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Fine-scale assessment of responses to roads by red foxes

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Preface

This thesis is written as the final step of my Master of Science in natural resource management at the Norwegian University of Life Science (NMBU), Faculty of Environmental Sciences and Natural Resource Management. This thesis is a part of the Red Fox Project at the university and is supported by the Norwegian Public Road Administration.

I want to give a big thanks to my supervisor at the university, Richard Bischof, for all crucial help with my thesis and for making it possible for me to write about my topic of interest. I also want to give a big thanks to my co-supervisor at The Norwegian Public Road Administration, Karianne Thøger- Haaverstad, for valuable input on my thesis and inspiration through my summer job at the office the summer of 2019.

Thanks to my partner, family and friends at the university for the love and support throughout my five years at Ås and through the process of writing my thesis.

Vestnes, June 2020

Emma Kuskemoen

Abstract

Anthropogenic alterations are prevalent in most landscapes today, and roads have a distinct impact on the ecosystems they intersect and on the wildlife populations inhabiting them. Understanding and quantifying wildlife responses to roads can aid the development of effective management and mitigation strategies. Despite numerous studies on road impacts, few studies have looked at detailed behavioural responses and examined drivers of the activity at a fine spatiotemporal scale.

To address the knowledge gap of detailed behavioural responses to roads in fragmented landscapes, this study utilizes fine scale GPS data with high-frequency bursts generated by tracking 21 red foxes (*Vulpes vulpes*) in Norway. Four different behavioural responses to roads were identified and a mixed multinomial logit model was used to assess how landscape features, individual traits and the climate influenced the responses to roads.

Sex of the foxes and proximity to development were the variables which best explained the foxes' probability to exhibit the recorded responses. Overall, the foxes were most likely to exhibit tracking, followed by crossing, being stationary and least likely to deflect when not near developed areas. When in proximity of development track became a less dominant behaviour, while the probability of being stationary increased. Additionally, great individual differences in road use between the foxes were observed.

The use of high-frequency bursts enabled me to identify and quantify detailed and short-lived behavioural responses to roads which would not be obtainable if the animals were tracked at a coarser spatiotemporal scale. This study has revealed that red foxes exhibit several behavioural responses to roads and utilize roads for movement. Additionally, the results suggest that roads near development are used mainly for forage and less for movement. This study highlights the need for high resolution tracking data when aiming to identify fine scale wildlife interaction with roads.

Sammendrag

Menneskeskapte endringer er i dag en dominerende del av de fleste landskap, og veier har stor påvirkningskraft på de økosystemene de fragmenterer. Kunnskap og kvantifisering av ville dyrs bruk av veier er et viktig verktøy for å utvikle effektive forvaltningsplaner og avbøtende tiltak. En rekke studier har undersøkt veiers effekt på ville dyr, men få har undersøkt i fin skala hvordan viltet beveger seg når de er i nærheten av vei og hvilke faktorer som påvirker bevegelsene.

På bakgrunn av dette er denne studien basert på høyfrekvens posisjonsdata der 21 rødrever (*Vulpes vulpes*) ble utstyrt med GPS halsbånd som samlet posisjoner med kort tidsintervall mellom. Fire typer adferdsmønster i nærheten av vei ble identifisert og en multinomisk logistisk regresjonsmodell ble brukt til å undersøke hvordan variasjoner i landskapet, individuelle forskjeller og klima påvirket de observerte bevegelsene.

Rødrevenes kjønn og tilstedeværelse av bebyggelse var de beste forklaringsvariablene for de observerte adferdsmønstrene. Resultatene viste at når revene var lengre enn 15 meter fra bebyggelse var sannsynligheten for de ulike adferdsmønstrene fordels slik fra høy til lav: 1) gå langs veien, 2) krysse veien, 3) være stillestående (minimale bevegelser med minst 1 min varighet) og 4) å reflektere veien (gå imot for deretter å snu uten å krysse). Ved tilstedeværelse av bebyggelse økte sannsynligheten for at revene viste stillestående adferd, mens det å følge veien ble mindre sannsynlig. Studien viste også at det er store individuelle forskjeller mellom hvordan dyrene reagerte og brukte veier.

Bruken av høyoppløst GPS data gjorde det mulig å både identifisere og tallfeste spesifikke adferdsmønstre rødrever har i møte med vei, adferdsmønstre som ikke ville være mulig å fange med mindre detaljerte data. Denne studien har vist at rødrever har flere ulike adferdsmønstre i møte med vei, og de bruker veier for å bevege seg i landskapet. I tillegg tyder resultatene på at veier i nærheten av bebyggelse i større grad benyttes for fødesøk og mindre for å bevege seg over store avstander. Denne studien fremhever viktigheten av brukt av høyoppløst GPS data i studier som har til hensikt å undersøke de finskala bevegelsene vilt viser i møte med vei.

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1. Introduction

Anthropogenic alterations are prevalent in most landscapes today, and roads are increasingly intersecting the terrestrial surface of the earth (Dulac, 2013; Forman & Alexander, 1998). As Forman (2003) puts it "transportation lies at the core of society" and infrastructure such as roads facilitate access to resources and supports increasing mobility demands. Global Roads Inventory Project developed by Meijer et al. (2018) estimated that roads currently stretch across the globe for more than 21.6 million km, a distance estimated to increase by up to 4.7 million km by 2050. While International Energy Agency (Dulac, 2013) estimated that 25 million km paved roads will be built by 2050, based on a current global road network consistent of 42 million km. Although estimates range widely among the aforementioned studies, there is a consensus of opinion that the global road network will expand during the decades to come. Most of the expansion of roads are expected to occur in developing nations and in areas with globally valuable ecosystems such as the Amazon or the Congo basin (Meijer et al., 2018), and Laurance et al. (2014) identified many areas where conflicts are expected to rise due to road expansion and environmental values in the future. Some reasons for these expected conflicts are grounded in the growing field of road ecology, which explores the complex relationship between roads and the natural environment (Forman & Alexander, 1998).

Roads have a distinct impact on the ecosystems they intersect and on the wildlife populations that are part of these ecosystems (Fahrig & Rytwinski, 2009). A complex and widespread network of roads causes fragmentation of landscapes, ultimately altering the ecosystems (Forman & Alexander, 1998). Through this process, many landscapes turn into complex matrix of small patches of remnant habitat more of less isolated by heavily utilized and modified areas, which restraints the wildlife population inhabiting it. Fahrig and Rytwinski (2009) found that the negative effects of roads and traffic on populations documented in studies outnumbered the positive effects by a factor of five. Fragmentation can cause habitat loss and degradation, as well as inaccessibility of resources (Habel et al., 2019; Jaeger et al., 2005). Roads can act as barriers for wildlife causing traffic induced mortality and isolation of subpopulations either due to physical barriers or road avoidance

(Jackson & Fahrig, 2011). Simultaneously, roads can have positive effects on population by providing corridors for movement (Bellamy et al., 2000; Mccleery et al., 2015), hence increasing connectivity, or by providing valuable habitat (Spooner, 2015). Connectivity between subpopulations are crucial for gene flow and to ensure sufficient genetic diversity for population resistance (Hamner et al., 2012). Corridors can be utilized by many species, including invasive species and roads as corridors can enhance their spread throughout a landscape and be of conservation concern (Dark, 2004; Gelbard & Belnap, 2003). Different road responses by species are also identified to alter predator-prey-interaction (Rogala et al., 2011). A significant amount of resources has been devoted to exploring the complex interaction between roads and wildlife, yet many effects remain unquantified (van der Grift et al., 2013; van der Ree et al., 2011; van Strien & Gret-Regamey, 2016).

Successful road mitigation requires a solid platform of knowledge on both positive and negative effects of roads on wildlife (Forman & Alexander, 1998). To reveal how roads affect population persistence it is necessary to combine information on several different factors due to the complex relationship between road and wildlife (Fahrig & Rytwinski, 2009; Jaeger et al., 2005). One factor to consider is the species behavioural responses to roads (Jaeger et al., 2005) both spatially and temporally (Corlatti et al., 2009). Information on the life history traits, like reproductive rates and movement ranges, of the species are important to examine the populations sensitivity to the mentioned negative effects of roads (Fahrig & Rytwinski, 2009; Jaeger et al., 2005). Jaeger et al. (2005) also pointed out the road characteristics, size and traffic volumes, to be additional important factors to take into consideration. Studies has shown a wide range of species-specific effects to roads, like variation in degree of road avoidance and mortality rates due to road traffic (Fahrig & Rytwinski, 2009), which implies a need to examine road use for multiple species at a time (Polak et al., 2019). Quantification of wildlife interaction with roads represents a useful tool, as understanding of the behavioural responses can aid the development of effective management and mitigation strategies.

Global Positioning System (GPS) telemetry has become a common method in wildlife tracking and is readily used in road ecology research (Loraamm et al., 2019; Pollock et al., 2019; Scrafford et al., 2018). Technical advances in the GPS technology, such as minimizing the size of GPS units and improved accuracy, have made it a powerful tool used to assess a wide range of ecological questions and species (Kays et al., 2015). Habitat selection is known to occurs at various scales (Johnson, 1980), and the equipment of GPS collars programmed to collect positions at certain intervals combined with high-resolution spatial data, permits research on animal movement at different scales. Shorter intervals between successive GPS fixes (inter-fix interval) will yield movement data of finer temporal scale, while simultaneously quickly increasing the battery expenditure and reducing the overall tracking time (Brown et al., 2012). The scale of which the movement patterns are examined, will heavily influence the patterns found (Beyer et al., 2013; Klaassen & Broekhuis, 2018). This can be illustrated by studies on moose in North America which have been found to prefer areas with moderate road densities at the landscape scale while avoiding roads on finer scale, as discussed by Beyer et al. (2013).

Despite numerous studies on road impacts, few studies have looked at fine scale responses of wildlife to roads. Most road ecology studies have utilized GPS with fixes rates of hours (Evans et al., 2019; Kite et al., 2016; Pollock et al., 2019) a few have used fix-rates of minutes (Baigas et al., 2017; Loraamm et al., 2019; Potapov et al., 2014) and very few have used fix-rates of seconds (Sur et al., 2020). The use of GPS fix-rates of one hour was used to identify habitat selection and road avoidance at the home-range scale by black bears (*Ursus americanus*) (Evans et al., 2019). A fix-rate of 2 hours revealed seasonal variation in grizzly bears (*Ursus arctos*) use of railways, though the authors pointed out that their GPS fix-rate might have been “too coarse to maximize biological relevance of the movement types [recorded]” (Pollock et al., 2019). A fix-rate of 20 to 30 minutes was used to quantify road crossings by lynx (*Lynx canadensis*) (Baigas et al., 2017). In highly fragmented landscapes a fix rate of 5 minutes (Potapov et al., 2014) and 10-12 minutes (Loraamm et al., 2019) was used to identify animals’ habitat selection in areas intercepted by roads and heavily influenced by human activity. A GPS fix rate of hours or even minutes may fail to catch short lived movement pattern or movement in relation to small landscape features (Bischof et al., 2019), and especially when these two are combined, such as when a rapid species cross or track a road. To my knowledge no study has used fix-rates of second to investigate animals fine scale responses to roads, except for other studies done in association with the Red Fox Project run by the Norwegian University of Life Science (NMBU), Norway (Bischof et al., 2019).

To address the knowledge gap of fine scale responses in fragmented landscapes, this study utilizes high-frequency bursts GPS data. The goal of this thesis is to demonstrate how GPS data at fine spatiotemporal scale can be used to assess wildlife's behavioural responses to roads in a highly fragmented landscape. Model species for the study was the globally abundant red fox (*Vulpes Vulpes*). Four different behavioural responses to roads were recorded: track, cross, stationary and deflection. The responses recorded were then linked with fine-scale spatial data (distance to open land, cover and development), sex of the foxes and presence of snow cover. In this thesis, I ask the following research questions with corresponding predictions:

The first research question asked is (**RQ. 1**): *What behavioural responses to road do red foxes exhibit and to what extent?* Based on current literature I predict that (**P.1**) the foxes will exhibit all road responses recorded in this study based on previous studies of the species in fragmented landscapes (Bischof et al., 2019; Frey & Conover, 2006; Hradsky et al., 2017; Toverud, 2019). Secondly, I predict that (**P. 2)** tracking will be the most pronounced response based on previous studies of canids (Bischof et al., 2019; Dickie et al., 2017; James & Stuart-Smith, 2000).

My second research question is (**RQ. 2**): *What factors can help predict activity by red foxes close to roads?* I predict that (**P. 3)** the foxes will be more likely to exhibit tracking and be stationary (the responses that intuitively require the most time spend in road habitat) when in proximity to cover and development, and less likely to exhibit these response when in proximity to open areas. Red foxes are known to utilize anthropogenic resources (Erb et al., 2012; Panek & Bresinski, 2002; Toverud, 2019) and the presence of cover has been shown to be preferred by wildlife in landscaped heavily affected by human activity (Ordiz et al., 2011) and in regards of road use in particular (Benitez-Lopez et al., 2010; Sunga et al., 2017). Lastly, I predict that (**P. 4**) foxes will be more likely to exhibit tracking and crossing when snow cover is present. An increase in use of roads and other landscape features with less snow during the winter have been identified for red foxes (Pozzanghera et al., 2016) as well as other taxa (Rolandsen et al., 2011).

2 Material and Methods

2.1 Study species

Red fox is a social species in the canid family that forms family groups, while being a solitary forager (Baker et al., 1998). Red foxes are a flexible, but mostly a crepuscular and nocturnal species (Monterroso et al., 2014). The species is widespread both globally and in Norway (Figure 1), and can be found in most landscapes ranging from harsh mountain areas to large cities (Eide, 2015). Red foxes are also invasive to many areas within the species' extent of occurrence (Gallant et al., 2020; Saunders et al., 2010) and are known to be a rapid disperser (Scott et al., 2014).

Red foxes show great flexibility when it comes to diet and is to be considered a generalist species, common foods can be rodents, eggs, insects, roe deer fawns (*Capreolus capreolus)* as well as berries, fruits, and grains (Eide, 2015). They are also known to scavenge and exploit anthropogenic food resources such as garbage and carrions from hunting (Bateman & Fleming, 2012; Stepkovitch et al., 2019). There are few restrictions on red fox hunting in Norway in regards of national laws for other huntable species (Viltloven, 1982) and live trapping in wooden traps are a common way to hunt the species. The hunting season lasts from the 15th of July to the 15th of April (Jakt- og fangsttider m.m. 1. april 2017–31. mars 2022, 2017) because females rear cubs during the from April to June.

***Figure 1**. Recorded observations (green circles) of red fox in Norway from the Norwegian Biodiversity Information Center database (observations from 11.08.1911 to 26.04.2020). Available at:* https://artskart.artsdatabanken.no/ *(accessed: 25.04.2020)*

2.2 Study area

The study was conducted in the south-eastern part of Norway (59°12´- 59°43´ N, 10°38´- 10°54´ E) (Figure 2). The study area consists of nine municipalities with the Oslo fjord bordering in the west. The total land area is 1269.21 km^2 (Kartverket, 2018a). Fox activity was recorded in the municipalities Frogn, Hobøl, Våler, Moss, Rygge, Råde and Fredrikstad, Vestby and Ås. The majority of the activity was within the last two, Ås and Vestby. The study area has elevations from zero to 280 meters above sea level (MASL) (Kartverket, 2018b).

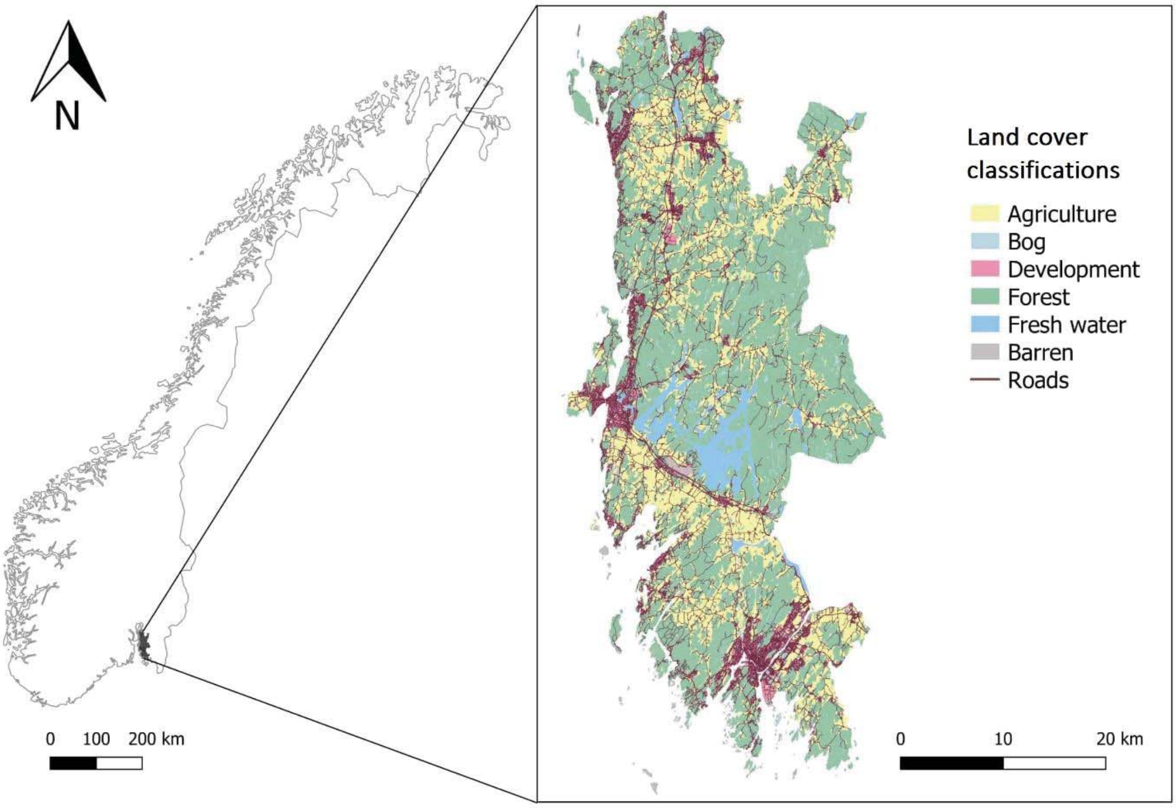

Figure 2. *Map of the study area's land cover types (to the right) and location in the south eastern Norway (to the left). The land cover classifications are agriculture (both arable land and pasture), bog, development (infrastructure, residential- and industrial areas), forest, fresh water and barren land. In addition, the road map for the area are marked.*

The weather station in Ås (59° 39' 37'' N, 10° 46' 54'' E, 93.3 MASL) reports that January and February are usually the coldest months with an average temperature of – 4.8 °C during the period from 1960 to 1990 and an average temperature of – 2.8 °C during the study period (January 2018 to November 2019). July is usually the warmest month with an average temperature of 14.8 °C during the period from 1960 to 1990 and 15.9 °C during the study period. During the study period of 2018 the snow covered the ground from new years to mid-April with some snow fall during late October and November. The snow covered the ground again from December 7th. In 2019 the snow lay until mid-February with a few days snow days later that month and in March. Later in 2019 there were only a few days with snow during the early to mid-November and from late November to early December. (Wolff et al., 2019; Wolff et al., 2020).

The study area can be described as a fragmented landscape dominated by forest and agricultural land, covering 60 % and 23 % of the area respectively (Kartverket, 2018a). Barren land covers 6 % of the study area, while residential areas and fresh water cover 4 % each (Kartverket, 2018a). About 2 % and 22 km^2 of the study area are roads (SSB, n.d.-e). Most of the forest consist of coniferous trees, but a good amount of mixed conifer-deciduous forests are present as well (NIBIO, n. d.). The most common coniferous species are Norway spruce (*Picea abies*) and Scots pine (Pinus Sylvestris). While the most common deciduous species is birch (*Betula ssp*.) with some elements of rowan (*Sorbus aucuaparia), Salix ssp*. and European aspen (*Populus tremula*). From 60 to 92 % of the forest are considered productive forest (SSB, n.d.-b). Protected land covered 44 % of the study area in 2017 (SSB, n.d.-d), meaning that less than 6 % of the forest is protected and therefore most likely being used for logging.

The study area had 201 510 inhabitants in 2018 (SSB, n.d.-c). As defined by Statistics Norway (2015) urban settlements are hubs of buildings with less than 50 metres apart with more than 200 inhabitants. If the distance exceeds 50 metres and the area between the buildings consist of area that cannot be developed for housing (e.g. parks, industrial areas, sport facilities or rivers), it can also be defines as urban settlements. The settlements not defined as urban are to be considered as rural settlements. By this definition the study area has predominantly urban settlements (73 %), and only 16 % of the inhabitants live in rural settlements (SSB, n.d.-a).

2.3 GPS telemetry

This study utilises GPS telemetry data generated by the Red Fox Project run by the University of Life Science (NMBU), Norway. The foxes were collared during the period from January 18th, 2018, to November 11th, 2019. Red foxes were captured in baited wooden box traps located in Ås and Vestby, during the period from January 2018 to November 2019. The animals were fitted with custom build GPS-collars with an integrated wear-and-tear mechanism (cotton string) which would allow the collars to eventually fall of. The average weight of the GPS-collars was 123 g, less than 2.3 % of the average body weight. For a more comprehensive description of the GPS units, see Bischof et al. (2019). In addition to collar fitting, sex and weight of each fox were recorded along with age-group based on size and appearance (juvenile/not juvenile). The capture and handling were in concordance with current laws and regulations and approved by the Norwegian Animal Research Authority (FOTS) on the behalf of the Norwegian Food Safety Authority (case ID: 2016/4769 and 18/211316).

The GPS collars were set to record position positions in bursts of 20 every 10 to 20 minutes (inter-fix interval), the position bursts recorded positions every 15 seconds (inter-bust interval). When active, the inter-burst and inter-fix could be set remotely by predefined commands passed on through SMS messages. The collected positions were immediately sent to an internet server for storing and availability. GPS error was determined using a reference unit (APX-15 GNSS/IMU). The test run by Bischof et al. (2019) yielded an accuracy of 10 cm for the reference unit and an median true error for our GPS units of 2.4 meters (CI: 0.6 – 10.1, n= 300 positions). To prevent the influence of capture and handling on the fox activity recorded, positions collected during the first 24 hours were excluded from analysis.

2.4 Behavioural assessment

The behavioural assessment process included data processing by identifying position sequences close to roads, as well as manually assessing the activity patterns. The data processing, plotting and later statistical analysis were conducted using R Studio 1.2.5033 (RStudio Team, 2019), powered by R version 3.6.1 (R Core Team, 2019), and associated packages. Google Earth Pro (Google, 2019) was used for quick assessment of the location of an activity and the surroundings, e.g. for confirming weather a crossing event was located at a site with an wildlife underpass. To link the GPS data with the surrounding habitat, a high-resolution map of the land cover types in the study area was obtained through the AR5-map from the Norwegian Institute of Bioeconomy Research (NIBIO, 2016). In addition, was a map of the road network obtained through the Norwegian Mapping Authority's geographic data portal (https://kartkatalog.geonorge.no/).

To select the position fixes close to roads, the distance from each position to the closest road was calculated using function st_distance in the sf package in R (Pebesma, 2018) by overlapping the GPS data and the road map. All burst with at least one position within the threshold distance of 10 meters from the road were included in the behaviour assessment and later statistical analysis. The threshold distance was set to 10 metres due to the previously mentioned error estimate of the GPS units (Bischof et al., 2019) and the interest of recording activity on or in close proximity of the road. The road buffer refers to the road and the two threshold distances on each side, covering a width of 20 metres with the road central line in the middle.

The bursts were selected, plotted with both the land cover and the road network maps, and assessed manually to identify the behaviour responses exhibited. To ensure consistent interpretation all assessments were conducted by one observer, my self. The four responses recorded were track, stationary, deflect and cross. The responses were recorded based on following conditions, which are illustrated in Figure 3 and 4:

Stationary if five or more successive point within the road buffer showed no clear direction and were clustered together within an approximately ten meters distance of each other (Figure 3 and 4). The threshold of five positions corresponds to ≥ one minute and was set in order to identify more persistent stational responses within the road buffer. When clear a stationary response also included positions outside the road buffer, the positions were included in the event.

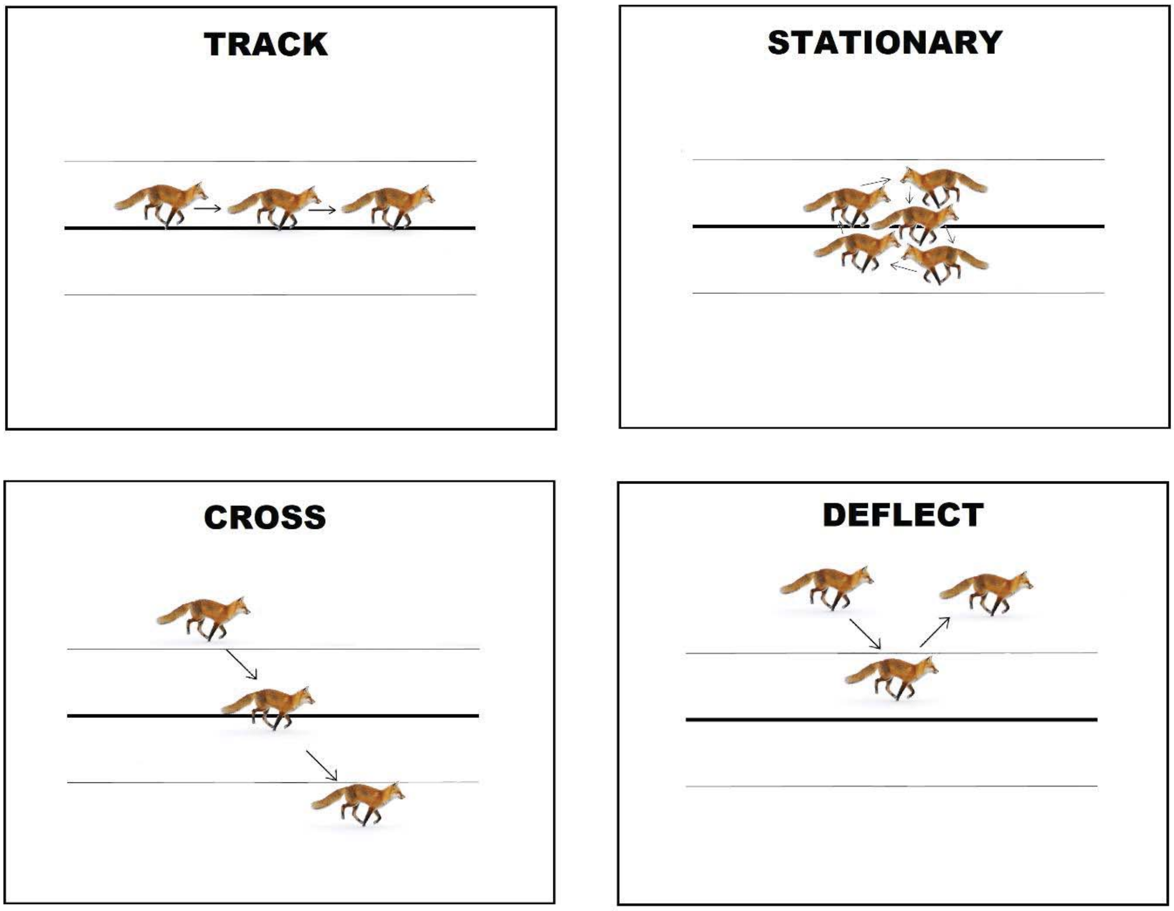

Figure 3. *A schematic presentation of the four behaviour responses recorded in this study. The small narrow lines represent the road buffer, the thick represent the road center line, the foxes represent the GPS positions fix and the arrows shows the direction of the movement pattern. Track equals ≥ 3 positions within the buffer in the direction of the road, cross equals one positions on either side of the buffer with or without positions within the buffer, stationary equals ≥ 5 positions clusters within the buffer and deflect equals two positions on the same side on the buffer with ≥1 position within.*

Cross if one position outside the buffer was followed by one position outside the buffer on the opposite side either with or without positions in between (within the buffer), se Figure 3 and 4. The duration of the identified crossing-response was set to start at the anterior position before entering the buffer and ending at the first position after exiting the road buffer. The cross response could be recorded in addition to a tracking or stationary event if the criteria for cross were met.

Deflect if one position outside the buffer was followed by at least one position within and then one outside the buffer on the same side as the first position (Figure 3 and 4). The duration of the identified deflect response was set to start at the anterior position before entering the buffer and ending at the first position after exiting the road buffer. The deflect activity could be recorded in addition to a tracking or Stationary event if the criteria for deflect were met.

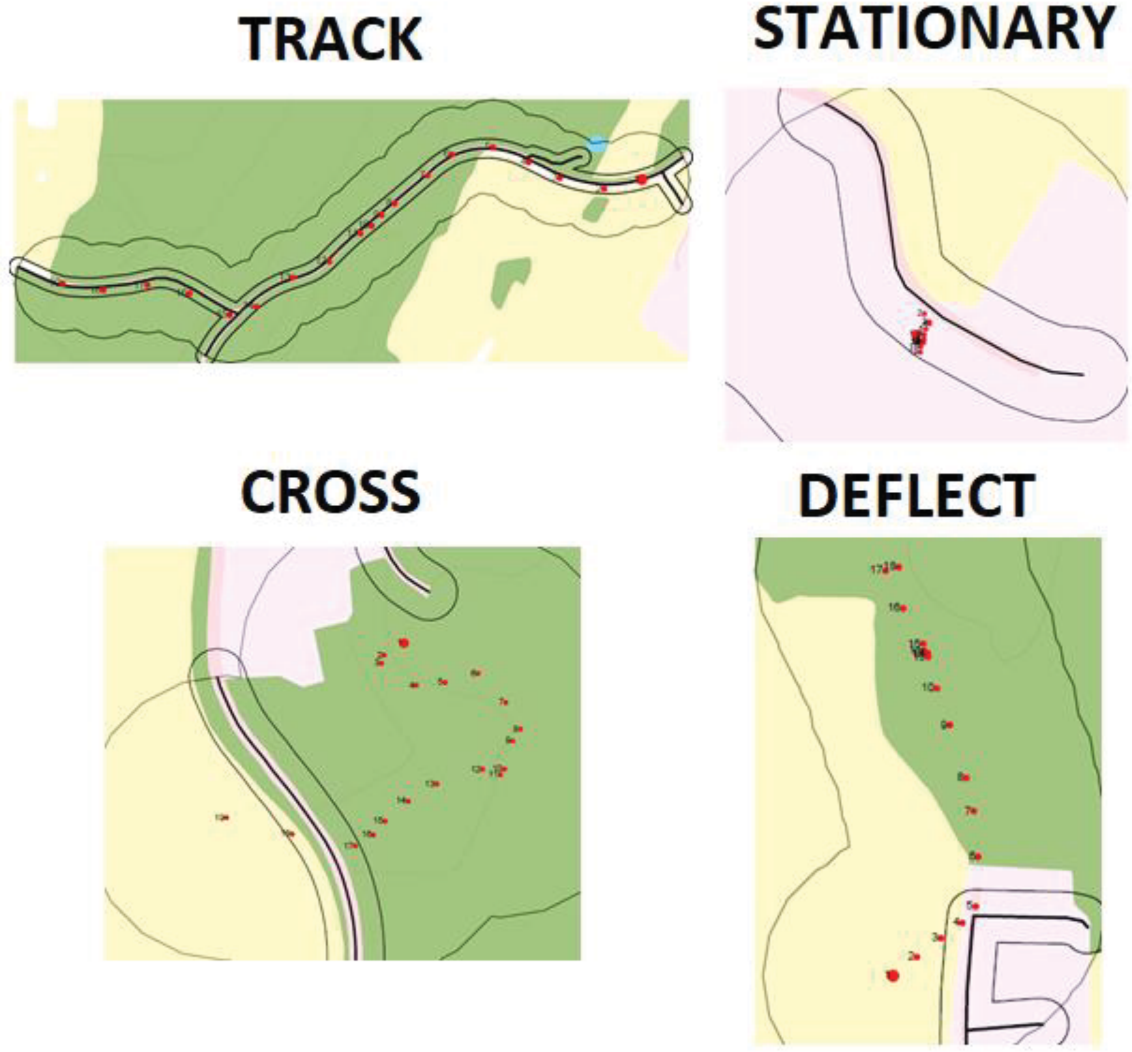

Figure 4. *Examples plots of real bursts exhibiting each behavioural response to roads recorded in this study (track, cross, stationary and deflect). The red dots represent the GPS positions, the black lines either represent the roads (thick), the road buffer or the 50 m focus- buffer. The coloring corresponds to the land cover types described in Figure 1.*

2.5 Exploring potential influential factors

The identified position sequences close to roads was further examined to investigate which factors influence the recorded behavioural responses to roads. The analysis was conducted using a multinomial logit regression (MLR) model. A multinomial model was suitable because the nominal response variable consists of four levels, the four different road responses recorded. The MLR also allowed for constructing mixed models which was needed to account for the non-independence in data by including both fixed and random effects.

Five predicting variables were included in the analysis: sex, snow cover and three categorical variables for land cover types/groups of land cover types. To create the latter, the st_distance function in the sf-package (Pebesma, 2018) was used to calculate the distance from each position to the different land cover types (Figure 2). The four land cover types/groups included were cover (forest and bog), open (barren and arable land) and development. The distance variables for one recorded response were calculated as the mean distance for the positions-fixes included in the response, and the distance variable for the grouped land cover types were the mean distance value to the land cover types included in the group. This information was included in the analysis as a categorical variable (0/1) by using a threshold distance of 15 meters (e.g. a distance to development <15 m equals 1; larger distance equal 0). In addition, sex of the individual fox (female/male) and presence of snow (0/1) were added as predictor variables.

The analysis only included positions with a recorded behavioural response to roads, and the dataset was aggregated by response, burst id and fox id after being transformed to a “long” format by using the melt-function in the reshape2 package (Wickham, 2007). All foxes were analysed jointly, and the analysis was conducted using the bayesx-function in R2BayesX package (Belitz et al., 2017; Umlauf et al., 2015). Level of significance used was $\alpha = 0.05$. All candidate models included fox id as a random effect the to account for the non-independence. Presence of cover, open areas, development, and snow cover, as well as sex, was included as fixed effects in different combinations to create the candidate models. The candidate models were compared and selected by using the Akaike information criterion (AIC) and the derived Akaike weights (AICw). The AIC comparison was performed for six different threshold distances for the land cover variables (development, cover and open), and the thresholds used was 5, 10, 15, 20, 25, 30 and 50 meters. This was used to evaluate the performance of the candidate models at different spatial scales. It was also used to examine which threshold distance yielded the most candidate models ranked better than the null model (the model not containing any predictor variables) as this threshold distance was selected for further analysis.

To ensure a comprehensive interpretation of the selected models, model outputs for all possible reference groups, meaning the four behavioural responses were generated and examined. The coefficient estimates from an MLR model are in log odds (logit), where a value > 0 equals “more likely than the response set as reference” and a value < 0 equals “less likely than the response set as reference”. For a brief visualisation of the most parsimonious (best ranked) models a bootstrap procedure with 500 iterations was used to make predictions, asses the fit of the models and construct the confidence intervals (CI). Due to technical constraints, the models used for this procedure were modified versions not including the random effects. Therefore, the plots were used for qualitative visualisation and not quantitative interpretation

3. Results

3.1 Fox trapping and GPS telemetry

Data from 21 GPS-collared foxes were included in this study, 8 of these were females and 13 were males (Table 1). The body weight of the foxes ranged from 3.5 to 7.9 kg, with a mean weight of 5.4 kg. Fourteen of the foxes were determined to be adults and seven to be juvenile based on their size and overall appearance. The sampling period per individual varied from 4.6 to 31.7 days, with a mean duration of 16.4 days and a standard deviation (SD) of 9 days. The entire data set for this study comprised of 69 099 GPS positions after removing the data from the first 24 hours after collaring. Number of positions per fox varied from a minimum of 1 309 to a maximum of 4 557, with a mean of 3 290 and a SD of 901. Fifteen percent (10 823 positions) of these were included in the analysis due to being a part of a burst with at least one position within the 10 metre road-buffer, a “road-burst”.

The number of positions per fox in the data set only containing positions from roads-bursts and road-positions (positions recorded with a behavioural response to roads), varied greatly depending on fox identity. Regarding road-bursts, fox 12 had the least positions with a total of 18, while fox 7 had the greatest amount with 1 138 positions. The mean number of road-burst positions per individual fox was 515.38 with a SD of 306.35. For road-positions, a total of 4 265 positions were recorded with a behavioural response. Fox 23 had the least recorded road-positions with a total of 3, while fox 25 had the most with 473 positions. The mean number of road-positions per fox was 203 and SD was 141.6 (Table 1).

Table 1. *Overview of the GPS-collared red foxes included in the study along with key numbers in the GPS data sets. The number of sampling days are measured after excluding the first 24h after collaring, road-burst refer to all burst with ≥ 1 position within the road buffer (10 meters) and road-positions refers to the positions recorded with a behavioural response to roads.*

Fox ID	Sex	Age group	Body weight (kg)	Date collared	Sampling days	Total positions	Positions in road-bursts	Road-positions/ sampling days
6	male	adult	7.9	18.01.2018	6.2	1911	344	55.5
7	male	adult	6.2	10.02.2018	10.9	3075	1138	104.4
8	male	adult	6.4	21.02.2018	4.6	1309	575	125.0
9	male	adult	5.9	22.02.2018	8.9	3719	440	49.4
11	female	adult	5.0	14.04.2018	10.8	3874	187	17.3
12	male	juvenile	4.6	27.07.2018	13.1	2536	18	1.4
13	female	juvenile	3.5	27.07.2018	11.0	3455	146	13.3
14	male	juvenile	4.9	03.08.2018	11.5	3762	79	6.9
15	male	juvenile	4.6	05.09.2018	12.9	4277	761	59.0
16	male	juvenile	4.0	07.09.2018	11.0	3702	868	78.9
17	female	juvenile	4.1	21.09.2018	9.2	4557	817	88.8
18	male	adult	6.5	12.11.2018	14.2	3512	757	53.3
19	female	adult	6.4	08.12.2018	7.9	2911	304	38.5
20	male	adult	5.5	09.12.2018	16.4	2891	528	32.2
21	female	adult	5.5	13.12.2018	27.8	3974	535	19.2
22	male	adult	5.5	17.01.2019	20.5	4142	201	9.8
23	female	adult	4.6	10.03.2019	27.0	4305	695	25.7
24	female	adult	4.3	24.03.2019	34.4	1807	668	19.4
25	male	adult	7.48	03.09.2019	23.1	4040	958	41.5
26	female	juvenile	4.58	15.11.2019	31.7	2385	484	15.3
27	male	adult	6.41	20.11.2019	30.4	2955	320	10.5

3.2 Behavioural assessment

A total of 664 events of behavioural responses to roads were recorded. Track was the most common response with 41 % of the recorded responses, while cross, stationary and deflect contribute to 28 %, 20 % and 11 % of the total, respectively (Figure 5).

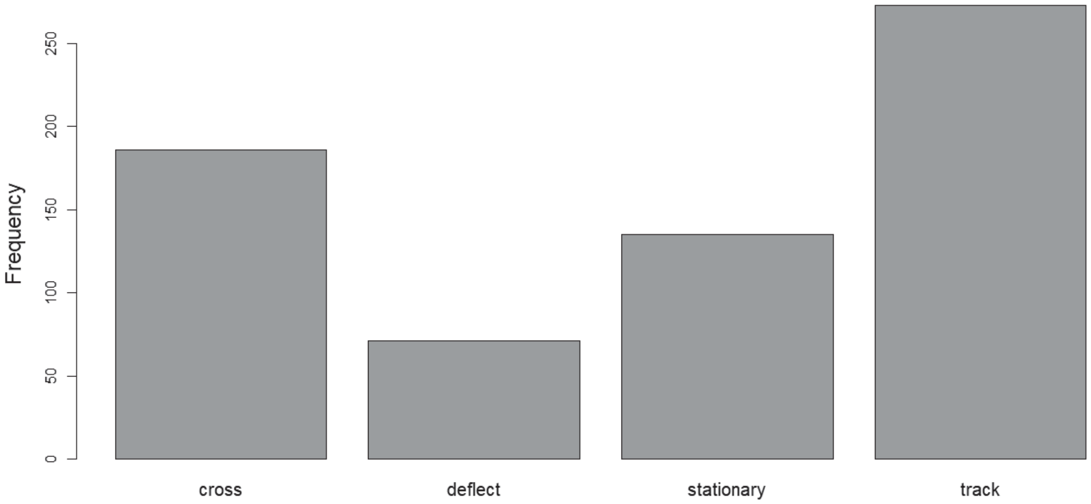

Figure 5. *Frequency of each examined behavioural response to roads (cross, deflect, stationary and track) recorded by manually assessing the GPS bursts with ≥ 1 positions within the road buffer of 10 meters.*

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The assessment of position sequences recorded with two or three different behavioural responses showed that there were six different activity combinations (Table 2). The total number of combined activity events recorded was 71, divided between 18 foxes. The most common combined activity was *track + cross* with 58 % (n= 41) of the events recorded combined activities, while the second most common with 20 % (n=14) of the events was *track + deflect*. The number of events combined activity events per fox ranged from 1 to 8, with a of mean of 3.89 and a SD of 2.37.

***Table 2**. Number of sequences of positions recorded with two or more behavioural responses, i.e. combined activities. Table shows the identified combined activities and the frequency of each.*

Combined activities	Frequency
Cross + stationary	7
Deflect + stationary	4
Track + cross	41
Track + cross + stationary	3
Track + deflect	14
Track + stationary	1

Tracking was exhibited by 19 foxes (Figure 7). A total of 273 tracking events were recorded portioned in 257 unique bursts, meaning that several bursts include more than one tracking event. The number of tracking events recorded per individual fox ranged from 1 to 36, with a mean of 14.37 and SD of 9.49. Mean tracking length was 88.55 m with a range from 6.13 m to 680.48 m and SD of 90 (Figure 8). Out of the 273 total tracking events 25 % (n= 59) were combined with other behavioural responses (Table 2).

Cross was recorded response for 19 of the foxes. The total number of crossing events were 186 crossing and 27 % (n= 51) of these were combined activities (Table 2). Recorded crossing events per individual fox ranged from 1 to 35, with a mean of 9.8 and a of SD of 8.7 (Figure 7). Several foxes were identified crossing the high-traffic-volume road intercepting the study area (the E6) using conventional bridges for vehicles, wildlife underpasses and overpasses as well as multipurpose underpasses (Figure 6).

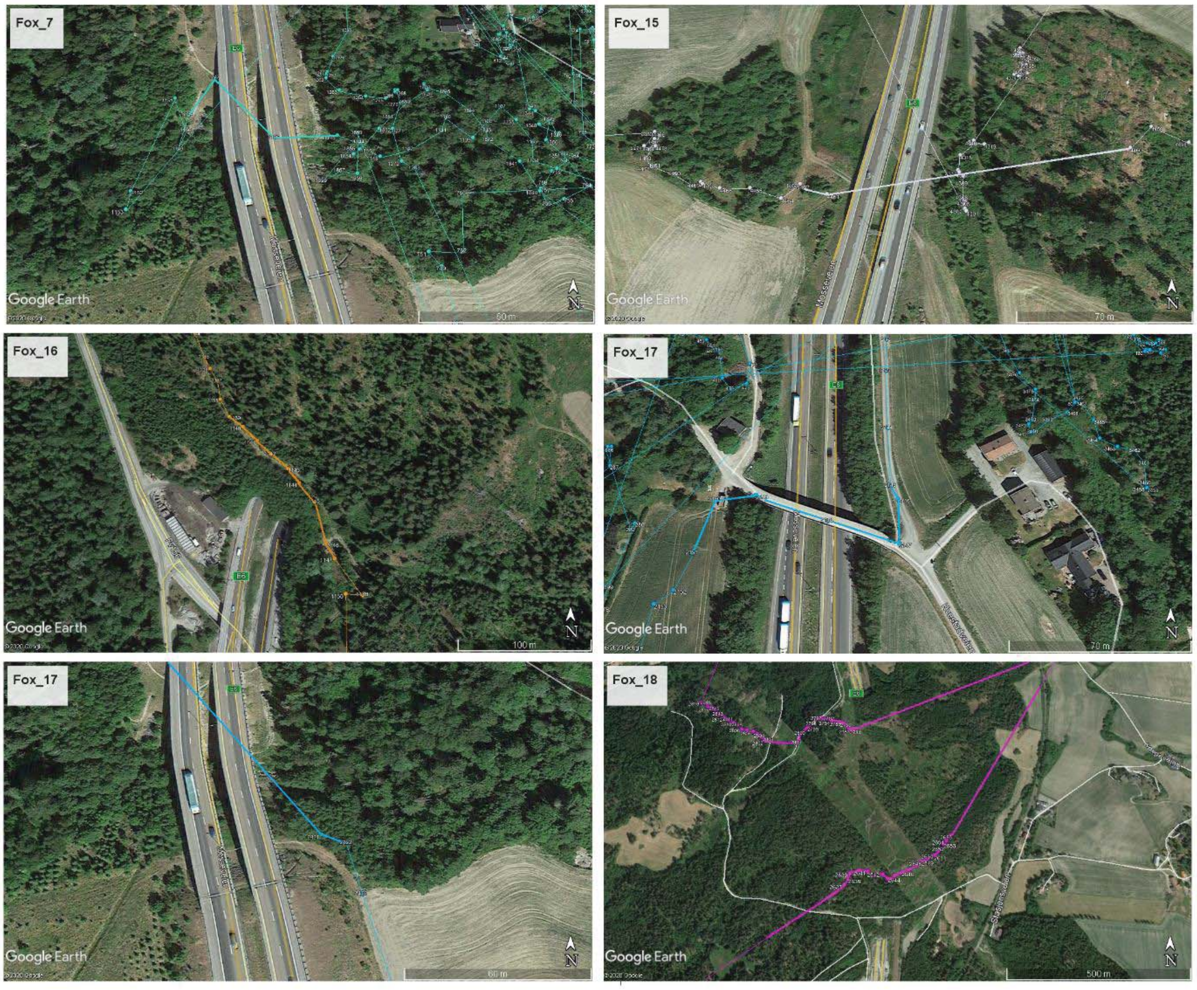


Figure 6. *Maps with GPS positions showing road crossing, of the high-traffic-volume E6 intercepting the study area. The maps show that several foxes utilized wildlife underpasses, wildlife overpasses, multipurpose underpasses, and a conventional vehicle bridge. The numbers indicate a position and the lines indicate the trajectory between successive positions.*

Deflecting events were recorded 71 times and by 19 of the individual foxes, 25 % (n= 18) of these deflecting responses were a part of a combined activity. The number of deflect events per individual fox ranged from 1 to 12, with a mean of 3.7 and a SD of 2.9 (Figure 7).

Stationary periods were exhibited by 19 of the foxes, and a total of 135 stationary events were recorded. Eleven percent (n= 15) of these were a part of a combined activity. The number of events per individual fox ranged from 1 to 18, with a mean of 7.16 and SD of 4.88 (Figure 7). The duration of the stationary events ranged from 60 seconds to 390 seconds. The mean stationary time was 121.3 seconds, with a SD of 75.52 (Figure 8).

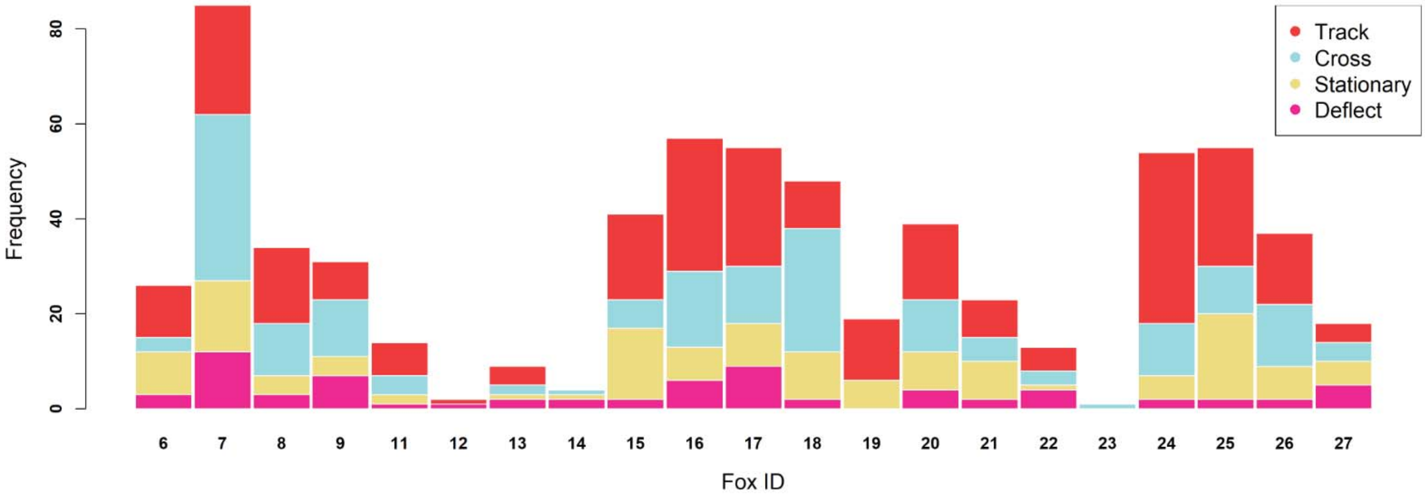


Figure 7. *Number of events recorded (frequency) of the four behavioural responses to roads (cross, deflect, stationary and track) per individual red fox tracked in this study.*

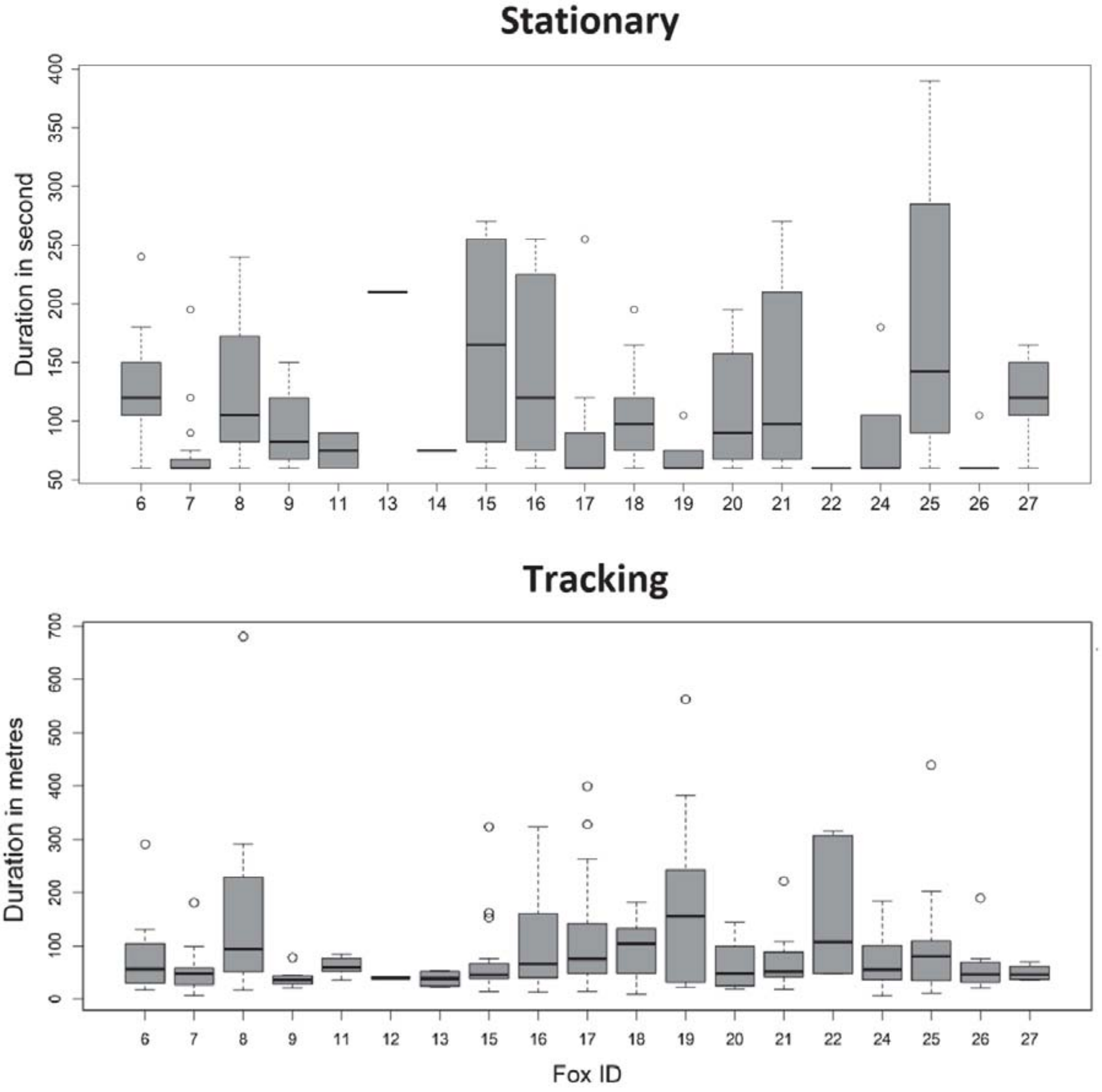


Figure 8. *Recorded duration of the behavioural responses track (in meters) and stationary (in seconds) per individual fox tracked in this study. The distribution of the recorded durations are displayed with the grey boxes representing 50 % of the durations(range from 25th quantile to 75th quantile), the thick black line representing the mean duration value and the whiskers (dashed lines) the 99.3 % of the durations. The open circles are the outliers and represent the rest 0.7 % of the durations.*

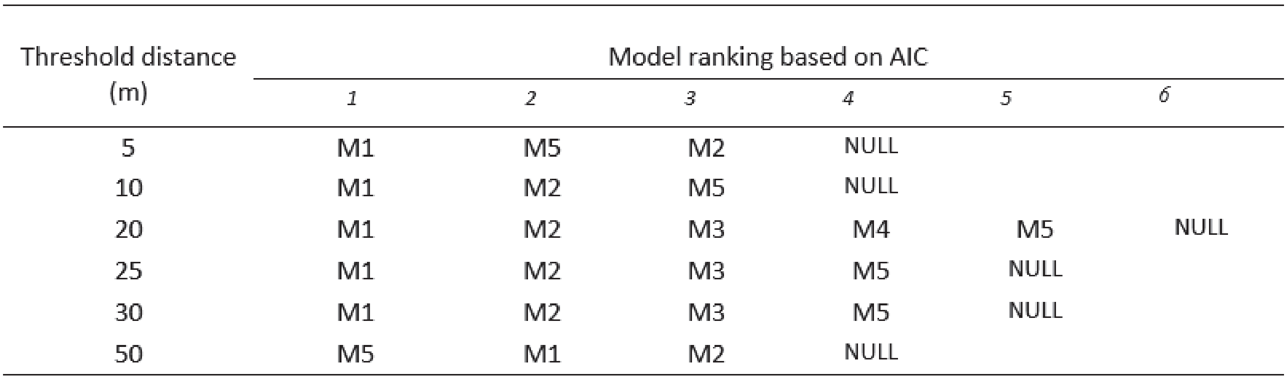
3.3 Exploring potential influential factors

The AIC comparison of the six threshold distances for the land cover variables (development, open and cover) resulted in the most candidate models ranked better than the null model for the threshold distance of 15 meters. The data set generated with this threshold distance was therefore used for the final AIC comparison and model selection. The top ranked model (M1) according to the AIC comparison process included the fixed effects; sex of the foxes and presence of development (within 15 meters of the response). The second-best model (M2) included presence of development only. The two top models, M1 and M2, carried the majority of the Akaike weights with 0.46 and 0.39 respectively (Table 3). Due to the small difference in AIC value between the two top-models, M2 were examined as well. Seven models were ranked better than the null-model based on the AIC comparison, and cover was the only variable not included in any of the models ranked better than the null. The AIC comparison test at different threshold-distances showed that M1 was the top-ranked model at all but one of the threshold distances tested (Table 4). At a threshold distance of 50 meters was M5 (the model containing sex only) ranked with the lowest AIC value.

Table 3. *Akaike Information Criterion (AIC) comparison table of the top ten models at a threshold-distance of 15 meters for the land-cover types (development, open and cover). The variables included in the models are the presence of development (dev), open areas and cover, plus presence of snow cover and sex of the foxes. All models included fox ID as a random effect in addition to the displayed fixed effects. NULL refers to the null model not containing any predictor variables. Furthermore, the table contains the raw AIC-values (AIC_i), the differences between the model i and the top-model ($\Delta_i AIC$), the AIC weights (w_i (AIC)) and the model ranking. Selected models are in bold.*

Model	Description	AIC_i	Δ_iAIC	w_i (AIC)	Rank
M1	**response ~ sex + dev**	**1571.18**	**0**	**0.46**	**1**
M2	**response ~ dev**	**1571.49**	**0.31**	**0.39**	**2**
M3	response ~ dev + snow	1574.82	3.64	0.07	3
M4	response ~ open + dev	1575.95	4.77	0.04	4
M5	response ~ sex	1578.85	7.67	0.01	5
M6	response ~ open + dev + snow	1579.25	8.07	0.01	6
M0	NULL	1580.01	8.83	0.01	7
M7	response ~ sex + cover + open + dev	1580.14	8.96	0.01	8
M8	response ~ sex + snow	1582.35	11.17	0.00	9
M9	response ~ sex + open	1583.41	12.23	0.00	10

Table 4. *Model comparison based on Akaike Information Criterion (AIC) for the six other threshold-distances for the land-cover types (development, open and cover) examined in this study. The model names refer to the descriptions provided in Table 3. NULL refers to the null model not containing any predictor variables and the table do only contain the candidate models ranked better than the null model.*



Threshold distance (m)	Model ranking based on AIC					
	1	*2*	*3*	*4*	*5*	*6*
5	M1	M5	M2	NULL		
10	M1	M2	M5	NULL		
20	M1	M2	M3	M4	M5	NULL
25	M1	M2	M3	M5	NULL	
30	M1	M2	M3	M5	NULL	
50	M5	M1	M2	NULL		

In M1, there was a trend for males being less likely to track than to be stationary (coef= -0.45, SE= 0.27, t= -1.66, p= 0.098) (Figure 9 and Table 5). I detected no other significant coefficients for different behavioural responses based on sex. Therefore, the other significant coefficients for females not in proximity to development (the intercept) were treated as valid for both sexes.

According to both M1 (Table 5) and M2 (Appendix A), the foxes were significantly more likely to track than to exhibit any of the other three behavioural responses when not in presence of development (Figure 9). M2 yielded significant values for the foxes to be more likely to cross than to be stationary (coef= 0.40, SE= 0.21, t= -5.09, p= < 0.001) when not in presence of development. While for M1 the differences in probability to cross compared to being stationary, and vice versa, was not significantly different from each other (p= 0.14) when not in presence of development. When not in proximity to development there was a trend for the foxes to be less likely to deflect than to be stationary (M1: p= 0.052), while compared to all other responses the log odds for deflection was negative and significant. All comparisons in M2 yielded significant values for deflection being the least likely response when not in proximity to development.

The presence of development decreased the probability of exhibiting tracking over being stationary (M1: coef= -0.70, SE= 0.24, t= -2,99, p= 0.003) and deflecting (M1: coef= -0.59, SE= 0.30, t= -1.97, p= 0.049) in both models. Meaning that tracking becomes a less prominent behaviour when in proximity to development. The presence of development also changed the pattern seen between stationary and cross, as stationary became more probable when in proximity to development (M1: coef= 0.67, SE= 0.26, t= 2.58, p= 0.01) in both models.

Table 5. *Model output for the best ranked model, M1, from the multinomial logit regression with all four behavioural responses as reference. The model contains sex of the fox and presence of development as fixed effects and fox id as random effect. The coefficient estimates are in log odds (logit). SE = standard error, intercept = for females when not in presence of development, male = male vs. female, dev = when development is present (within 15 m).*

Reference	Variable	Estimate	SE	t value	p value	
Track	Intercept: cross	-0.7643	0.2592	-2.9488	0.0033	**
	Male: cross	0.4	0.3166	1.2633	0.207	
	Dev: cross	0.0559	0.2371	0.2358	0.8137	
	Intercept: deflect	-1.9524	0.3521	-5.5444	<2e-16	***
	Male: deflect	0.6747	0.4109	1.6421	0.1011	
	Dev: deflect	0.5863	0.3065	1.9127	0.0563	.
	Intercept: stationary	-1.1971	0.2622	-4.5648	<2e-16	***
	Male: stationary	0.3912	0.3133	1.2486	0.2123	
	Dev: stationary	0.7632	0.3133	3.1656	0.0016	**
Cross	Intercept: deflect	-1.1953	0.3568	-3.3497	0.0009	***
	Male: deflect	0.2182	0.4135	0.5278	0.5979	
	Dev: deflect	0.4665	0.3191	1.462	0.1442	
	Intercept: stationary	-0.448	0.3062	-1.4631	0.1439	
	Male: stationary	-0.0556	0.3651	-0.1523	0.879	
	Dev: stationary	0.6737	0.2615	2.5768	0.0102	*
	Intercept: track	0.7402	0.2352	3.1469	0.0017	**
	Male: track	-0.4457	0.2853	-1.5623	0.1187	
	Dev: track	-0.1171	0.2333	-0.5021	0.6158	
Stationary	Intercept: cross	0.4373	0.3025	1.4456	0.1488	
	Male: cross	-0.0446	0.3594	-0.124	0.9014	
	Dev: cross	-0.6514	0.2604	-2.5015	0.0126	*
	Intercept: deflect	-0.7515	0.3863	-1.9453	0.0522	.
	Male: deflect	0.2407	0.4463	0.5393	0.5899	
	Dev: deflect	-0.1143	0.3254	-0.3512	0.7255	
	Intercept: track	1.1955	0.2331	5.1285	<2e-16	***
	Male: track	-0.4526	0.2734	-1.6553	0.0984	.
	Dev: track	-0.7049	0.236	-2.987	0.0029	**
Deflect	Intercept: cross	1.1444	0.3377	3.3889	0.0007	***
	Male: cross	-0.1417	0.3909	-0.3626	0.717	
	Dev: cross	-0.5173	0.3148	-1.6435	0.1008	
	Intercept: stationary	0.7073	0.3549	1.9929	0.0467	*
	Male: stationary	-0.1534	0.4086	-0.3754	0.7075	
	Dev: stationary	0.1906	0.3198	0.596	0.5514	
	Intercept: track	1.9005	0.2948	6.4462	<2e-16	***
	Male: track	-0.5488	0.3382	-1.6225	0.1052	
	Dev: track	-0.5856	0.297	-1.9716	0.0491	*

Significance codes 0 ‘***’ 0.001 ‘**‘ 0.01 ‘*’ 0.05 ‘.’

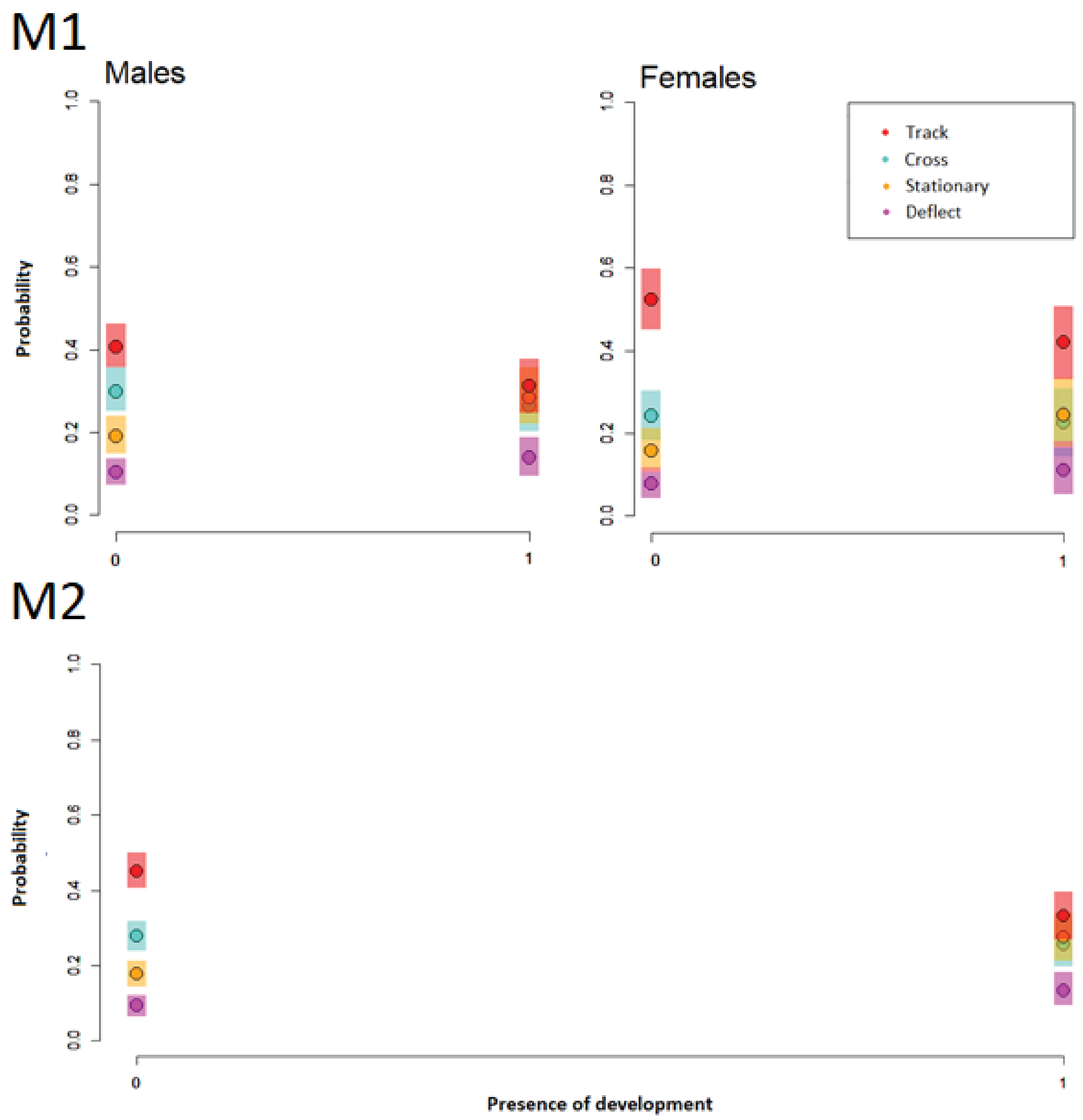


Figure 9. *Probability of foxes exhibiting one of the four behavioral responses (track, cross, stationary, deflect) when approaching within 10 meters of a road as predicted by the top-models, M1 and M2 (Appendices A and B), without random effects and with "track" as reference. M1 contains sex of the foxes and presence of development as fixes effects, while M2 contains only presence of development. The Figure shows the model predictions based on 500 iterations of bootstrapping. Colored circles represent the mean predicted value and the colored area represent the confidence interval (CI). Zero equals no presence of development within 15 meters and 1 equals presence of development (within 15 meters).*

4. Discussion

The fine-scale approach of this study made it possible to find evidence for and quantify the occurrence of specific fine-scale responses of foxes to roads. The assessment of potential influential factors showed that sex of the foxes and proximity to development best explained the foxes' probability to exhibit the recorded responses. Overall, foxes were most likely to exhibit tracking, followed by crossing, being stationary and least likely to deflect when not near developed areas. When in proximity of development track became a less dominant behaviour, while the probability of being stationary increased (Figure 9). The study also identified great individual variation in the frequency of road encounters with a behavioural response and in the duration of the exhibited behaviours (Figure 7 and 8).

4.1 Behavioural assessment

The behavioural assessment yielded numerous events of each behavioural response, showing road use by red foxes in accordance with my first prediction (P.1). Use of road habitat have been reported by a wide range of species such as grey wolves (*Canis lupus*) (Dickie et al., 2017; James & Stuart-Smith, 2000), coyotes (*Canis latrans*) (Murray & St Clair, 2015), African wild dogs (*Lycaon pictus*) (Abrahms et al., 2016), tasmanian devils (*Sarcophilus harrisii*), striped skunks (*Mephitis mephitis*) and racoons (*Proycon lotor*) (Frey & Conover, 2006). Studies on red foxes have also found patterns of road use (Bischof et al., 2019; Frey & Conover, 2006; Hradsky et al., 2017). Therefore, the identified road use by red foxes are consistent with results from previous studies of wildlife.

This study was conducted in a patchy and fragmented landscape, and previous studies of urban wildlife have also identified road use (Hradsky et al., 2017; Loraamm et al., 2019). In regard of road use in fragmented landscapes, few have studied detailed behavioural responses like in this study, but rather examined selection of road habitat. Studies of the latter have shown road use by e.g. fishers (*Martes pennant*) in New York (Loraamm et al., 2019) and invasive red foxes in urban Australia (Hradsky et al., 2017). Using partly the same data set as I, Bischof et al. (2019) and (Toverud, 2019) identified road use and selection towards road habitat for red foxes examined in this study. Thus, the recorded road use in this study substantiate that roads can facilitate movement of urban wildlife.

Previous studies on wildlife movement around road have mainly focused on the behavioural responses cross (Asari et al., 2019; Baigas et al., 2017; Murray & St Clair, 2015) and track (Andersen et al., 2017; Dickie et al., 2017; James & Stuart-Smith, 2000) and few have studied multiple responses at once. One exception is Pollock et al. (2019) who examined a similar set of behavioural responses as this study, but at a much coarser scale with fix-intervals of 2 hours and without the use of bursts. Consequently, the findings in this study provide new insight of a species' diversity of behavioural responses to roads in a fragmented landscape.

The great variation in the number of road encounters and behavioural responses to roads recorded per individual red fox imply that individual traits impact the road use. The number of position fixes recorded with a behavioural response varied from less than 0.00 % to 17 % of total collected positions per fox (Table 1). The frequency of recorded responses (Figure 8) and duration of the responses (Figure 9) also illustrate individual variation, although not being adjusted for sampling duration. Sex was the only individual specific factor used to explain the range of responses in this study, and although several studies have found females to be more sensitive to roads than males (Jerosch et al., 2018; Sawaya et al., 2019) this was not supported by my results. An explanation for the lack of sex differences detected might be explained by other studies which linked sex with reproductive status of the animal. Kite et al. (2016) found female grizzly bears to avoid roads at longer distances during breeding season, as opposed to in dispersal season, and Evans et al. (2019) found female black bears with cubs to be more reluctant to approach roads than non-reproducing females. This suggests that the sex differences in road use will be most prominent during breeding season, and might explain the lack of sex differences detected in this study as only one fox was tracking during this period (fox 11 was tracked for 10 days in April, Table 1). Therefore, the results of this study are not representative for the red foxes' responses to road throughout the year, as minimal data was collected during breeding season and time of year was not included as a predictor variable in the analysis (RQ.2).

My second prediction (P.2) was regarding tracking, as tracking of roads and other anthropogenic linear features has frequently been documented or inferred. African wild dogs were found to use roads for movement (Abrahms et al., 2016), as well were striped skunks, racoons and red foxes in a wetland area intercepted by roads (Frey & Conover, 2006). Wolverines (*Gulo gulo luscus)* were also found to use roads for movement (Scrafford et al., 2017), and grey wolves selected anthropogenic linear structures such as roads and pipelines in Alberta, Canada (Dickie et al., 2017). In conformance with both existing literature and my second prediction, tracking was the most prominent behavioural response recorded in this study.

Researchers have pinpointed several hypotheses for why tracking behaviour occurs along roads. Dickie et al. (2020) and James and Stuart-Smith (2000) both examined grey wolves and found prominent differences in tracking behaviour between wolves and caribous, suggesting that road use by predators can facilitate more effective movement and therefore food search. This hypothesis was supported by Frey and Conover (2006) as well. Predators and scavengers have been recognized to increase speed when tracking (Abrahms et al., 2016; Bischof et al., 2019; Dickie et al., 2017; Scrafford et al., 2018), which can further support that roads permits more effective foraging as well as foraging opportunities such as road kills and garbage (Frey & Conover, 2006). Another driver for the increased travel speed while tracking roads have been suggested to be related to higher perceived risks, as wildlife are more exposed while on roads and roads usually indicate human activity. Therefore, can increased speed while tracking roads be explained as a trade- off between more effective foraging and higher mortality risks (Bischof et al., 2019; Scrafford et al., 2018).

4.2 Exploring potential influential factors

The statistical analyses showed that the presence of development was the most influential factor for explaining the variation in recorded behavioural responses to roads. The presence of development was included as a predictor variable in either the best or the second-best model for all threshold distances according to the AIC comparison process. This suggests that development do influence the red foxes' road responses at distances ranging from 5 to 50 meters. The top models predicted that the presence of development would decrease the probability of a fox exhibiting tracking, even though tracking was the most common response recorded. This contradicts my third prediction (P.3) where I predicted that the behavioural responses requiring the most time spent in road habitats (stationary and tracking) to be more prominent when in proximity to development and cover, as opposed to open areas. My results show that foxes spent less time following roads when near human settlements than further away, which might imply that the animals use roads when approaching developed areas as identified by Hradsky et al. (2017). The decreased probability of tracking when near development can be caused by the foxes either avoiding roads when navigating in these areas or that the animals keep their activity to the edge of developed areas, but further research are needed to determine this.

According to the top models the probability of a fox exhibiting stationary periods increases when in proximity to development, which is in accordance with my third prediction. This might imply that developed areas provide more foraging opportunities as identified by Hradsky et al. (2017) and Stepkovitch et al. (2019), and that the stationary events recorded indicate either search of food or handling/consumption of food items. This assumption can be partly supported by findings in Andersen et al. (2017), which found similar mesopredator species to utilize roads for foraging. Physical surveys of activity clusters by Toverud (2019), which worked with a data set containing 16 of the same foxes as I, found that foxes were significantly more likely to forage very close to infrastructure. These two studies did not link the identified foraging activity close to roads to presence of development, therefore further research is needed to identify the reasons behind the apparent increase of stationary periods when in presence of development.

Contrary to my third prediction, presence of cover was not included in any of the candidate models ranked better than the null model at any of the tested threshold distances, suggesting that cover did not explain the variation in the recorded road responses. Open was included in one of the models ranked better than null for two threshold distances, but not included in the most parsimonious models. This suggest that the presence of open areas might influence the fox's behavioural responses when close to roads, although this was not fully supported by the results of this study. The lack of effects of cover is not in accordance with a range of previous studies who have found cover to be a significant predictor of road use (Benitez-Lopez et al., 2010; Sunga et al., 2017; Toverud, 2019). Toverud (2019) found that red foxes' selection towards infrastructure increased with the presence of cover. Other mammals have also been found to prefer areas with vegetation when approaching roads (Benitez-Lopez et al., 2010; Sunga et al., 2017). A potential explanation of the lack of effects can be the choice of land cover types included in the variable. Areas classified as bog was included in the cover- variable since it often contains scattered to dense vegetation and can also include areas that meets the criteria for "forest" (Ahlstrøm et al., 2019). Toverud (2019) included only "forest" in the cover variable and found it to be a significant predictor at a threshold distance of 27 meters.

The prediction of cover being an influential factor was based on studies who examined habitat preference by comparing available habitat to used habitat (Benitez-Lopez et al., 2010; Sunga et al., 2017; Toverud, 2019). The design of my study did not allow for assessing road use in regards of habitat preference, since no controls were taken, this might explain the inconsistency with present literature. Meaning that the results of this study do not necessarily contradict previous studies, but do not support the hypothesis that the presence of cover influence the probability of foxes to exhibit one road responses over the other.

Lastly, I predicted (P.4) that presence of snow cover would positively affect the probability to use the roads for activities linked to transportation (track and cross). This prediction was not fully supported by the findings as the two best ranked models did not contain snow as a predictor variable. However, the third ranked model, M3, contained snow which does imply that the presence of snow can explain some of the variation in the recorded responses. As mentioned under the discussion of P.3 this study did not include controls and therefore not make predictions regarding changes in use versus not use of roads as examined by (Pozzanghera et al., 2016; Rolandsen et al., 2011). This might explain the lack of effects of snow cover, and the results suggest that presence of snow cover does not influence the probability of foxes to exhibit one road response over the other.

Another factor which could have influenced the results is the snow data itself. Although the data on snow cover was temporally matched with movement data, the use of weather station data could have caused spatial mismatches due to the distances between the weather station and certain tracked foxes. Rolandsen et al. (2011) identified snow depth to be the most influential weather variable for predicting vehicle collisions with moose (*Alces alces)*, but this was only present for the areas with mean snow depths ranging from 50 to 70 cm, which is not the case for the study area of this thesis (Wolff et al., 2019; Wolff et al., 2020). Consequently, the results of this study might be more area specific and less applicable to areas of other environmental conditions.

4.3 Implications

With the use of high-frequency bursts and GPS data at fine spatiotemporal scale this study shows that GPS telemetry is a great tool for examining detailed wildlife movements. This study presents a framework which can be used to quantify fine scale movements in relation to small landscape features where GPS tracking at a coarser scale easily can overlook the encounters the animals have with these features (Bischof et al., 2019). There is little research on wildlife's decision making upon road encounters and little is known about the relationship between the exhibited responses. Therefore, this study contributes to the platform of knowledge on the subject and the methods used can be developed further to examine the mechanisms behind the animal's reaction patterns and road use. The framework of this study can also be used for quantifying the occurrence of behavioural responses to roads across a gradient of environmental change. This can provide insight into a species' vulnerability to roads and the cumulative effects the road network has on wildlife populations.

My result highlight that development and roads can facilitate movement as well as providing potential foraging opportunities for wild animals. Red foxes have previously been shown to utilize human settlements as steppingstones for dispersal into new areas and developed areas have been identified to cause population growth of the species (Elmhagen et al., 2018; Panek & Bresinski, 2002). The combination of roads and development might therefore provide new dispersal routes for red foxes and be of special interest for the wildlife management as the species are a rapid disperser (Scott et al., 2014), easily dispersing long distances (Walton et al., 2018). To reduce the likelihood of an unwanted population growth or spread of the species my results support that management strategies should include minimizing their access to anthropogenic food sources, which can be achieved by e.g. rapid removal of road kills and minimizing animals' access to dung piles and garbage close to roads.

This study has implications for both wildlife managers and researchers as it illustrates a method of how GPS telemetry can be used to better examine fine scale behavioural responses wildlife exhibit close to roads. The use of burst of position-fixes, as used in this study, makes it possible to track wildlife movement with two different fix rates (inter-burst-interval and inter-fix-interval). This allows for the collection of fine-scale temporal data while maximizing the batter longevity, as the high-frequency bursts produces fine scale GPS data while the use of longer inter-burst-intervals reduces the battery expenditure. Most importantly the combination of data on finer and coarser scale allows for multiscale analysis, although fine scale movements have been the emphasis of this thesis. Depending on the spatial and temporal scale of which wildlife are examined they will exhibit different habitat preferences (Beyer et al., 2013; Klaassen & Broekhuis, 2018; Zimmermann et al., 2014) and this makes multiscale analysis crucial for establishing a comprehensive knowledge on how wildlife use the landscape.

4.5 Recommendations for future research

This study illustrates a framework for examining detailed road use and can be developed further to study different species as well as answering other research questions regarding road ecology. One important factor for determining roads' effect on wildlife is road traffic, which was not included as a predictor variable in this study due to uncertainties regarding the quality of road traffic data in the study area. Traffic are known to affect both wildlife movement and persistence, as traffic induced mortality can deplete wildlife populations (Jackson & Fahrig, 2011) and increased road traffic can reinforce road avoidance behaviour as identified by Mccleery et al. (2015) and Scrafford et al. (2018). Consequently, further research on fine scale behavioural responses should include road traffic as one of the predictor variables to fully elucidate the different factors affecting road use.

In addition to road traffic, the inclusion of other road characteristics such as the roads width, surface or purpose/use (e.g. road for forestry or a multi-lane highway) could help identify how the different part of the road network effect the wildlife. Andersen et al. (2017) examined how two mesopredator species used sealed, unsealed and four-wheel-drive roads and found the animals to use the road types differently. Along sealed roads the movement patterns were straight and of greater speed, while along unsealed and four-wheel-drive roads the movement patterns were more tortuous and slower. Andersen et al. (2017) suggested that sealed roads were used for examining stretches for road kills and the other road types were used for hunting. Zimmermann et al. (2014) also found road type to be an important predictor of wolves' road use. Combining road characteristics and traffic volumes with the behavioural responses exhibited close to roads are recommended for future research.

Other factors known to impact animals' use of roads are time of day (Toverud, 2019; Zimmermann et al., 2014) , sex (Jerosch et al., 2018; Sawaya et al., 2019), reproductive status (Evans et al., 2019; Zimmermann et al., 2014) and whether it is breeding or dispersal season (Frey & Conover, 2006; Kite et al., 2016). Including these factors in future road ecology research at a fine scale can strengthen the predictions of species' road use and their sensitivity to roads, as well as explaining the great individual variation in behavioural responses to roads identified in this study.

The behaviour assessment process poses a bias due to the manual recordings. The response recordings are all based on one observer's ability to consistently examine the movement plots, hence there is a potential risk of misinterpretation and ignored behavioral patterns. This can cause underestimation of the frequency of a response as well as causing effects to go undetected. A critical assumption for applying my presented quantification method is that the bias is random, and no specific response is recorded wrongly more frequently than the others. Automating the assessment process would improve this part of the methodology.

5. Conclusion

GPS telemetry is a powerful and frequently used method in wildlife research (Kays et al., 2015), but yet few have used the tool to examine the detailed and fine scale behavioural responses wildlife have when encountering roads. High resolution tracking data enabled me to identify and quantify detailed and short-lived behavioural responses red foxes exhibit when encountering roads, which would not be obtainable if the animals were tracked at a coarser spatiotemporal scale. This study has revealed that the animals exhibit several behavioural responses to roads and utilize road for movement as tracking was the most prominent response. My results also suggest that roads near development is used for forage and less for movement than roads further away from human settlements.

This study highlights the need for high resolution tracking data when aiming to identify how wildlife interacts with roads at fine scale. Additionally, the study demonstrates a framework which can be used to clarify fine scale movement patterns in relation to other small landscape features as well. With this study I hope to illustrate the opportunities GPS telemetry with high-frequency bursts provide for multiscale analysis and for clarifying how wildlife interacts with the road network. Comprehensive knowledge on fine scale movements, which to large extent are lacking today, will allow for more informed decisions regarding wildlife management and road mitigation.

6. References

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Appendix A

Model output for the second-best ranked model, M2, from the multinomial logit regression with all four behavioural responses as reference. The model contains presence of development as fixed effect and fox id as random effect. SE = standard error, intercept = for females when not in presence of development, dev = when development is present (within 15 m).

Reference	**Variable**	**Estimate**	**SE**	**t value**	**p value**	
Track	Intercept: cross	-0.5135	0.1619	-3.1708	0.0016	**
	Dev: cross	0.0828	0.2359	0.3509	0.7258	
	Intercept: deflect	-1.516	0.2091	-7.2506	<2e-16	***
	Dev: deflect	0.6291	0.3037	2.0714	0.0387	*
	Intercept: stationary	-0.9527	0.1695	-5.6197	<2e-16	***
	Dev: stationary	0.796	0.2399	3.3178	0.001	***
Cross	Intercept: deflect	-1.055	0.2073	-5.0879	<2e-16	***
	Dev: deflect	0.4659	0.3153	1.4774	0.1401	
	Intercept: stationary	-0.4851	0.1894	-2.5616	0.0107	*
	Dev: stationary	0.6618	0.2601	2.5448	0.0112	*
	Intercept: track	0.4537	0.1535	2.9561	0.0032	**
	Dev: track	-0.1389	0.2327	-0.5968	0.5509	
Stationary	Intercept: cross	0.4056	0.1852	2.1902	0.0289	*
	Dev: cross	-0.6622	0.2591	-2.5556	0.0108	*
	Intercept: deflect	-0.5947	0.2294	-2.5925	0.0098	**
	Dev: deflect	-0.1118	0.3226	-0.3465	0.7291	
	Intercept: track	0.9008	0.1581	5.6979	<2e-16	***
	Dev: track	-0.7412	0.2362	-3.1375	0.0018	**
Deflect	Intercept: cross	1.0476	0.2047	5.1169	<2e-16	***
	Dev: cross	-0.5324	0.3128	-1.7019	0.0893	.
	Intercept: stationary	0.6008	0.2211	2.7176	0.0068	**
	Dev: stationary	0.1707	0.3183	0.5364	0.5919	
	Intercept: track	1.538	0.1901	8.0905	<2e-16	***
	Dev: track	-0.6241	0.2963	-2.1058	0.0356	*

Significance codes 0 ‘***’ 0.001 ‘**‘ 0.01 ‘*’ 0.05 ‘.’

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