chrysocyon brachyurus)*. Due to often high numbers of GPS fixes at these clusters, overall accuracy was sufficient to locate the real cluster in most cases. Despite these errors, the analyses presented are still valid, as the analysis regarding selection within the home range (A-RQ1) excluded inactive/resting locations, and the analysis of location and activity at clusters (A-RQ2) was based on ground-truthing clustered locations, and sufficient evidence at site was required in order to include the observation in analysis.

The frequency of reliable information went up when tracking conditions were favorable. This is reflected by the increased relative frequency of these tracking conditions in the data selected for analysis, compared to the dataset including all observations. Logically, snow cover was of high relevance, and made important evidence such as tracks, urine, scats, rest sites, blood and prey remains much more visible.

Determining habitat selection based on the assumption of use versus availability alone, may often be too simplistic. Habitat selection changes depending on the specific requirements of activity the animal is performing at any given time or place (Mysterud & Ims 1998). Optimally, the behavior should be studied at the scale that it is relevant to the animal making the decision (Boyce 2006; Fortin et al. 2005b). By conducting my analysis at two primary scale levels, and including small scale variations within these, further light was shed on the way human presence shape red fox decisions.

At the broader scale within the home range, the step-level null model provided a suitable availability sample, and helped determine the overall selection strength towards my specific features. The inclusion of time and available cover in the analysis further helped to disentangle when the specific habitat elements mattered, and in what way. Boyce (2006) imply that different habitat features should be treated as such, and that the presence of objects such as roads may be viewed more as buffered densities in the landscape than discrete patches. Simply put, their effects stretch further than their geographical extent. This justifies my use of a buffer of varying size around the infrastructure. An additional link between my data and Boyce's contention are my findings that effects upon selection gradually decreased as distance to the feature increased.

As Johnson (1980) argues, the highest order of selection, governs the selection of all the lower levels. By his definition, the highest order refers to the specific resources and food items preferred at a feeding site. Studies of resource selection are often limited by the resolution of either their telemetry data, or the resolution of their covariates such as land cover maps. They are therefore inhibited to, or do not seek to investigate the whole picture of how an animal makes its decisions (Boyce 2006). Compared to conventional studies, my study has both high detail in GPS data and covariates. Not being limited by these factors, I was able to zoom further in to the level of specific behaviors and get a glimpse of how specific resources are exploited, as well as the likely reason the fox chose to be in that particular spot at that particular time.

Generally speaking, any scenario involving questions about the relationship between an animal (suited for GPS monitoring), and its spatial and temporal relationship to specific features in its habitat, could potentially be shown by applying variations of the methods presented here. As technology is predicted to develop further, the tradeoff between resolution/battery life may become obsolete. Until that point is reached, using high frequency GPS bursts is one solution to partially solve this tradeoff. Another potential solution to this problem appears to be the use of accelerometers to recreate movement paths in very high detail between locations provided from the GPS unit, allowing for a dynamic fix schedule related to activity, and longer FIs (Berlincourt et al. 2015; Brown et al. 2012).

Because GPS monitoring is an invasive approach, researchers should aim to minimize animal stress and suffering during all parts of the process, including minimizing necessary deployments by maximizing utility from each deployment. The methods used in this study help achieve this, by deriving as much information as possible from each deployment, given the technological constraint of battery capacity.

4.6 Relevance to management – Further research

The results presented here have implications for the management of red foxes, as well as the species they affect. These animals are able to disperse distances up to hundreds of kilometers (Allen & Sargeant 1993; Gosselink et al. 2010). Due to the advantage foxes often gain from human presence such as agriculture, predation pressure from foxes may be elevated in the surrounding areas (Shapira et al. 2008). In some cases red foxes contribute to further decline in endangered species (Aarvak et al. 2017; Henriksen & Hilmo 2015; Noren et al. 2017). This interaction may be important in changing surrounding ecosystems where human develop the landscape. Locally in the presented study area for example, roe deer are an important game species, and is likely targeted seasonally by the red fox (Panzacchi et al. 2008). If the goal is to limit red fox abundance, documenting the specific types of food subsidies foxes gain from humans may raise awareness and potentially help eliminate the presence of some of these. To show an example, Contesse et al. (2004) found; “85% of the households provided anthropogenic food which were accessible to foxes”. I found several food sources visited by the fox which could easily have been removed, such as large dung piles in relationship with animal agriculture, carcass remains left by hunters (occasionally as bait), fruit, bird feeders and open compost piles. Limiting such resources can have substantial population effects (Bino et al. 2010), and I propose that measures such as this should be taken more seriously in the management of generalist predators such as the red fox.

I suggest that adapted versions of the methods used in this study can be useful for research and management of carnivores, as well as wildlife in general. I will relate this to Scandinavian management especially, however some of these examples may be applicable in other areas. Linnell et al. (2015) points to several gaps in knowledge regarding large carnivores and golden eagles (*Aquila chrysaetos*) relevant to management in Norway, that may be filled by using some of the methods presented here. For example, the need for better knowledge regarding how both Eurasian lynx (*Lynx lynx)*, and grey wolf relates to infrastructure, and how this affects predator-prey interactions with roe deer is mentioned. High frequency GPS bursts, perhaps tagging both predator and prey, combined with field inspections to verify kill rates, would likely contribute to answering these questions. The method of tagging both predator and prey simultaneously is also highly relevant in the case of predation upon domestic sheep (*Ovis aries*). Few topics are as hotly contested as this one in Norway, and much could be gained by greater nuance in our knowledge. For example, Linnell et al. (2015) points to wolverine (*Gulo gulo)*, and golden eagle as understudied species in this context.

Further developments and testing based on the methods demonstrated and mentioned in this study seems to be a worthy aim to pursue. In doing this, researchers could gain better and more precise information when studying cases such as those mentioned in the previous paragraph. Moreover, these type of methods could improve data materials in any scenario where detailed knowledge about the behavior of wildlife towards specific features in their habitat is demanded.

5. Conclusion

My findings show that high frequency GPS bursts, combined with subsequent field observation of relocation clusters, can provide detailed insights of how animals relate to specific features in their habitat. In the case study conducted, foxes timed their use of anthropogenic areas to exploit available food subsidies, while avoiding direct contact with humans. They also used cover for this purpose close to infrastructure. The spatio-temporal patterns of selection pointing to such a conclusion were found both at the home range scale and at the finer scale of specific activities. This suggests infrastructure is a shaping factor of how red foxes use fragmented, human-dominated landscapes. Direct and indirect human-derived food sources such as dung piles, open compost piles, fruit, bird feeders and carcasses from animal agriculture and hunting were repeatedly visited by foxes in the study, indicating that these should be removed if the goal is to reduce food subsidies available to foxes.

To minimize the impacts of tagging on animals, GPS monitoring studies should aim at maximizing utility of each deployment. One way of achieving this is showed here by combining a method that optimizes the tradeoff between temporal resolution and battery life, with extensive field inspections of recorded locations. Combining studies at various scales will also likely help to develop a more complete picture of an animals' behavior, which in turn will help managers and law makers make better decisions regarding them. I suggest further development and deployment of these methods will likely help answer questions and inform policy regarding wildlife that is challenged by an increasingly human-dominated environment - and indeed all cases where fine-scale behavioral knowledge of animals is needed.

6. References

Aarvak, T., Øien, J. & Karvonen, R. (2017). Development and key drivers of the Fennoscandian Lesser White-fronted Goose population monitored in Finnish Lapland and Finnmark. *the Lesser White-fronted Goose Fennoscandian population at key staging and wintering sites within the European flyway*: 29.

Allen, S. H. & Sargeant, A. B. (1993). Dispersal patterns of red foxes relative to population-density. *Journal of Wildlife Management*, 57 (3): 526-533.

Angerbjörn, A., Eide, N. E., Dalén, L., Elmhagen, B., Hellström, P., Ims, R. A., Killengreen, S., Landa, A., Meijer, T. & Mela, M. (2013). Carnivore conservation in practice: replicated management actions on a large spatial scale. *Journal of Applied Ecology*, 50 (1): 59-67.

Baker, S. E. & Macdonald, D. W. (2000). Foxes and foxhunting on farms in Wiltshire: a case study. *Journal of Rural Studies*, 16 (2): 185-201.

Bateman, P. W. & Fleming, P. A. (2012). Big city life: carnivores in urban environments. *Journal of Zoology*, 287 (1): 1-23.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). *Fitting Linear Mixed-Effects Models Using lme4*. Journal of Statistical Software, 67(1), 1-48.

Beckmann, J. P., Murray, K., Seidler, R. G. & Berger, J. (2012). Human-mediated shifts in animal habitat use: Sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. *Biological Conservation*, 147 (1): 222-233.

Berlincourt, M., Angel, L. P. & Arnould, J. P. Y. (2015). Combined Use of GPS and Accelerometry Reveals Fine Scale Three-Dimensional Foraging Behaviour in the Short-Tailed Shearwater. *Plos One*, 10 (10): 16.

Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D. & Kark, S. (2010). Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology*, 47 (6): 1262-1271.

Birnie-Gauvin, K., Peiman, K. S., Gallagher, A. J., de Bruijn, R. & Cooke, S. J. (2016). Sublethal consequences of urban life for wild vertebrates. *Environmental Reviews*, 24 (4): 416-425.

Bischof, R., Gjevestad, J. G. O., Ordiz, A., Eldegard, K. & Milleret, C. (2018). *High frequency GPS bursts 1 and path-level analysis reveal linear feature tracking by red foxes*: Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås, Norway. Faculty of Science and Technology, Norwegian University of Life Sciences, PO Box 5003, NO-1432 Ås. Unpublished manuscript.

Bivand, R. & Lewin-Koh, N. (2019). *maptools: Tools for Handling Spatial Objects. R package version 0.9-5.*

Bivand R.S., Pebesma E.J. & (2005). *Classes and methods for spatial data in R. R News 5 (2),.*

Boitani, L., Barrasso, P. & Grimod, I. (1984). Ranging behaviour of the red fox in the Gran Paradiso National Park (Italy). *Bollettino di zoologia*, 51 (3-4): 275-284.

Bonnell, T. R., Dutilleul, P., Chapman, C. A., Reyna-Hurtado, R., Hernandez-Sarabia, R. U. & Sengupta, R. (2013). Analysing small-scale aggregation in animal visits in space and time: the ST-BBD method. *Animal Behaviour*, 85 (2): 483-492.

Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions*, 12 (3): 269-276.

Brown, D. D., Lapoint, S., Kays, R., Heidrich, W., Kummeth, F. & Wikelski, M. (2012). Accelerometer-Informed GPS Telemetry: Reducing the Trade-Off Between Resolution and Longevity. *Wildlife Society Bulletin*, 36 (1): 139-146.

Brown, J. S., Laundré, J. W. & Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of mammalogy*, 80 (2): 385-399.

Butchart, S. H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P., Almond, R. E., Baillie, J. E., Bomhard, B., Brown, C. & Bruno, J. (2010). Global biodiversity: indicators of recent declines. *Science*, 328 (5982): 1164-1168.

Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365 (1550): 2157-2162.

Coelho, C. M., de Melo, L. F. B., Sabato, M. A. L., Rizel, D. N. & Young, R. J. (2007). A note on the use of GPS collars to monitor wild maned wolves Chrysocyon brachyurus (Illiger 1815) (Mammalia, Canidae). *Applied Animal Behaviour Science*, 105 (1-3): 259-264.

Coffin, A. W. (2007). From roadkill to road ecology: a review of the ecological effects of roads. *Journal of transport Geography*, 15 (5): 396-406.

Conover, M. R. (2001). *Resolving human-wildlife conflicts: the science of wildlife damage management*: CRC press.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F. & Deplazes, P. (2004). The diet of urban foxes (Vulpes vulpes) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mammalian Biology*, 69 (2): 81-95.

DeCesare, N. J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G. J., Neufeld, L., Bradley, M., Whittington, J., Smith, K. G., Morgantini, L. E., et al. (2012). Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications*, 22 (4): 1068-1083.

Diaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B. & Ferreras, P. (2016). Drivers of red fox (Vulpes vulpes) daily activity: prey availability, human disturbance or habitat structure? *Journal of Zoology*, 298 (2): 128-138.

Doncaster, C. P. & Macdonald, D. W. (1997). Activity patterns and interactions of red foxes (Vulpes vulpes) in Oxford city. *Journal of Zoology*, 241: 73-87.

Elbroch, L. M., Lowrey, B. & Wittmer, H. U. (2017). The importance of fieldwork over predictive modeling in quantifying predation events of carnivores marked with GPS technology. *Journal of Mammalogy*, 99 (1): 223-232.

Forester, J. D., Im, H. K. & Rathouz, P. J. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology*, 90 (12): 3554-3565.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T. & Mao, J. S. (2005a). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology,* 86 (5): 1320-1330.

Fortin, D., Morales, J. M. & Boyce, M. S. (2005b). Elk winter foraging at fine scale in Yellowstone National Park. 145 (2): 334-342.

Frair, J. L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N. J. & Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365 (1550): 2187-2200.

Google. (2019). *Google Earth.*

Gosselink, T. E., Piccolo, K. A., van Deelen, T. R., Warner, R. E. & Mankin, P. C. (2010). Natal Dispersal and Philopatry of Red Foxes in Urban and Agricultural Areas of Illinois. *Journal of Wildlife Management,* 74 (6): 1204-1217.

Grunewald, C., Breitbach, N. & Bohning-Gaese, K. (2010). Tree visitation and seed dispersal of wild cherries by terrestrial mammals along a human land-use gradient. *Basic and Applied Ecology*, 11 (6): 532-541.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P. & Collins, C. D. (2015). Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science advances*, 1 (2): e1500052.

Hebblewhite, M. & Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365 (1550): 2303-2312.

Hengl, T., Roudier, P., Beaudette, D. & Pebesma, E. (2015). *plotKML: Scientific Visualization of Spatio-Temporal Data. Journal of Statistical Software, 63(5), 1-25.*

Henriksen, S. & Hilmo, O. (2015). Norsk rødliste for arter 2015. *Artsdatabanken, Norge,* 6.

Hradsky, B. A., Robley, A., Alexander, R., Ritchie, E. G., York, A. & Di Stefano, J. (2017). Human-modified habitats facilitate forest-dwelling populations of an invasive predator, Vulpes vulpes. *Scientific Reports*, 7: 12.

Humphries, N. E., Weimerskirch, H., Queiroz, N., Southall, E. J. & Sims, D. W. (2012). Foraging success of biological Levy flights recorded in situ. *Proceedings of the National Academy of Sciences of the United States of America*, 109 (19): 7169-7174.

Jahren, T., Storaas, T., Willebrand, T., Moa, P. F. & Hagen, B. R. (2016). Declining reproductive output in capercaillie and black grouse-16 countries and 80 years. *Animal Biology*, 66 (3-4): 363-400.

Janko, C., Schroder, W., Linke, S. & Konig, 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 (3): 245-250.

Johnson, D. D. & Ganskopp, D. C. (2008). GPS collar sampling frequency: effects on measures of resource use. *Rangeland Ecology & Management*, 61 (2): 226-231.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61 (1): 65-71.

Kartverket. (2012). Høyeste fjelltopp i hver kommune. In *Kartverket*. Available at: https://www.kartverket.no/kunnskap/fakta-om-norge/Hoyeste-fjelltopp-i-kommunen/hoyeste-fjelltopp-i-hver-kommune/ (accessed: 25.02.2019).

Kartverket. (2017). *Kommunegrenser Norge*. Kartkatalog.geonorge.no: Geonorge.

Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. *Environmental Pollution*, 159 (8-9): 1974-1983.

Lempp, C., Jungwirth, N., Grilo, M. L., Reckendorf, A., Ulrich, A., van Neer, A., Bodewes, R., Pfankuche, V. M., Bauer, C., Osterhaus, A., et al. (2017). Pathological findings in the red fox (Vulpes vulpes), stone marten (Martes foina) and raccoon dog (Nyctereutes procyonoides), with special emphasis on infectious and zoonotic agents in Northern Germany. *Plos One*, 12 (4): 20.

Lindstrom, E. R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., Lemnell, P. A., Martinsson, B., Skold, K. & Swenson, J. E. (1994). Disease reveals the predator - sarcoptic mange, red fox predation, and prey populations. *Ecology,* 75 (4): 1042-1049.

Linnell, J. D., Tveraa, T., Hansen, I., Andrén, H., Persson, J., Sand, H., Wikenros, C., Zimmermann, B., Odden, J. & Stien, A. (2015). Kunnskapsstatus og kunnskapsbehov for forvaltning av rovvilt i Norge.

Lloyd, H. G. (2013). Habitat requirements of the Red fox. In *The red fox: symposium on behaviour and ecology*, pp. 7-25: Springer.

Lombardi, J. V., Comer, C. E., Scognamillo, D. G. & Conway, W. C. (2017). Coyote, fox, and bobcat response to anthropogenic and natural landscape features in a small urban area. *Urban Ecosystems,* 20 (6): 1239-1248.

Lovdata. (2017). *Forskrift om jakt- og fangsttider samt sanking av egg og dun for jaktsesongene fra og med 1. april 2017 til og med 31. mars 2022*. lovdata.no: Lovdata.

Lowry, H., Lill, A. & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews,* 88 (3): 537-549.

Luniak, M. (2004). *Synurbization–adaptation of animal wildlife to urban development*. Proc. 4th Int. Symposium Urban Wildl. Conserv. Tucson. 50-55 pp.

Macdonald, D. (1977). On food preference in the red fox. *Mammal review,* 7 (1): 7-23.

Macdonald, D. W. (1976). Food caching by red foxes and some other carnivores. *Zeitschrift für Tierpsychologie*, 42 (2): 170-185.

Macdonald, D. W. & Reynolds, J. C. (2004). 5.3 Red fox Vulpes vulpes. In *Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan*, pp. 129-136: IUCN Gland, Switzerland.

McKeown, B. (2018). *Navigating the Red Fox's Cognitive Map: How recursive use of resource locations influence movement patterns and the notion of a home range*.

McKinney, M. L. & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14 (11): 450-453.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127 (3): 247-260.

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11 (2): 161-176.

Miljødirektoratet. (2016). Forskrift om utøvelse av jakt, felling og fangst med kommentarer, instrukser og avtaler. Miljødirektoratet.no. 25-30 pp.

Mills, K. J., Patterson, B. R. & Murray, D. L. (2006). Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Society Bulletin*, 34 (5): 1463-1469.

Moen, A. & Odland, A. (1998). *Nasjonalatlas for Norge: vegetasjon*: Statens kartverk.

Mysterud, A. & Ims, R. A. (1998). Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology*, 79 (4): 1435-1441.

NIBIO. (2017). *AR5 Area resource map*: Norwegian institute of bioeconomics.

NMBU. (2019). Meteorological data for Ås. In *NMBU*. Available at: https://www.nmbu.no/fakultet/realtek/laboratorier/bioklim/meteorologiske-data (accessed: 25.02.2019).

Noren, K., Angerbjorn, A., Wallen, J., Meijer, T. & Sacks, B. N. (2017). Red foxes colonizing the tundra: genetic analysis as a tool for population management. *Conservation Genetics*, 18 (2): 359-370.

Palacios, V. & Mech, L. D. (2011). Problems with studying wolf predation on small prey in summer via global positioning system collars. *European Journal of Wildlife Research*, 57 (1): 149-156.

Pandolfi, M., Forconi, P. & Montecchiari, L. (1997). Spatial behaviour of the red fox (Vulpes vulpes) in a rural area of central Italy. *Italian Journal of Zoology*, 64 (4): 351-358.

Panzacchi, M., Linnell, J. D. C., Serrao, G., Eie, S., Odden, M., Odden, J. & Andersen, R. (2008). Evaluation of the importance of roe deer fawns in the spring-summer diet of red foxes in southeastern Norway. *Ecological Research*, 23 (5): 889-896.

Pebesma, E. (2018). *The R Journal, Simple Features for R: Standardized Support for Spatial Vector Data.* p. sf package.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R. & Cheung, W. W. (2010). Scenarios for global biodiversity in the 21st century. *Science,* 330 (6010): 1496-1501.

Postlethwaite, C. M. & Dennis, T. E. (2013). Effects of Temporal Resolution on an Inferential Model of Animal Movement. *Plos One,* 8 (5): 11.

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S. & Brashares, J. S. (2009). The Rise of the Mesopredator. *Bioscience*, 59 (9): 779-791.

R Core Team. (2013). *R: A language and environment for statistical computing.*: R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. (2018). *Package: splines, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL*

Recio, M. R., Mathieu, R. S., Maloney, R. & Seddon, P. J. (2010). *First results of feral cats (Felis catus) monitored with GPS collars in New Zealand*: New Zealand Ecological Society.

Reynolds, J. & Tapper, S. (1996). Control of mammalian predators in game management and conservation. *Mammal Review*, 26 (2-3): 127-155.

Ryan, P. G., Petersen, S. L., Peters, G. & Gremillet, D. (2004). GPS tracking a marine predator: the effects of precision, resolution and sampling rate on foraging tracks of African Penguins. *Marine Biology*, 145 (2): 215-223.

Sabarros, P. S., Gremillet, D., Demarcq, H., Moseley, C., Pichegru, L., Mullers, R. H. E., Stenseth, N. C. & Machu, E. (2014). Fine-scale recognition and use of mesoscale fronts by foraging Cape gannets in the Benguela upwelling region. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 107: 77-84.

Salek, M., Drahnikova, L. & Tkadlec, E. (2015). Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammal Review*, 45 (1): 1-14.

Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A. S., Stuart, S. N. & Temple, H. J. (2008). The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, 322 (5899): 225-230.

Schofield, G., Bishop, C. M., MacLean, G., Brown, P., Baker, M., Katselidis, K. A., Dimopoulos, P., Pantis, J. D. & Hays, G. C. (2007). Novel GPS tracking of sea turtles as a tool for conservation management. *Journal of Experimental Marine Biology and Ecology*, 347 (1-2): 58-68.

Servín, J., Rau, J. R. & Delibes, M. (1991). Activity pattern of the red fox Vulpes vulpes in Doñana, SW Spain. *Acta Theriologica*, 36 (3-4): 369-373.

Shapira, I., Sultan, H. & Shanas, U. (2008). Agricultural farming alters predator-prey interactions in nearby natural habitats. *Animal Conservation*, 11 (1): 1-8.

Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D. W. (2004). *Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan*: IUCN Gland.

Soulsbury, C. D., Baker, P. J., Iossa, G. & Harris, S. (2010). Red foxes (Vulpes vulpes). In *Urban carnivores: ecology, conflict, and conservation*, pp. 63-79: JHU Press.

SSB. (2016). Folkemengd og areal, etter kommune (SÅ 57). In *Statistisk sentralbyrå*. Available at: https://www.ssb.no/262531/folkemengd-og-areal-etter-kommune-sa-57 (accessed: 25.02.2019).

SSB. (2018). *Folkemengde i tettbygde og spredtbygde strøk. Kommune. 1. januar.* ssb.no: Statistisk Sentralbyrå. Available at: https://www.ssb.no/beftett (accessed: 19.02.2019).

SSB. (2019a). 07366: Produktivt skogareal (dekar), etter region, statistikkvariabel og år. In *Statistisk sentralbyrå*. Available at: https://www.ssb.no/statbank/table/07366/ (accessed: 25.02.2018).

SSB. (2019b). Bosetting og areal etter kommune. In *Kommuneprofilen.no*. Kommuneprofilen online database (Kommuneprofilen). Available at: https://www.kommuneprofilen.no/profil/Kommunefakta/Bosetting_Areal_kommune.aspx (accessed: 25.02.2019).

SSB. (2019c). Felte småvilt, etter region, småvilt, statistikkvariabel og intervall (år). In *Statistisk sentralbyra*. Available at: https://www.ssb.no/statbank/table/07514/ (accessed: 25.02.2019).

SSB. (2019d). Kommunefakta. In *SSB*. Available at: https://www.ssb.no/kommunefakta (accessed: 25.02.2019).

Stillfried, M., Belant, J. L., Svoboda, N. J., Beyer, D. E. & Kramer-Schadt, S. (2015). When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes*, 120: 30-39.

Therneau, T. (2015). *package "survival: A Package for Survival Analysis in S_. version 2.38*.

Thurfjell, H., Ciuti, S. & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, 2 (1): 4.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365 (1550): 2163-2176.

Treves, A. & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation biology*, 17 (6): 1491-1499.

Turchin, P. (1998). *Quantitative analysis of movement*: Sinauer assoc. Sunderland (mass.).

Venables, W. N. & Ripley, B. D. (2002). *Mass package: Modern Applied Statistics with S. Fourth Edition.*: Springer, New York. .

Weimerskirch, H., Pinaud, D., Pawlowski, F. & Bost, C. A. (2007). Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *American Naturalist*, 170 (5): 734-743.

Wiens, J. A. (1989). Spatial Scaling in Ecology. *Functional Ecology*, 3 (4): 385-397.

Wilson, R. P. & McMahon, C. R. (2006). Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment*, 4 (3): 147-154.

Zeller, K. A., McGarigal, K., Cushman, S. A., Beier, P., Vickers, T. W. & Boyce, W. M. (2016). Using step and path selection functions for estimating resistance to movement: pumas as a case study. *Landscape Ecology*, 31 (6): 1319-1335.

Appendix 1

Summary of cluster visitation protocol:

- Identify clusters in Google Earth based on previously mentioned criteria, save as .kml.
- Convert the file to .gpx through an online conversion service.
- Load .gpx file to handheld GPS (Garmin 60CX)
- Navigate to cluster
- Search in the immediate area around the cluster for signs of fox presence and likely activity.
- Record predetermined parameteres in google sheets, take photo documentation, and collect scats/hair if present. The main objective was to find the likely activity of the fox at the cluster, but several other parameters like habitat, terrain, tracking conditions and signs of the fox were also recorded.

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