

Habitat selection and diel activity patterns of red fox as a function of contrasting wolf activity levels in a Danish wolf territory

Master thesis by
Sofie Amund Kjeldgaard



AARHUS UNIVERSITY



Photo credit: Alex Sand Frich

Dansk titel: Habitatsselektion og døgnaktivitetsmønstre hos rød ræv som funktion af varierende ulveaktivitets-niveauer i et dansk ulveterritorium

English title: Habitat selection and diel activity patterns of red fox as a function of contrasting wolf activity levels in a Danish wolf territory

60 ECTS-point specialeprojekt:

Sofie Amund Kjeldgaard, 201507077

- Institut for Biologi, Aarhus Universitet
 - o Sektion for Økoinformatik og Biodiversitet.
- Institut for Bioscience, Aarhus Universitet
 - o Sektion for Faunaøkologi
- Naturhistorisk Museum Aarhus
 - o Research & Collections

Aflevering: 08/06-2021

Forsvar: 30/06-2021

Vejledere:

Jens-Christian Svenning

Institut for Biologi, Aarhus Universitet
Sektion for Økoinformatik og Biodiversitet.

Peter Sunde

Institut for Bioscience, Aarhus Universitet, Kalø
Sektion for Faunaøkologi

Kent Olsen

Naturhistorisk Museum Aarhus
Research & Collections

Forside:

Med tilladelse fra fotograf Alex Sand Frich, billede taget i Danmark i 2021, af en ulv med en ræv i munden.

Forord

Denne opgave består af to dele. Del A består af en udvidet introduktion og redegørelse for de elementer, der ligger til grund for og indgår i del B, der er et udkast til en videnskabelig artikel målrettet tidskriftet *Mammalian biology*.

Dette speciale kunne ikke være blevet til uden en lang række personer. Generering af data og klargøring af variabler til analyserne er i høj grad blevet til i samarbejde med Rebecca Lyhne. Vi har været heldige at kunne sparre med hinanden igennem de fire måneder, vi tastede data ind, for at sikre en konsekvent indtastningsprocedure. Datasættet indeholdt observationer indtastet af flere forskellige personer, derfor gennemgik vi sammen alle indtastede serier i databasen og rettede observationerne til, for at sikre at data var sammenligneligt. Undervejs i indtastningsprocessen rettede jeg indtastningsmanualen til, så den afspejlede den procedure vi benyttede. Jeg har bidraget med 6739 indtastede observationer i det datasæt, der er brugt i dette speciale, som i del B bliver beskrevet som datasæt A.

Sideløbende med indtastningen gennemgik Rebecca og jeg i fællesskab alle observationerne af ulve fra 2017, 2018 og 2019 og fik koblet kameraplacering på og lavet UTM-koordinater. Ulveobservationerne er indtastet i et separat datasæt, som i del B bliver beskrevet som datasæt B. Efter kameraplaceringen blev koblet på, er det blevet muligt at sammenligne de to datasæt. Vi har i den proces også hjulpet de frivillige med at rette en række fejl og mangler i den protokol, der bliver fulgt når kameraerne tømmes.

Rebecca og jeg var tre gange ude i felten for at assistere de to frivillige med dataindsamlingen, for på den måde at få en forståelse for arbejdet bag de billeder vi tastede ind til projektet. Vi har i den forbindelse set størstedelen af de kameraplaceringer, vi har brugt data fra. Det har været uundværligt at være med i den del af processen, da det har givet os en forståelse for de muligheder og mangler, der er i kameraovervågning af pattedyr.

Takket være Fonden Frands Christian Frantsens legat fik vi yderligere mulighed for at bidrage med den fremtidige overvågning af store pattedyr. Vi modtog hver især et legat til at indkøbe vildtkameraer, som vi, i samarbejde med de to frivillige, satte op i efteråret 2020 på 10 vilkårligt udvalgte placeringer i undersøgelses-området. Vi har siden indsamlet data fra disse kameraer månedligt, ved brug af samme indsamlingsmetode som det data vi har benyttet i vores projekter.

I forbindelse med databehandling har vi ligeledes assisteret hinanden med klargøring af de variabler, vi skulle bruge i vores egne analyser. Variablerne er blevet udregnet ved hjælp af R og QGIS. Vi har i forbindelse med inddelingen af døgnet i tidsperioder delt arbejdet op, så Rebecca fik kodet omregningen af tiden til UTC og beregnet solvinklen for hver observation. Jeg fik lokaliseret de observationer, der ikke var indtastet i den korrekte tid, så tidspunkter kunne blive rettet til, inden hele tidsdatasættet blev omregnet til UTC. Vi fik assistance af Oskar Hansen til at skrive et stykke kode, der kunne udregne de datoer i vores serier, hvor kameraet havde været aktivt, men hvor der ikke var observeret nogen arter. Derudover fik vi tilsendt de shapefiler, som blev benyttet til arbejdet med habitatsvariabler i QGIS af Martin Mayer.

Foruden de inkluderede analyser i artikel-udkastet, blev der kørt en overlap-analyse for at sammenligne vores studie og data på ræve fra et tidligere studie. Dette studie inkluderede observationer af ræve fra Danmark og Tyskland, fra før ulvene etablerede sig helt i Danmark. Denne analyse blev ekskluderet på grund af for mange afvigelser i indsamlingsmetoden.

Jeg vil gerne sige en stor tak til Fonden Frands Christian Frantsens legat, for økonomisk at gøre det muligt for Rebecca og mig at få sat kontrolkameraer op i forsøgsområdet, som i fremtiden kan bidrage til viden om interaktionerne mellem rovdyr i Danmark. Jeg vil også gerne sige tak til Lars Haugaard med flere fra Faunaøkologi-sektionen på Kalø, som har hjulpet med at realisere muligheden for at få kontrolkameraerne sat op.

Både med arbejdet i QGIS, med R og i den videre skriveproces har vi lavet analyserne sideløbende og diskuteret, hvilke fremgangsmåder der var mest meningsfulde for de videre analyser. Det har været en fornøjelse og meget givende at samarbejde med Rebecca Lyhne under dette speciale.

Foruden et stor tak til Rebecca Lyhne, Martin Mayer og Oskar Hansen for deres hjælp til ovennævnte, så vil jeg også gerne sige en meget stor tak til mine vejledere, Jens-Christian Svenning, Peter Sunde og Kent Olsen, for deres hjælp og vejledning igennem speciale-processen. Det har været en fornøjelse at have jer som vejledere, selvom de fleste møder endte med at være over zoom og på trods af nogle stressede perioder, som især skyldtes COVID-19 restriktioner. Jeg vil også gerne sige tak til Christina, Marianne og de andre på Naturhistorisk Museum Aarhus for deres hjælp og støtte undervejs. Tak til Andreas, Cecilie, Matilde, Mette og min familie for hjælp og moralsk opbakning undervejs. Tusind tak til Oskar for hjælp, støtte og tolerance, især i de stressede perioder. Sidst men på ingen måde mindst vil jeg sige et kæmpestort tak til Thomas og

Søren, som frivilligt tog Rebecca og mig under deres vinger. Tak for at introducere os til jeres store arbejde med dataindsamling, lære os at sætte vildtkameraer op og hjælpe os med opsætning af vores egne. Det var været en stort fornøjelse og månedens højdepunkt at være i felten med jer det sidste halve år.

Table of content

PART A - GENERAL INTRODUCTION OF TOPICS	7
1) INTRODUCTION	7
2) PREDATORY INTERACTIONS	8
3) FOCUS SPECIES	13
<i>Red fox (Vulpes vulpes)</i>	<i>13</i>
<i>Grey wolf (Canis lupus)</i>	<i>15</i>
4) STUDYING CARNIVORES AND INTERACTIONS	16
5) PREDATORS IN DENMARK	18
REFERENCES	24

Part A - General introduction of topics

1) Introduction

An ecosystem is defined as a specific community of species and the physical environment they live in (Krebs, 2009). Species in these communities can be divided into different trophic levels based on their role in the ecosystem. The characterization varies in the literature, so the definition from the book “Ecology – The Experimental Analysis of Distribution and Abundance” by Krebs from (2009) is used here. For communities including mammals, the first and largest level, based on biomass, is the primary producers (mostly plants), the second level is the primary consumers (e.g., herbivores), the third level is the secondary consumers (e.g., carnivores), and the fourth and “highest” level is the tertiary consumers (e.g., higher carnivores). The secondary and tertiary consumer levels are lower in abundance than primary consumers, because of their place at the top of the trophic levels, (Ripple et al., 2014). These different levels can be occupied by one or several coexisting species (Fleming et al., 2017).

Communities are shaped and affected by bottom-up and top-down trophic processes (Krebs, 2009). Bottom-up control is when nutrient supply from the lower level controls the ecosystem (Krebs, 2009). Top-down control is when higher trophic levels control communities via predation or by being present in a habitat (Fleming et al., 2017; Ripple et al., 2014; Ritchie and Johnson, 2009). A recent study by le Roux et al. have found variation in the extent of top-down effects in prey species is higher in intermediate size prey and not in small prey species, despite the smaller species have more potential predators (le Roux et al., 2019).

Globally Carnivora comprise of 250 terrestrial species (Hunter and Barrett, 2018). The species are distributed in many different habitats across the globe (Ripple et al., 2014) and they are included in different higher trophic levels. The highest level of carnivore species is tertiary consumers, called apex predators or top predators (hereafter referred to as top predators), they are the largest species in Carnivora, not preyed on by other species (Fleming et al., 2017; Wallach et al., 2015). The secondary consumers, the mesopredators are smaller predatory species that are both a predator, as well as prey and competitor of top predators (Krebs, 2009; Prugh et al., 2009). Predatory species can play a crucial role in regulating communities via top-down effects, some as keystone species that help structure communities (Estes et al., 2011).

It is relevant to mention humans (*Homo sapiens*), because of their impact on ecosystems and species within. Worm and Paine (2016) has proposed that humans should be defined as a hyperkeystone species, because of how humans can affect and structure how keystone species, like large predators, structure ecosystems (Estes et al., 2011). As the human population has increased and have claimed more land for settlements, agriculture, and infrastructure more conflicts have arisen, resulting in the decline in number and distribution of predatory species worldwide with cascading trophic effects (Estes et al., 2011; Ripple et al., 2014). From a human perspective, predators are often seen in a negative way, in part because of their predation on livestock (Ugarte et al., 2019) or direct threat for human, with predator attacks (Linnell et al., 2002), as seen with tigers (*Panthera tigris*) and leopards (*Panthera pardus*) in a reserve in central India (Dhanwatey et al., 2013). A new study showed economic benefits larger than the cost of predation on livestock from having a top predator in the ecosystem, by reducing the deer-car collisions (Raynor et al., 2021). In recent years in Europe, for some predator species, their population numbers are on the rise, and they are reappearing in their former habitats (Chapron et al., 2014). In other parts of the world, predators are being reintroduced to ecosystems from which they had disappeared (Beschta and Ripple, 2009).

With both disappearance and reappearance of large predatory species from ecosystems, there can be several outcomes for other species in their interactions with these predators, this can both be behavioral changes (Haswell et al., 2020) and changes in population numbers affecting the entire ecosystem (Lindström et al., 1995). ‘

2) Predatory interactions

The goal for any individual is to maximize its fitness and acquire a sufficient energy intake to reach reproductive maturity and successfully reproduce (Davies et al., 2012). Interactions with other species are affecting the possibility of reaching this goal (Davies et al., 2012). Predators interact with both competitors and prey in their environment through direct effects, like top-down control of populations by consumption, and indirect effects on the behavior just by being present in a system (Estes et al., 2011; Lima, 1998; Ripple et al., 2014). These interactions can affect feeding choices, activity patterns, habitat selection and reproduction of both competitors and prey, resulting in large changes in the structure of ecosystems (Lima, 1998).

Predator-prey interactions have both lethal and non-lethal effects, with the lethal effect being direct predation (Lima, 1998). While predation has a negative effect on the individual

animal killed, it can be beneficial on a population level, controlling the population number and allowing better foraging opportunities for the remaining individuals (Peacor, 2002). Encounters between a predator and prey have several potential outcomes, described in a flow chart made by Lima and Dill in (1990) (Fig. 1).

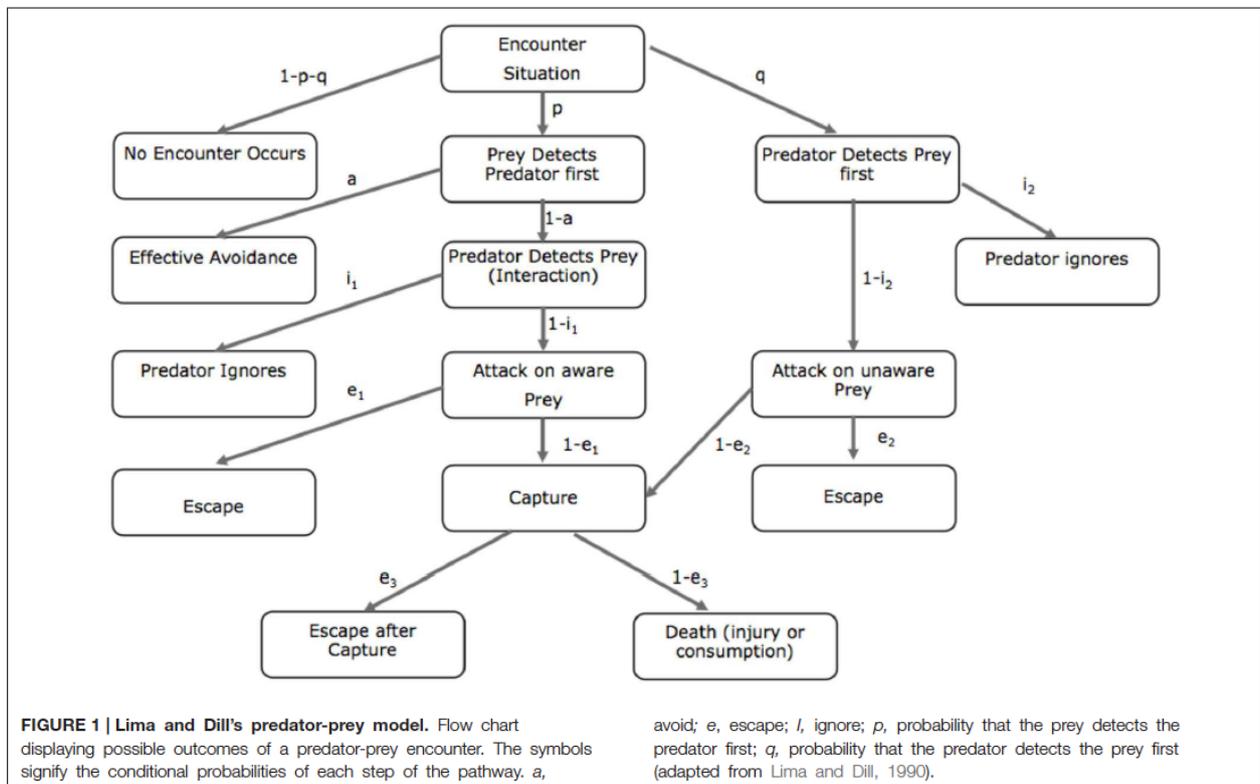


Figure 1: Figure showing Lima and Dill's predator-prey model, obtained from (Mobbs et al., 2015), where it has been adapted from the original flow chart made by (Lima and Dill, 1990).

Avoiding lethal encounters with predators and navigating in a landscape of fear requires behavioral changes, known as anti-predator behavior (Lima and Dill, 1990). The anti-predator behavior is from prey species point of view, a tradeoff between optimal foraging opportunities and safety (Brown and Kotler, 2004). Predation risk varies throughout an individual's lifetime, both on temporal, seasonal, spatial and life history scales (e.g., there is a higher predation risk in breeding periods when offspring are small and vulnerable (Caravaggi et al., 2018; Sih et al., 2000). There is a need to be able to make anti-predator decisions in time, e.g., how long to forage, and in space e.g., avoiding areas with high risk (Brown and Kotler, 2004; Lima and Dill, 1990). Prey uses different cues to perceive predation risk, olfactory cues being important (Kuijper et al., 2014; Mayer et al., 2020), but also visual cues (Kuijper et al., 2014). The cues used might shift between open and closed landscape depending on habitat (Kuijper et al., 2014). The study by

Kuijper et al. (2014) found that the presence of wolf scat raised vigilant behavior of red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) in a forested area but found no effect of variation in habitat visibility. A study found that hare (*Lepus europaeus*) avoided areas where unfamiliar scent and where scent from red fox (*Vulpes vulpes*) was placed. Hares showed more vigilance during foraging in response to the scent of foxes (Mayer et al., 2020).

The *risk allocation* hypothesis is proposed by Lima and Bednekoff (1999) as a way to explain how prey navigate temporal variation in predation risk, between environments with high and low predation risk. The result of their theoretical analysis showed that animals living in environments of high predation risk limit anti-predator behavior to temporal periods with high risk (Lima and Bednekoff, 1999). They show less anti-predator behavior in low-risk periods in these high-risk environments to have a sufficient energy intake. In low-risk environments animals exhibit anti-predator behavior in response to even low amount of risk because they have enough time to forage sufficiently, while still showing anti-predator behavior (Lima and Bednekoff, 1999). *Landscape of fear* is defined as “the spatially explicit distribution of perceived predation risk as seen by a population” (Bleicher, 2017). As the definition states, it is a concept that, like the *risk allocation* hypothesis, is a way to explain how individuals in a population perceive variations in predation risk on a spatial scale in an area (Bleicher, 2017; Laundre et al., 2010).

A lot of focus has been on simple single-predator-prey interactions (Ritchie and Johnson, 2009), but in many ecosystems there is more than one predator, giving rise to intraguild interactions where species close in trophic levels act as both a predator and competitor for resources (Fedriani et al., 2000). Predatory species face many of the same decisions and tradeoffs as prey species does, when encountering a competing predator (Lima, 1998). The direct effects of a predator-predator interaction are the same as between predator and prey, but the interaction can happen for different reasons (Polis, 1981; Polis et al., 1989). When resource competition between two predators can develop into interference competition or intraguild predation, that occurs when one animal harms or kills the competitor utilizing a common resource, even when the resource is not limited (Krebs, 2009; Petroelje et al., 2021; Polis et al., 1989). A study has found support for interference competition, with the abundance of coyotes (*Canis latrans*) being limited by the competition with a larger predator grey wolf (*Canis lupus*) (Berger and Gese, 2007). It can also happen as intraspecific killing, when another predator is killed and afterwards eaten as a resource in itself (Polis, 1981).

The indirect effect of predator-predator interactions is, like with predator-prey interaction, causing behavioral changes in the subdued species, but the presence of top predators can affect the number of mesopredators present in an ecosystem, defined as mesopredator suppression (Ritchie and Johnson, 2009). The presence of one species might indirectly suppress another if they change their behavior due to fear (Haswell et al., 2020). As seen in a long-term study from Serengeti National Park in Tanzania, Africa, it showed a suppression of one mesopredator species, wild dog (*Lycaon pictus*), after a tripling in population numbers of the top predator lion (*Panthera leo*) (Swanson et al., 2014). Population numbers of another mesopredator species, cheetah (*Acinonyx jubatus*) remained unchanged (Swanson et al., 2014). It was found that wild dogs were present in habitats with a low density of lions before the rise in lion population numbers, where cheetahs were found in areas with a higher lion density (Swanson et al., 2014).

As a result, mesopredators living in an ecosystem with a top predator face a dilemma between being able to obtain enough food for reproduction and avoid being killed in the process. To combat this, mesopredators can adapt to the presence of predators by changing their behavior, the same way prey species do (Karanth et al., 2017). For example, as seen in a study from Croatia, where they found that foxes changed their foraging behavior in sites with wolf urine present, as a result they spent less time visiting food patches and even left food (Haswell et al., 2018). On a temporal scale plasticity in diel activity patterns can be a way for predators to coexist. Either by the mesopredator avoiding potential lethal interactions by being active at other times than the top predator (Karanth et al., 2017) or by being active in the darkest times at night, to avoid being seen by larger predators when moving around (Haswell et al., 2020). Mesopredators can also be attracted to top predators, because of how they can benefit from being present near top predators, in order to utilize leftover resources (Ferretti et al., 2021).

When a top predator disappears from an area it will have cascading effects down the ecosystem (Estes et al., 2011). For mesopredators, it can result in what is called the *mesopredator release* hypothesis where the absence of a top predator results in an increase in the population numbers of mesopredators (Prugh et al., 2009). Mesopredators will therefore pose a larger threat to prey because of a rise in population numbers (Prugh et al., 2009; Soulé et al., 1988). The concept was first described by Soulé et al. in (1988) regarding the effect of coyotes on gray foxes (*Urocyon cinereoargenteus*) and domestic cats (*Felis catus*) in California, United States. It was observed that the absence of coyotes resulted in an increase in the population of foxes and the domestic cats, which in turn resulted in the extinction of several bird species (Soulé et al., 1988). The effects of

mesopredator release have been documented in several ecosystems. In the United States it was found that the reintroduction of wolves reversed the mesopredator release of coyotes that had happened in the absence of a top predator, allowing less predation on rodents in the areas close to wolves established dens (Miller et al., 2012). A Swedish study from 1995 found strong evidence of a *mesopredator release* effect on the smaller predator (mesopredator) pine marten (*Martes martes*) following the decline of foxes due to sarcoptic mange (Lindström et al., 1995). Another study from Sweden documented a lower abundance of red fox (*Vulpes vulpes*) in periods with lynx (*Lynx lynx*) present and a larger population of mountain hare (*Lepus timidus*) (Elmhagen et al., 2010). A similar pattern between the two species were found in a newer study in Sweden and Finland from a 220-year period (Pasanen-Mortensen et al., 2017). They found the same pattern in newer studies, where bottom-up changes resulted in an increase in population of mesopredators, because of a rise in food availability of prey species (Pasanen-Mortensen et al., 2017).

In Australia *mesopredator release* and *mesopredator suppression* have been documented in an ecosystem with the introduced top predator dingo (*Canis lupus dingo*) and the, for Australia, invasive mesopredator red fox (Feit et al., 2019; Letnic et al., 2012; Letnic and Dworjanyn, 2011). The removal of the top predator dingo resulted in mesopredator release of the mesopredator fox (Letnic et al., 2012). The presence of dingoes in an area resulted in a suppression of foxes and a larger abundance of an endangered rodent dusky hopping mouse (*Notomys fuscus*) that from scat analysis was found to be a preferred prey species of red foxes (Letnic and Dworjanyn, 2011).

These intraguild interactions have been documented in several ecosystems around the world, both in marine and terrestrial systems and across different classes: A review by Ritchie & Johnson from (2009) found 94 studies of vertebrate predators on mesopredators in these systems.

3) Focus species

Two species for which these interactions are highly relevant to study are the top predator grey wolf (*Canis lupus*; hereafter referred to as wolf) and the smaller mesopredator red fox (*Vulpes vulpes*; hereafter referred to as fox) (Castelló, 2018). Both species are widespread and present across the world (Boitani et al., 2018; Hoffmann and Sillero-Zubiri, 2021), with fox being the most widespread canid species (Hoffmann and Sillero-Zubiri, 2021). Wolves have been persecuted along with many of the world's largest carnivores and have been absent from many of the species former habitats, but wolves are on the rise again in Europe (Chapron et al., 2014) and their reappearance in the ecosystems are facilitating changes in interactions between these two species.

Red fox (*Vulpes vulpes*)



Figure 2: Picture of a fox, taken with one of the control cameras in the Ulfborg territory in Western Jutland.

Fox is, with an average weight around 5.3 kg (Faurby et al., 2020; Smith et al., 2003) considered a medium size carnivore in the canid family. A keystone mammalian predator in some ecosystems in Europe (Meisner et al., 2014) and functioning as a mesopredator (Elmhagen et al., 2010; Haswell et al., 2020), but also a top predator in systems lacking larger terrestrial carnivores, as seen in Sweden (Lindström et al., 1995). It is a solitary species, only living in pairs during breeding periods from December-January. After a gestation period of 51-53 days, the female gives birth to between 3-10

pups in a den. The first period is spent near the den, but after 6-12 months the pups will start to migrate, often over long distances, to establish their own territories (Castelló, 2018).

The fox is a very adaptable species, with habitats ranging from tundra (Hoffmann and Sillero-Zubiri, 2021) to desert (Letnic and Dworjanyn, 2011) and even has populations within cities, in close proximity to humans. In habitats near cities, they are in some cases benefitting from being near humans, e.g., foraging on human leftovers (Bateman and Fleming, 2012; Hoffmann and Sillero-Zubiri, 2021). They prefer rich biotopes, with abundant food sources, like arable fields, farmland, or pastures (Castelló, 2018).

They are adaptable opportunistic with a variable diet across latitude, seasons, that varies between insects, birds, and mammals (Hoffmann and Sillero-Zubiri, 2021; Soe et al., 2017). Studies have found that the presence of lynx or another top predator, allow foxes to scavenge on leftover prey as well (Bassi et al., 2018; Castelló, 2018). They have mainly nocturnal activity patterns (Castelló, 2018), but studies have found seasonal variations (Caravaggi et al., 2018), inconsistent diel activity patterns (Ikeda et al., 2016) and changes in the pattern as a response to other predators and moderated by human activity (Haswell et al., 2020).

Population size is highly variable across their large distribution range (Hoffmann and Sillero-Zubiri, 2021). Foxes are globally classified as Least concern (LC) on IUCN's redlist with a stable population trend, but in some local areas they are classified as threatened due to hunting practices (Hoffmann and Sillero-Zubiri, 2021). They are in many countries thought of as pests and is therefore under hunting and culling laws (Hoffmann and Sillero-Zubiri, 2021). They have been introduced to Australia with highly negative consequences to local fauna (Letnic and Dworjanyn, 2011).

Grey wolf (*Canis lupus*)



Figure 3: Picture of a wolf, taken with one of the control cameras in the Ulfborg territory in Western Jutland.

Wolf is, with an average weight around 32.2 kg (Faurby et al., 2020; Smith et al., 2003), the largest extant species in the canid family (Castelló, 2018), who functions as a top predator in many ecosystems (Ferretti et al., 2021; Newsome and Ripple, 2015). It is a social species, often living in large packs, with exceptions, for example in European populations, where hunting has impacted pack size, resulting in smaller packs (Castelló, 2018). The breeding period is from January-February and between 5-6 pups are born in a den in the end of April-May (Castelló, 2018). During the first period, the pups stay close to the den, following a period where they will be placed in a rendezvous spot by the adults, where they wait for the adults to return with food (Mills et al., 2010). Wolves have territories ranging from 100- 300 km² that varies in size seasonally (Castelló, 2018).

They will defend the territory from other competing wolves and their habitat varies from forest, steppe zones to peat bogs in some countries (Castelló, 2018). They have also established territories that include farmland areas (Castelló, 2018). Population numbers of wolves in Europe are not fully known, because of variation in available information from different countries in its distribution range (Boitani et al., 2018).

Wolves are opportunistic predators, with a diet composition across their distributional range, depending on which prey species is most abundant. Prey species varies from deer species, fish, and livestock, but also smaller mammal species and varies over season (Castelló, 2018).

Wolves are primarily nocturnal, but studies have shown variation in the activity pattern in relation to human activity, where it has been found that wolves living in areas far from human activity shows more diurnal activity patterns (Theuerkauf et al., 2007) compared to wolves living closer to humans (Mancinelli et al., 2019).

Because of human persecution, the population numbers were at a minimum in the 1970s (Boitani et al., 2018), but because of conservations efforts, protective legislation and a general change in public opinions, population numbers are on the rise again in Europe (Chapron et al., 2014). Now globally classified on IUCN's redlist as Least Concern (LC) (Boitani et al., 2018).

4) Studying carnivores and interactions

Studying terrestrial carnivores in nature is not easy because of lower population sizes and their often nocturnal, elusive, and solitary behaviors is making it difficult to gain knowledge of the abundance and distribution of these species. Non-invasive methods have been sought after and tried by researchers for decades (Burton et al., 2015; Kucera and Barrett, 2011) It is often time-consuming, expensive, and requires comprehensive knowledge of potential habitats or travel routes of the species. With the development in technology, it has gotten easier to achieve knowledge, especially using non-invasive methods (Kucera and Barrett, 2011). Different non-invasive methods, and combinations of them, are used to explore behavior and distribution of these species and to gain valuable knowledge (Ferretti et al., 2021; Haswell et al., 2018).

Collection of hair samples used to identify species, is an old method. Previously, species groups could be identified using identification keys on the collected hair (Kendall et al., 2008), but with affordable DNA analysis methods, it is now possible to identify species and, in some cases, even individuals (Kendall et al., 2008; Long et al., 2007; Monterroso et al., 2014). Hair samples are often collected using hair snares, where wires are being hung along travel routes or next to bait stations that can lure species to the snare (Schmidt and Kowalczyk, 2006).

Another method used to detect presence and gain knowledge about a species, is active collection of scats. As with hair samples, it is to some extent possible to identify species or species groups from scat alone, but by using DNA analysis methods species identifications is becoming more accurate (Harrington et al., 2010). Collected scat can also be used for gaining valued information about a species diet (Wachter et al., 2012).

Mapping of species movement can be done using the previously mentioned methods, but also by using observations of tracks. This method requires a terrain feasible for the animals to leave trackable trails. The method is used during snow periods (Wikenros et al., 2017) and can be used to gain paramount knowledge of species movement, as seen in an article by Bojarska et al. (2017) where snow-tracking was used to identify kill sites of wolves in commercial forests. Collection of scats, hair and following tracks, requires knowledge about the targeted species biology and behavior in a landscape and even though it is a noninvasive method, it requires active searches and training of people partaking in tracking, for the methods to be most effective.

Remotely triggered camera traps are another non-invasive method that does not require active searching as scat collection and track observations. The use of camera traps in species monitoring has been increasing and is now used worldwide (O'Connell et al., 2011). First developed in the beginning of the 1990 as a non-lethal method for documenting the distribution of elusive and rare carnivore species in the United State of America (Kucera and Barrett, 2011). Since then, the method has progressed and developed into a widely used method for estimating population size, movement and behavior of mammals and birds (Burton et al., 2015; Johnson et al., 2009), especially well used for more elusive carnivore species (Kucera and Barrett, 2011). A study found camera traps to be a more efficient method to detect mesopredators, compared to using hair snares (Monterroso et al., 2014).

For species where each individual is distinguishable (e.g., due to coat patterns), like tigers, it is possible to identify different individuals and via a capture – recapture method, to detect their movement and presence in a landscape via camera traps (Karanth et al., 2004). Cameras can be placed along travelling routes in the landscape to detect species passing by (Tourani et al., 2020). Olfactory lures can also be used to lure species in front of the camera (Tourani et al., 2020), as done in a study by Haswell et al. (2018), where foxes were studied using lures with wolf urine.

One of the primary disadvantages when using camera trapping in monitoring is imperfect detection of all individuals present in research areas (Burton et al., 2015). The probability of detection is influenced by many factors and knowledge of the ecology of a species (Caravaggi et al., 2017). Some of the most important factors include camera placement, where extensive knowledge of species travelling routes is needed and the quality of cameras used. A cameras detection zones, sensitivity and trigger time are all key factors (Burton et al., 2015; Wellington et al., 2014).

Camera trapping is gaining leverage as a useful tool for examining temporal activity patterns in species (Caravaggi et al., 2018; Frey et al., 2017). It is an effective tool in monitoring changes or overlap in activity patterns in relation to other species (Ikeda et al., 2016) or human-driven changes (Haswell et al., 2020). Camera traps are considered a non-intrusive method for capturing these behavioral changes and interactions between species (Caravaggi et al., 2018). A study from 2016 have found that light and sounds when a camera was triggered influenced some individuals, but this pattern was inconsistent between species (Meek et al., 2016). Indicating that individual's detection of camera traps needs to be taken into consideration, when using camera traps for observation of behavioral changes.

5) Predators in Denmark

Denmark is a smaller country (42.937 km²), the most recent assessment of land cover categories, from 2018, showed that Denmark is heavily dominated by agricultural areas 59.9% (Danmarks Statistik, 2021a). Included in this is field crops, improved grasslands, fruit plantations and some tree plantations, but it is not clear whether all managed forest areas are included in the category (Danmarks Statistik, 2018). There are 7.3% urban areas (e.g., buildings and built-up areas) and 5.5% infrastructural areas (Danmarks Statistik, 2021a). Of the remaining areas, there is 22.1% terrestrial areas that can be classified as nature areas. There is 13.1% managed forested areas and 9% open semi-natural areas (Danmarks Statistik, 2021a), as seen above, most areas in Denmark are managed in some way or another. With approximately 5.8 million inhabitants, there are approximately 135.1 people pr km² (Danmarks Statistik, 2021b). This makes Denmark a heavily cultivated country, with few fragmented nature areas and many species have had to adapt to living in human-modified habitats or near humans.

Denmark has a history of several terrestrial, carnivorous, mammalian species, that has been present in different periods during the last 10.000 calendar years before present day *cal. BP*, see table 1 for first and last appearance along with the average weight of each mentioned species (Aaris-Sørensen, 2009). Wolverine (*Gulo gulo*) and polar bear (*Ursus maritimus*) has had a single documented record each around 10.000 years BP (Aaris-Sørensen, 2009). Top- and mesopredators that have been present in Denmark during the Holocene period, but have disappeared again consists of brown bear (*Ursus arctos*), lynx and wild cat (*Felis silvestris*) (Aaris-Sørensen, 2009). Since the disappearance of these species and until the beginning of 1800, the largest terrestrial predators in

the country were wolf, badger, fox, pine marten and beech marten (*Martes foina*) (Aaris-Sørensen, 2009). In recent times, new predatory species have arrived in the country. Raccoon dog (*Nyctereutes procyonoides*) was introduced to Europe and has since spread to the country, with the first observation in 1980 (Miljøstyrelsen, 2021), it has been heavily hunted with the goal of eradication but is still present in the country (Skov- og Naturstyrelsen, 2010). Another species introduced to Europe, that has appeared in Denmark is racoon (*Procyon lotor*), it has only been observed a few times after 2007 and is considered a relatively rare species (Miljøstyrelsen, 2017).

Table 1: The first and last appearance of each larger, native terrestrial predator that has been present in Denmark during the last 10.000 calendar years before present (cal. BP). Sorted from highest average weight. First and last appearance obtained from Aaris-Sørensen (2009). Average weight has been obtained from Faurby et al. (2020), original source (Smith et al., 2003).

Species	First appearance	Last appearance	Average weight
brown bear (<i>Ursus arctos</i>)	ca. 13.400 cal. BP	4800-4400 cal. BP	180.5 kg
grey wolf (<i>Canis lupus</i>)	ca. 12.700-12.400 cal. BP	1813 reappeared 2012 (Sunde and Olsen, 2018)	32.2 kg
lynx (<i>Lynx lynx</i>)	ca. 9500 cal. BP	7000-5500 cal. BP	17.9 kg
badger (<i>Meles meles</i>)	11.600-11300 cal. BP	extant	13 kg
golden jackal (<i>Canis aureus</i>)	2015 (Andersen, 2017)	extant	10.3 kg
raccoon (<i>Procyon lotor</i>)	after 1945 (Baagøe and Ujvári, 2007)	extant	6.5 kg
red fox (<i>Vulpes vulpes</i>)	ca. 9500 cal. BP	extant	5.3 kg
raccoon dog (<i>Nyctereutes procyonoides</i>)	1980 (Miljøstyrelsen, 2021)	extant	4.0 kg
beech marten (<i>Martes foina</i>)	No data	extant	1.5 kg
pine marten (<i>Martes martes</i>)	ca. 9500 cal. BP	extant	1.3 kg

Apart from humans (Worm and Paine, 2016), the top predator in the danish ecosystems has been the wolf in most of the Holocene, but due to being persecuted and hunted to regional extinction, the last wolf was killed in 1813 in Denmark (Aaris-Sørensen, 2009). Following this, the functionally top predator in the ecosystem was the fox, with humans and dogs being the only enemy (Peter Sunde, pers. comm.). Large predators are on the rise again in Europe, as mentioned before (Chapron et al., 2014). After 200 years absence, wolves have returned to the

country, with the first documented observation of a wolf made in a nature area in Thy, Northern Jutland, on the 14 October 2012 (Sunde and Olsen, 2018). This observation solidified the return of the previous top predator to the country (Sunde and Olsen, 2018). Along with the reappearance of wolves, another large predator, the golden jackal (*Canis aureus*) has returned to the country with a few individuals, with the first documented observation made in 2015 (Andersen, 2017).

Foxes are present across most of the country, except in a few islands (Madsen et al., 2020; Pagh et al., 2007). Population estimates of fox in Denmark, can only be estimated from the number of individuals killed via hunting (Elmeros, 2019) because there is no known count of the population size in Denmark (Pagh, 2011). Since 1940 it has been mandatory for danish hunters to report the number of killed wildlife each hunting season and in season 2019-20, 31.036 individuals of fox were killed by hunters (Madsen et al., 2020). The population yield has been decreasing by 1.4% the last 25 hunting seasons (Madsen et al., 2020). They are on the latest danish redlist evaluation classified as near threatened (NT), meaning that the population is in decline, because of a 10 % decrease in population numbers over the last three generations of foxes (approximately 17 years). The declining population is in the report proposed to be in part because of *Canine distemper*, a disease killing many foxes in Jutland in 2012 (Elmeros, 2019). A study found an increase in reproduction following the outbreak, indicating the population is on the rise again (Pagh et al., 2018). Foxes are under no protection in Denmark, they are a huntable species and whether they have a viable population and is eligible to be hunted is reassessed every third or fourth year by the Environmental Agency and the Wildlife Council (Madsen et al., 2020). They have closed hunting seasons and can be hunted in the winter period between September 1st and January 31st (Madsen et al., 2020). They are allowed to be regulated with permission year-round (Madsen et al., 2020).

Wolves in Denmark are with DNA test confirmed to be from the Central European population (Boitani et al., 2018) and have established territories throughout Jutland, with individuals moving freely between Denmark and Germany (Olsen et al., 2021). Wolves are in Denmark classified as vulnerable (VU) (Elmeros and Sunde, 2019), since their return to the country, there have been a fluctuating number of wolves and four documented established wolf pairs in the country and two documented successful breeding attempts. Per March 2021, there were nine or ten wolves in the country (Olsen et al., 2021). Wolves are protected under Habitat Directive appendix IV in Europe under the EU council (European Union, 2013). Countries under the European Union are obliged to protect species inside and outside of natura 2000 areas (Miljøministeriet, 2021).

Because of this “The National Monitoring Program on Wolves in Denmark” was established, the program is managed by the Natural History Museum in Aarhus (NHMA) and Aarhus University (AU) and the data collection and monitoring is partly fulfilled by a group of volunteers and from observations collected by the general public (Sunde and Olsen, 2018). The collection effort consists of several elements; excursions, specific search trips, collection of DNA samples (scat, hair, saliva, urine, or blood) and camera trap monitoring in areas with known or expected wolf populations (Olsen et al. 2021). Collected observations is after collection assessed and verified by professionals using SCALP criteria (Reinhardt et al., 2015) that is developed for a standardized monitoring of lynx populations in Europe (Breitenmoser et al., 2006).

From the latest monitoring status report from 3rd of March 2021, there has been a total of 27 different individuals of wolves in Denmark that have been confirmed by DNA (Olsen et al., 2021), one individual has been killed by a human and several other has disappeared without a trace (Sunde et al., 2021). Several of these wolves have been documented from the first established and successful wolf territory in Denmark “Ulfborg territory” in Western Jutland (Olsen et al., 2021). The area consists of a mosaic plantations and heathland and the first area there was documented a wolf couple was in a plantation area in Western Jutland (Thorsen et al., 2019). Since 2016, the area has been occupied by at least three different wolf couples, where there have been two successful breeding periods, one in 2017 and one in 2019 and a short period with only one wolf present in the area (Thorsen et al., 2019).

Ulfborg territory has been monitored, using camera traps since 2016 with a varying number of cameras managed by a group of volunteers (Kent Olsen, pers. comm.). The monitoring has focus of capturing wolves, and therefore cameras has been placed and moved around to optimize the possibility of capturing observations of wolves (Unpublished Camera Protocol). The number, model and quality of camera traps has improved since 2016 from Bushnell Trophy Cam HD aggressor (Bushnell, 2017) to Bushnell Core DS (Bushnell, 2020) and Reconyx Ultrafire XS8 (Reconyx, 2015). Because of the group of very dedicated volunteers, large amount of data has been collected of wolves and all the other large species moving around in Ulfborg territory. The data collected in the Ulfborg territory, is the foundation for this thesis.

6) What this thesis will contribute to

Fox has since the extinction of wolves 200 years ago been acting as top predator in terrestrial Danish ecosystems, with only humans and dogs as potential enemies. With the reappearance of wolves in Denmark, it is interesting to understand how and if the activity patterns and habitat use of foxes has been affected.

There have only been a few studies on wolves and their effect on other species in Denmark after their reappearance. One study by Thorsen et al. (2019) about wolves' diel activity patterns in Denmark, done on data collected between 2013-19, primarily from Ulfborg territory. Another study has been done by the undersigned and Andreas Bennetsen Boe as a part of a biological project in the spring semester 2020 and not yet published. The study examined the diel activity pattern and explanatory variables (e.g., human activity, deer activity, time of day and time period) that best explained the activity patterns of wolves, the study was done on data collected between 2016-20 (Boe and Kjeldgaard, 2020). Both studies were done using data from two different databases, but at the time there were no unique identification number linking the two. As a part of this thesis this has been established, allowing analysis on a spatial scale as well as the temporal scale. Concurrently there have yet to be conducted studies exploring the interactions between wolves and mesopredators in Denmark. This study will therefore be a piece in the puzzle of understanding the effects reappearing top predators can have on the Danish ecosystem on both a temporal and spatial scale.

Wolf, and to some extent fox, is considered a nuisance and an unwanted part of the nature in Denmark, as seen with how they are being portrayed in literature and the public opinion of them. Because of this, there is a need to gain and share as much knowledge as possible about the behavior of these species in Denmark.

“The National Monitoring Program on Wolves in Denmark” is to my knowledge, the most extensive on-going camera monitoring programs in Denmark right now, especially the data from the Ulfborg territory in Western Jutland. It is therefore possible to use the data for gaining knowledge of these intraguild interactions between predators, but also between predators, prey species and predators, and human activity.

Since the data collected in Ulfborg territory has been collected with the target of capturing wolves, then as a part of the project behind this thesis, several camera traps were placed in Ulfborg territory at randomly selected locations, following the same camera protocol established

for the monitoring program, but not with the main target for capturing wolves. This data will hopefully be a key element in clarifying whether the data collected on other species in the wolf targeted monitoring is comparable with data collected with the randomly placed cameras.

This study will specifically examine what variables best explains the habitat selection of foxes and wolves and if the presence and activity of wolves affect the distribution of foxes on spatial, temporal, and spatiotemporal scales. The predictions in the study will be the following, as also stated in the manuscript (part B):

- we expect that wolves and foxes differ in their response to human settlements, we predict:
 - the distance to human settlement is negatively correlated with the presence of foxes
 - the distance to human settlement is positively correlated with the presence of wolves
- If foxes are attracted by the presence of wolves, as found by Ferretti et al. (2021), we predict that:
 - the presence of foxes per camera day is positively correlated with the local activity index of wolves
- If foxes are avoiding wolves, we predict:
 - the presence of fox per camera day is negatively correlated with the local activity index of wolves.
- If foxes are seeking to minimize detection or encounter rates with wolves, we predict:
 - foxes that live sympatrically with wolves to be more nocturnally active (because it is easier to escape detection when active in the dark)
- If foxes do not seek to minimize detection or encounter rates with wolves, we predict that:
 - foxes express a lower diel overlap in activity with wolves (to reduce encounter rates) than foxes living allopatrically from wolves.
- If the presence of wolves does not affect diel activity patterns of foxes, we predict:
 - similar diel activity patterns of foxes in areas where more wolves were present and areas where fewer wolves were present.

References

- Aaris-Sørensen, K., 2009. Diversity and dynamics of the mammalian fauna in Denmark throughout the last glacial-interglacial cycle, 115-0 kyr BP, *Fossils and Strata*. Wiley-Blackwell, West Sussex.
- Andersen, L.W., 2017. Artsidentifikation og slægtskabsanalyse af to dødfundne guldsjakaler (*Canis aureus*) i Danmark - Notat fra DCE - Nationalt Center for Miljø og Energi 1–11.
- Baagøe, H.J., Ujvári, M., 2007. Vaskebjørn (*Procyon lotor*), in: *Dansk Pattedyratlas*. Copenhagen, pp. 184–85.
- Bassi, E., Battocchio, D., Marcon, A., Stahlberg, S., Apollonio, M., 2018. Scavenging on ungulate carcasses in a mountain forest area in northern Italy. *Mammal Study* 43, pp. 33–43.
<https://doi.org/10.3106/ms2016-0058>
- Bateman, P.W., Fleming, P.A., 2012. Big city life: Carnivores in urban environments. *J. Zool.* 287, pp. 1–23.
<https://doi.org/10.1111/j.1469-7998.2011.00887.x>
- Berger, K.M., Gese, E.M., 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.* 76, pp. 1075–1085. <https://doi.org/10.1111/j.1365-2656.2007.01287.x>
- Beschta, R.L., Ripple, W.J., 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biol. Conserv.* 142, pp. 2401–2414.
<https://doi.org/10.1016/j.biocon.2009.06.015>
- Bleicher, S.S., 2017. The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ* 5, pp. 1–22. <https://doi.org/10.7717/peerj.3772>
- Boe, A.M.B., Kjeldgaard, S.A., 2020. Analyse af danske ulves (*Canis lupus*) aktivitetmønstre og mulige forklaringsvariable. Unpublished work. Aarhus University & Natural History Museum Aarhus.
- Boitani, L., Phillips, M., Jhala, Y., 2018. *Canis lupus* (errata version published in 2020). IUCN Red List Threat. Species 2018 e.T3746A163508960. <https://doi.org/https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T3746A163508960.en>
- Bojarska, K., Kwiatkowska, M., Skórka, P., Gula, R., Theuerkauf, J., Okarma, H., 2017. Anthropogenic environmental traps: Where do wolves kill their prey in a commercial forest? *For. Ecol. Manage.* 397, pp. 117–125. <https://doi.org/10.1016/j.foreco.2017.04.013>
- Breitenmoser, U., Breitenmoser-Würsten, C., von Arx, M., Zimmermann, F., Ryser, A., Angst, C., Molinari-Jobin, A., Molinari, P., Linnell, J., Siegenthaler, A., Weber, J.-M., 2006. Guidelines for the monitoring of lynx. *Kora Bericht*, pp. 1–31.
- Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7, pp. 999–1014. <https://doi.org/10.1111/j.1461-0248.2004.00661.x>
- Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* 52, pp. 675–685. <https://doi.org/10.1111/1365-2664.12432>
- Bushnell, 2020. Instruction Manual - Bushnell CORE and CORE DS.
- Bushnell, 2017. Instruction Manual - Bushnell Trophy Cam HD Agressor.
- Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M.V., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J., Wood, M.D., 2017. A review of camera trapping for conservation behaviour research. *Remote Sens. Ecol. Conserv.* 3, pp. 109–122. <https://doi.org/10.1002/rse2.48>
- Caravaggi, A., Gatta, M., Vallely, M.-C., Hogg, K., Freeman, M., Fadaei, E., Dick, J.T.A., Montgomery, W.I., Reid, N., Tosh, D.G., 2018. Seasonal and predator-prey effects on circadian activity of free-ranging mammals revealed by camera traps. *PeerJ* 6, pp. 1–27. <https://doi.org/10.7717/peerj.5827>
- Castelló, J.R., 2018. *Canids of the World*. Princeton University Press, New Jersey.

<https://doi.org/10.2307/j.ctv39x6vm>

- Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balečiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mystajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* (80-.). 346, pp. 1517–1519. <https://doi.org/10.1126/science.1257553>
- Danmarks Statistik, 2021a. Danmarks Statistik – Areal. URL <https://www.dst.dk/da/Statistik/emner/geografi-miljoe-og-energi/areal/areal> (accessed 14 may 2021).
- Danmarks Statistik, 2021b. Danmarks Statistik – Folketal. URL <https://www.dst.dk/da/Statistik/emner/befolkning-og-valg/befolkning-og-befolkningsfremskrivning/folketal> (accessed 14 may 2021).
- Danmarks Statistik, 2018. Land cover - v3:2018. URL <https://www.dst.dk/en/Statistik/dokumentation/nomenklaturer/arealdaekke> (accessed 26 may 2021).
- Davies, N.B., Krebs, J.R., West, S.A., 2012. *An introduction to behavioural ecology*, fourth. ed. Wiley-Blackwell, London.
- Dhanwatey, H.S., Crawford, J.C., Abade, L.A.S., Dhanwatey, P.H., Nielsen, C.K., Sillero-Zubiri, C., 2013. Large carnivore attacks on humans in central India: A case study from the Tadoba-Andhari Tiger Reserve. *Oryx* 47, pp. 221–227. <https://doi.org/10.1017/S0030605311001803>
- Elmeros, M., 2019. Den Danske Rødliste - Ræv (*Vulpes vulpes*). Den danske Rødliste. URL <https://bios.au.dk/forskningraadgivning/temasider/redlistframe/soeg-en-art/#37232> (accessed 27 may 2021).
- Elmeros, M., Sunde, P., 2019. Den Danske Rødliste - Ulv (*Canis lupus*). Den danske Rødliste. URL <https://bios.au.dk/forskningraadgivning/temasider/redlistframe/soeg-en-art/#5919> (accessed 12 may 2021).
- Elmhagen, B., Ludwig, G., Rushton, S.P., Helle, P., Lindén, H., 2010. Top predators, mesopredators and their prey: Interference ecosystems along bioclimatic productivity: Gradients. *J. Anim. Ecol.* 79, pp. 785–794. <https://doi.org/10.1111/j.1365-2656.2010.01678.x>
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pritchard, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. *Science* (80-.). 333, pp. 301–306. <https://doi.org/10.1126/science.1205106>
- European Union, 2013. Council directive 2013/17/EU - of 13 May 2013. *Off. J. Eur. Union.* (accessed 6 June 2021).
- Faurby, S., Pedersen, R.Ø., Davis, M., Schowanek, S.D., Jarvie, S., Antonelli, A., Svenning, J.C., 2020. PHYLACINE 1.2.1: An update to the Phylogenetic Atlas of Mammal Macroecology. <https://doi.org/10.5281/zenodo.3690867>
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., York, E.C., 2000. Competition and intraguild predation among three sympatric carnivores. *Oecologia* 125, pp. 258–270. <https://doi.org/10.1007/s004420000448>

- Feit, B., Feit, A., Letnic, M., 2019. Apex Predators Decouple Population Dynamics Between Mesopredators and Their Prey. *Ecosystems* 22, pp. 1606–1617. <https://doi.org/10.1007/s10021-019-00360-2>
- Ferretti, F., Pacini, G., Belardi, I., Cate, B.T.E.N., Sensi, M., Oliveira, R., Rossa, M., Burrini, L., Lovari, S., 2021. Recolonizing wolves and opportunistic foxes: Interference or facilitation? *Biol. J. Linn. Soc.* 132, pp. 196–210. <https://doi.org/10.1093/biolinnean/blaa139>
- Fleming, P.J.S., Nolan, H., Jackson, S.M., Ballard, G.A., Bengsen, A., Brown, W.Y., Meek, P.D., Mifsud, G., Pal, S.K., Sparkes, J., 2017. Roles for the Canidae in food webs reviewed: Where do they fit? *Food Webs* 12, pp. 14–34. <https://doi.org/10.1016/j.fooweb.2017.03.001>
- Frey, S., Fisher, J.T., Burton, A.C., Volpe, J.P., 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens. Ecol. Conserv.* 3, pp. 123–132. <https://doi.org/10.1002/rse2.60>
- Harrington, L.A., Harrington, A.L., Hughes, J., Stirling, D., Macdonald, D.W., 2010. The accuracy of scat identification in distribution surveys: American mink, *Neovison vison*, in the northern highlands of Scotland. *Eur. J. Wildl. Res.* 56, pp. 377–384. <https://doi.org/10.1007/s10344-009-0328-6>
- Haswell, P.M., Jones, K.A., Kusak, J., Hayward, M.W., 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia* 187, pp. 573–583. <https://doi.org/10.1007/s00442-018-4133-3>
- Haswell, P.M., Kusak, J., Jones, K.A., Hayward, M.W., 2020. Fear of the dark? A mesopredator mitigates large carnivore risk through nocturnality, but humans moderate the interaction. *Behav. Ecol. Sociobiol.* 74, pp. 1–9. <https://doi.org/10.1007/s00265-020-02831-2>
- Hoffmann, M., Sillero-Zubiri, C., 2021. *Vulpes vulpes* (amended version of 2016 assessment). IUCN Red List Threat. Species 2021 e.T23062A193903628. <https://doi.org/https://www.iucnredlist.org/species/23062/193903628>
- Hunter, L., Barrett, P., 2018. Introduction, in: *A Field Guide to the Carnivores of the World*. Bloomsbury Wildlife, London, pp. 6–13.
- Ikeda, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K., Koizumi, I., 2016. Seasonal and diel activity patterns of eight sympatric mammals in northern Japan revealed by an intensive camera-trap survey. *PLoS One* 11, pp. 1-16. <https://doi.org/10.1371/journal.pone.0163602>
- Johnson, A., Vongkhamheng, C., Saithongdam, T., 2009. The diversity, status and conservation of small carnivores in a montane tropical forest in northern Laos. *Oryx* 43, pp. 626–633. <https://doi.org/10.1017/S0030605309990238>
- Karanth, K.U., Chundawat, R.S., Nichols, J.D., Kumar, N.S., 2004. Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. *Anim. Conserv.* 7, pp. 285–290. <https://doi.org/10.1017/S1367943004001477>
- Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., Samba Kumar, N., 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proc. R. Soc. B Biol. Sci.* 284, pp. 1-11. <https://doi.org/10.1098/rspb.2016.1860>
- Kendall, Katherine C, McKelvey, Kevin S, 2008. Chapter 6 - Hair collection methods, in: *noninvasive survey methods for North American carnivores*. Washington, D. C., pp. 135–176.
- Krebs, C.J., 2009. *Ecology - The experimental analysis of distribution and abundance*, Sixth. ed. Pearson, San Francisco.
- Kucera, T.E., Barrett, R.H., 2011. Chapter 2 - A History of Camera Trapping, in: *Camera Traps in Animal Ecology: Methods and Analyses*. pp. 9–24. <https://doi.org/10.1007/978-4-431-99495-4>
- Kuijper, D.P.J., Verwijmeren, M., Churski, M., Zbyryt, A., Schmidt, K., Jedrzejewska, B., Smit, C., 2014. What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS One* 9, pp. 1–12. <https://doi.org/10.1371/journal.pone.0084607>

- Laundre, J.W., Hernandez, L., Ripple, W.J., 2010. The Landscape of Fear: Ecological Implications of Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~! Open Ecol. J. 3, pp. 1–7.
<https://doi.org/10.2174/1874213001003030001>
- le Roux, E., Marneweck, D.G., Clinning, G., Druce, D.J., Kerley, G.I.H., Cromsigt, J.P.G.M., 2019. Top-down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography (Cop.)*. 42, pp. 1115–1123. <https://doi.org/10.1111/ecog.03791>
- Letnic, M., Dworjanyn, S.A., 2011. Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? *Ecography (Cop.)*. 34, pp. 827–835.
<https://doi.org/10.1111/j.1600-0587.2010.06516.x>
- Letnic, M., Ritchie, E.G., Dickman, C.R., 2012. Top predators as biodiversity regulators: The dingo *Canis lupus dingo* as a case study. *Biol. Rev.* 87, pp. 390–413. <https://doi.org/10.1111/j.1469-185X.2011.00203.x>
- Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions: What are the ecological effects of anti-predator decision-making? *Bioscience* 48, pp. 25–34.
- Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *Am. Nat.* 153, pp. 649–659. <https://doi.org/10.1086/303202>
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, pp. 619–640.
- Lindström, E.R., Brainerd, S.M., Helldin J. O, Overskaug, K., 1995. Pine marten - red fox interactions: a case of intraguild predation? *Ann. Zool. Fennici* 32, pp. 123–130.
- Linnell, J.D.C., Andersen, R., Andersone, Ž., Balčiauskas, L., Blanco, J., Boitani, L., Brainerd, S., Breitenmoser, U., Kojola, I., Liberg, O., Others, 2002. The fear of wolves: a review of wolf attacks on humans. *NINA Oppdragsmeld.* 731, pp. 1–65.
- Long, R.A., Dononvan, T.M., Mackay, P., Zielinski, W.J., Buzas, jeffrey S., 2007. Comparing scat detection fogs, cameras, and hair snares for surveying carnivores. *J. Wildl. Manage.* 71, pp. 2018–2025.
<https://doi.org/10.2193/2006-292>
- Madsen, A., Christensen, T., Madsen, J., Balsby, T., Bregnballe, T., Clausen, K., Clausen, P., Elmeros, M., Fox, A., Frederiksen, M., Hansen, H., Haugaard, L., Heldbjerg, H., Mayer, M., Mikkelsen, P., Nielsen, R., Pedersen, C., Pedersen, I., Sterup, J., Therkild, O., 2020. Vildtbestande og jagttider i Danmark. Det biologiske grundlag for jagttidsrevisionen 2022 - Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, pp. 1-168. Aarhus.
- Mancinelli, S., Falco, M., Boitani, L., Ciucci, P., 2019. Social, behavioural and temporal components of wolf (*Canis lupus*) responses to anthropogenic landscape features in the central Apennines, Italy. *J. Zool.* 309, pp. 114–124. <https://doi.org/10.1111/jzo.12708>
- Mayer, M., Fog Bjerre, D.H., Sunde, P., 2020. Better safe than sorry: The response to a simulated predator and unfamiliar scent by the European hare. *Ethology* 126, 704–715. <https://doi.org/10.1111/eth.13019>
- Meek, P., Ballard, G., Fleming, P., Falzon, G., 2016. Are we getting the full picture? Animal responses to camera traps and implications for predator studies. *Ecol. Evol.* 6, pp. 3216–3225.
<https://doi.org/10.1002/ece3.2111>
- Meisner, K., Sunde, P., Clausen, K.K., Clausen, P., Fællø, C.C., Hoelgaard, M., 2014. Foraging ecology and spatial behaviour of the red fox (*Vulpes vulpes*) in a wet grassland ecosystem. *Acta Theriol. (Warsz.)*. 59, pp. 377–389. <https://doi.org/10.1007/s13364-014-0178-9>
- Miljøministeriet, 2021. EU's naturbeskyttelsesdirektiver. URL <https://mst.dk/natur-vand/natur/international-naturbeskyttelse/eu-direktiver/naturbeskyttelsesdirektiver/> (accessed 14 may 2021).
- Miljøstyrelsen, 2021. Mårhund (*Nyctereutes procyonoides*). Artsleksikon. URL <https://mst.dk/natur-vand/natur/artsleksikon/pattedyr/maarhund/> (accessed 6 june 2021).

- Miljøstyrelsen, 2017. Faktaark for invasive arter – Vaskebjørn – (*Procyon lotor*). URL <https://mst.dk/media/121587/vaskebjoern.pdf> (accessed 26 may 2021).
- Miller, B.J., Harlow, H.J., Harlow, T.S., Biggins, D., Ripple, W.J., 2012. Trophic cascades linking wolves (*Canis lupus*), coyotes (*Canis latrans*), and small mammals. *Can. J. Zool.* 90, pp. 70–78. <https://doi.org/10.1139/Z11-115>
- Mills, K.J., Patterson, B.R., Murray, D.L., 2010. Direct Estimation of Early Survival and Movements in Eastern Wolf Pups. *J. Wildl. Manage.* 72, pp. 949–954. <https://doi.org/10.2193/2006-457>
- Mobbs, D., Hagan, C.C., Dalglish, T., Silston, B., Prévost, C., 2015. The ecology of human fear: Survival optimization and the nervous system. *Front. Neurosci.* 9. <https://doi.org/10.3389/fnins.2015.00055>
- Monterroso, P., Rich, L.N., Serronha, A., Ferreras, P., Alves, P.C., 2014. Efficiency of hair snares and camera traps to survey mesocarnivore populations. *Eur. J. Wildl. Res.* 60, pp. 279–289. <https://doi.org/10.1007/s10344-013-0780-1>
- Newsome, T.M., Ripple, W.J., 2015. A continental scale trophic cascade from wolves through coyotes to foxes. *J. Anim. Ecol.* 84, pp. 49–59. <https://doi.org/10.1111/1365-2656.12258>
- O’Connell, A.F., Nichols, J.D., Karanth, U.K., 2011. *Camera Traps in Animal Ecology - Methods and Analyses*. Springer US.
- Olsen, K., Sunde, P., Vedel-Smith, C., Hansen, M.M., Thomsen, P.F., 2021. Statusrapport fra den national overvågning af ulv (*Canis lupus*) i Danmark - 4. kvartal 2020 - Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, pp. 1-21 – Notat nr. 2021|21.
- Pagh, S., 2011. Baggrund for regulering af ræv, pp. 1-36.
- Pagh, S., Asferg, T., Madsen, A.B., 2007. Ræv (*Vulpes vulpes*), in: Baagøe, H.J., Thomas S. Jensen (Eds.), *Dansk Pattedyratlas*. Gyldendal, Copenhagen, pp. 176–181.
- Pagh, S., Chriél, M., Madsen, A.B., Jensen, T.W., Elmeros, M., Asferg, T., Hansen, M.S., 2018. Increased reproductive output of Danish red fox females following an outbreak of canine distemper. *Canid Biol. Conserv.* 21, pp. 12–20.
- Pasanen-Mortensen, M., Elmhagen, B., Lindén, H., Bergström, R., Wallgren, M., van der Velde, Y., Cousins, S.A.O., 2017. The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change. *J. Anim. Ecol.* 86, pp. 566–576. <https://doi.org/10.1111/1365-2656.12633>
- Peacor, S.D., 2002. Positive effect of predators on prey growth rate through induced modifications of prey behaviour. *Ecol. Lett.* 5, pp. 77–85. <https://doi.org/10.1046/j.1461-0248.2002.00287.x>
- Petroelje, T.R., Kautz, T.M., Beyer, D.E., Belant, J.L., 2021. Interference competition between wolves and coyotes during variable prey abundance. *Ecol. Evol.* 11, pp. 1413–1431. <https://doi.org/10.1002/ece3.7153>
- Polis, G.A., 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.* 12, pp. 225–251. <https://doi.org/10.1146/annurev.es.12.110181.001301>
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The Ecology and Evolution of Intraguild Predation - Potential Competitors that eat each other. *Annu. Rev. Ecol. Evol. Syst.* 20, pp. 297–330.
- 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, pp. 779–791. <https://doi.org/10.1525/bio.2009.59.9.9>
- Raynor, J.L., Grainger, C.A., Parker, D.P., 2021. Wolves make roadways safer, generating large economic returns to predator conservation. *Proc. Natl. Acad. Sci.* 118, e2023251118. <https://doi.org/10.1073/pnas.2023251118>
- Reconyx, 2015. *Instruction Manual - Reconyx UltraFire XS8*.
- Reinhardt, I., Kluth, G., Nowak, S., Mysłajek, R.W., 2015. Standards for the monitoring of the Central European wolf population in Germany and Poland, Bfn-Skripten.

- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science*. 343, pp. 1-13
<https://doi.org/10.1126/science.1241484>
- Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12, pp. 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Schmidt, K., Kowalczyk, R., 2006. Using scent-marking stations to collect hair samples to monitor eurasian lynx populations. *Wildl. Soc. Bull.* 34, pp. 462–466. [https://doi.org/10.2193/0091-7648\(2006\)34\[462:USSTCH\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2006)34[462:USSTCH]2.0.CO;2)
- Sih, A., Ziemba, R., Harding, K.C., 2000. New insights on how temporal variation in predation risk shapes prey behavior. *Trends Ecol. Evol.* 15, pp. 3–4. [https://doi.org/10.1016/S0169-5347\(99\)01766-8](https://doi.org/10.1016/S0169-5347(99)01766-8)
- Skov- og Naturstyrelsen, 2010. *Indsatsplan mod mårhund i Danmark*.
- Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H., Haskell, J.P., 2003. Body mass of late quaternary mammals. *Ecology* 84, pp. 3403–3403. <https://doi.org/10.1890/02-9003>
- Soe, E., Davison, J., Süld, K., Valdmann, H., Laurimaa, L., Saarma, U., 2017. Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox *Vulpes vulpes*: a quantitative review. *Mamm. Rev.* 47, pp. 198–211. <https://doi.org/10.1111/mam.12092>
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M., Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2, pp. 75–92. <https://doi.org/10.1111/j.1523-1739.1988.tb00337.x>
- Sunde, P., Collet, S., Olsen, K., Matzen, J., Thomsen, P.F., Michler, F., Hansen, M.M., Vedel-smith, C., 2021. Where have all the young wolves gone? Traffic and cryptic mortality create a wolf population sink in Denmark and northernmost Germany, pp. 1–10. <https://doi.org/10.1111/conl.12812>
- Sunde, P., Olsen, K., 2018. *Ulve (Canis lupus) i Danmark 2012-2017 Oversigt og analyse af tilgængelig bestandsinformation - DCE – Nationalt Center for Miljø og Energi*. <https://doi.org/10.13140/RG.2.2.24365.18403>
- Swanson, A., Caro, T., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E., Packer, C., 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. *J. Anim. Ecol.* 83, pp. 1418–1427. <https://doi.org/10.1111/1365-2656.12231>
- Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S., Radler, S., 2007. Human impact on wolf activity in the Bieszczady Mountains, SE Poland. *Ann. Zool. Fennici* 44, pp. 225–231.
- Thorsen, H., Olsen, K., Sunde, P., 2019. Danske ulves (*Canis lupus lupus*) døgnaktivitets-mønster studeret med brug af vildtkameraer. *Flora og Fauna* 125, pp. 1–11.
- Tourani, M., Brøste, E.N., Bakken, S., Odden, J., Bischof, R., 2020. Sooner, closer, or longer: detectability of mesocarnivores at camera traps. *J. Zool.* 312, pp. 259–270. <https://doi.org/10.1111/jzo.12828>
- Ugarte, C.S., Moreira-Arce, D., Simonetti, J.A., 2019. Ecological attributes of carnivore-livestock conflict. *Front. Ecol. Evol.* 7, pp. 1–9. <https://doi.org/10.3389/fevo.2019.00433>
- Wachter, B., Blanc, A.S., Melzheimer, J., Höner, O.P., Jago, M., Hofer, H., 2012. An advanced method to assess the diet of free-ranging large carnivores based on scats. *PLoS One* 7. <https://doi.org/10.1371/journal.pone.0038066>
- Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J., Shanas, U., 2015. What is an apex predator? *Oikos* 124, pp. 1453–1461. <https://doi.org/10.1111/oik.01977>
- Wellington, K., Bottom, C., Merrill, C., Litvaitis, J.A., 2014. Identifying performance differences among

trail cameras used to monitor forest mammals. *Wildl. Soc. Bull.* 38, pp. 634–638.
<https://doi.org/10.1002/wsb.425>

Wikenros, C., Aronsson, M., Liberg, O., Jarnemo, A., Hansson, J., Wallgren, M., Sand, H., Bergström, R.,
2017. Fear or food - Abundance of red fox in relation to occurrence of lynx and Wolf. *Sci. Rep.* 7, pp.
1–10. <https://doi.org/10.1038/s41598-017-08927-6>

Worm, B., Paine, R.T., 2016. Humans as a hyperkeystone species. *Trends Ecol. Evol.* 31, pp. 600–607.
<https://doi.org/10.1016/j.tree.2016.05.008>

Table of content

PART B – ARTICLE MANUSCRIPT.....	2
RESUME	2
ABSTRACT.....	3
KEYWORDS	3
METHOD	6
<i>Study area.....</i>	<i>6</i>
<i>Data analysis.....</i>	<i>8</i>
<i>Predictions</i>	<i>10</i>
<i>Spatial distribution.....</i>	<i>10</i>
<i>Temporal distribution.....</i>	<i>10</i>
RESULTS.....	11
<i>Predictions</i>	<i>13</i>
<i>Spatial distribution.....</i>	<i>13</i>
<i>Temporal distribution.....</i>	<i>18</i>
DISCUSSION.....	19
<i>Synopsis.....</i>	<i>19</i>
<i>Spatial distribution.....</i>	<i>19</i>
<i>Temporal distribution.....</i>	<i>20</i>
<i>Spatiotemporal distribution.....</i>	<i>20</i>
ACKNOWLEDGMENTS.....	23
REFERENCES.....	24
APPENDIX 1 – DATA SELECTION AND DATA GENERATION	28
<i>1.1 Data selection.....</i>	<i>28</i>
<i>1.2 Data generation.....</i>	<i>28</i>
APPENDIX 2 – ADDITIONAL TABLES	29
<i>2.1 – Pearson’s correlation of variables from Table 3 and Table 6.....</i>	<i>29</i>
<i>2.2 – Pearson’s correlation of variables used in Table 10.....</i>	<i>29</i>
APPENDIX 3 – QGIS WORK.....	29
<i>3.1 Heatmaps of wolf activity.....</i>	<i>29</i>
<i>3.2: Correlation matrix two observation type.....</i>	<i>30</i>
<i>3.3: Correlation matrix for combined observations in 6-months periods.....</i>	<i>31</i>
<i>3.4: Heatmap figure of winter and summer periods</i>	<i>31</i>
<i>3.5: Figure of human activity heatmap</i>	<i>32</i>
APPENDIX 4 – R CODE	32

Part B – Article manuscript

Submission plan

The article in part B is written with manuscript submission as original research article to *Mammalian biology* in mind. While the article type should not be longer than 7,000-8,000 words, this manuscript version is 9546 words, to include several details, relevant for the Master thesis that would not be included in the final submission.

Journal

Mammalian biology

Title

Habitat selection and diel activity patterns of red fox as function of contrasting wolf activity levels in a Danish wolf territory.

Resume

Top prædatorer regulerer artsamfund igennem top-down trofiske interaktioner eller igennem *landscape of fear* ved at modificere adfærd og aktivitetsmønstre hos mesoprædatorer. Derfor kan manglende top prædatorer lede til *mesopredator release*. I 2012 blev den første ulv dokumenteret i Danmark i 200 år. Om og hvordan grå ulv, som top prædator, regulerer habitatselektion og døgnaktivitetsmønstre hos rød ræv efter ulvens genindvandring, blev undersøgt i dette studie. Vi brugte data indsamlet igennem det nationale ulveovervågningsprogram med kamerafælder i perioden 2017-2019. Specifikt er den rumlige og tidsmæssige fordeling af ulv, ræv og en række miljøvariabler blevet kvantificeret. *Generalized linear mixed models* (GLMM) og modelselektion blev brugt til at undersøge effekten af ulvens tilstedeværelse på ræve. Endvidere undersøgte vi om perioder med henholdsvis høje og lave ulveaktivitets-niveauer påvirkede ræve ved brug af en overlap-analyse. Vi fandt, at den rumlige fordeling af ulve blev beskrevet med en model, der indeholdt den gennemsnitlige vegetationshøjde med en negativ korrelation. Den rumlige fordeling af ræve blev bedst beskrevet med en model, der indeholdt afstanden til nærmeste hus med en negativ korrelation. Modeller som indeholdt aktiviteten og tilstedeværelse af ulve, var ikke bedre til at beskrive den rumlige fordeling af ræve end afstanden til nærmeste hus. De temporære aktivitetsmønstre var ikke signifikant forskellig mellem ræv og ulv i perioder med høje og lave ulveaktivitets niveauer. Resultaterne indikerer en potentiel rumlig adskillelse og et tidsmæssigt overlap i aktiviteten mellem de to arter, som vil være relevant at undersøge nærmere i et studie med flere studieområder.

Abstract

Top predators regulate species communities through top-down trophic interactions or through *landscape of fear* by modifying behavior and activity patterns of mesopredators. Thus, absence of top predators can lead to mesopredator release. The first grey wolf in 200 years was documented in Denmark in 2012. Here we investigate if and how wolf as top predator regulate habitat selection and diel activity of red fox after the reappearance. We used data collected in the national wolf population monitoring program with camera traps in 2017-2019. Specifically, we quantified the spatial and temporal distribution of wolf and fox and several environmental variables. Generalized linear mixed models (GLMM) and model selection was used to investigate the effect of wolf presence on foxes. Further we investigated if periods with high or low wolf activity levels influenced fox using an overlap analysis. We found that the spatial distribution of wolves, was best described by a model including mean vegetation height with a negative correlation. The spatial distribution of foxes was best described by a model including distance to nearest house with a negative correlation. Models including activity and presence of wolves was not better at explaining the presence of foxes, than the distance to nearest house. Temporal activity patterns were not significantly different between fox and wolf in periods with high and low wolf activity levels. The results indicate a potential spatial segregation and a temporal overlap in the activity of the two species, that could be relevant to examine closer in a study containing more study sites.

Keywords (4-6)

Vulpes vulpes, *Canis lupus*, intraguild interactions, camera traps, model selection, overlap

Introduction

Large carnivores are often keystone species in terrestrial ecosystems (Estes et al., 2011; Prugh et al., 2009). Predators regulate species communities via top-down effects caused by both direct and indirect interactions (Estes et al., 2011; Ripple et al., 2014; Ritchie and Johnson, 2009). The effect of indirect predation leads prey species to live in a *landscape of fear*, where they make a tradeoff between predation risk and food intake, affecting both their habitat choice and behavior (Bleicher, 2017; Laundre et al., 2010) and affecting population numbers of prey species (Lima, 1998).

Carnivores are found on several trophic levels depending on their role in the ecosystem (Ripple et al., 2014). Top predators (apex predators), the largest predators, are few in numbers due to their size and consequently larger home range (Wallach et al., 2015). Their dietary preferences for large herbivores including livestock leaves them often in conflict with humans and as a result they are often hunted to extirpation (Estes et al., 2011; Ripple et al., 2014). Combined with habitat loss, extirpations lead to many larger carnivore species being at risk of extinction (Prugh et al., 2009; Ripple et al., 2014).

Mesopredators are both hunter and hunted, as they are at risk of being predated and controlled by top predators (Ritchie and Johnson, 2009). Some mesopredators choose to avoid top predators by changing foraging behavior when coexisting with top predators (Haswell et al., 2018). Mesopredators may however also benefit from staying in proximity of top predators in order to utilize prey killed by top predators (Ferretti et al., 2021; Pereira et al., 2014). Mesopredators coexisting with top predators, may therefore tradeoff benefits and risks (Rossa et al., 2021).

The absence of top predators in an ecosystem can lead to trophic cascades (Estes et al., 2011) and to mesopredator release, where the lack of predation risk and population control from the larger predator leads to an increase in mesopredator populations. First documented by Soulé et al. (1988), extirpation of coyotes (*Canis latrans*), gave way to a mesopredator release through increasing numbers of gray foxes (*Urocyon cinereoargenteus*), and domestic cats (*Felis catus*), resulting in the local extinction of several bird species. Mesopredator release increases predation on prey species and change population dynamics or lead to extinction of prey species (Ritchie and Johnson, 2009; Soulé et al., 1988).

Recolonization of top predators can likewise lead to suppression of mesopredators. Examples include recolonization of lynx (*Lynx lynx*), in Sweden and Finland leading to suppression of foxes (Pasanen-Mortensen et al., 2017). Wolves lead to suppression of coyotes in The United States of America (Berger and Conner, 2018), and wolves and lynx lead to a suppression of foxes in Sweden (Elmhagen and Rushton, 2007).

The distribution and abundance of large predators are increasing throughout Europe (Chapron et al., 2014). In Denmark, grey wolf (*Canis lupus*; hereafter referred to as wolf) was historically top predator in the terrestrial ecosystem, though hunted to extirpation, with the last individual seen in 1813 (Madsen et al., 2013). Due to the extirpation of wolf, Denmark has been without a terrestrial top predator for the last 200 years. In 2012, observations documented the return of a wolf to the country. Since, a varying number of wolves have been present in the country and closely monitored by a national wolf monitoring program (Olsen et al., 2021; Sunde and Olsen, 2018). The wolf is the largest species of the canids, with an average weight of 32kg (Faurby et al., 2020; Smith et al., 2003). In Europe wolf are elusive top predators living in larger established territories, preferably areas avoiding humans or with little human contact (Carricondo-Sanchez et al., 2020; Gurarie et al., 2011). When in habitats closer to humans, a more nocturnal activity pattern, with activity peaks around dusk and dawn is pronounced (Ciucci et al., 1997; Haswell et al., 2020; Mancinelli et al., 2019; Thorsen et al., 2019).

Red fox (*Vulpes vulpes*; hereafter referred to as fox), is a smaller canid species with an average weight of 5.3kg (Faurby et al., 2020; Smith et al., 2003) and normally mesopredator. However, in the absence of wolf, fox has been the top predatory terrestrial mammal in Denmark with humans and dogs as its only enemy (Pagh et al., 2007; Peter Sunde, pers. comm.). Foxes are opportunistic predators, feeding on several smaller species (Castelló, 2018). They have adapted to anthropogenic landscapes and proximity to humans (Bateman and Fleming, 2012; Hoffmann and Sillero-Zubiri, 2021). The activity patterns of foxes vary from primarily nocturnal (Caravaggi et al., 2018) to be cathemeral, with inconsistency activity patterns throughout the day (Ikeda et al., 2016).

As wolves and foxes differ in their response to anthropogenic environments (Kuijper et al., 2016), studying their interactions in areas with a high human population density is therefore of interest. Interactions between foxes and recolonized wolf populations, have been studied in North America (Newsome and Ripple, 2015; Sivy et al., 2018), but only in a few European communities (Chapron et al., 2014). A new study from Italy found that foxes were not avoiding sites with high wolf activity, instead staying close and benefitting from leftover prey (Ferretti et al., 2021). In contrast, a study from Croatia found that foxes were avoiding wolves on a temporal scale by being more nocturnal (Haswell et al., 2020).

Here, we investigate if and how reappearance of wolf suppresses red fox. Specifically, we investigate how the distribution of foxes and wolves have changed in Denmark's first wolf pack territory in Western Jutland from 2017-2019. We investigate spatial distribution and temporal dis-

tribution. Specifically for spatial distribution, we expect that wolves and foxes differ in their response to human settlements, specifically (1) the distance to human settlement is negatively correlated with the presence of foxes and positively correlated with the presence of wolves. (2) If foxes are attracted by the presence of wolves, as found by Ferretti et al. (2021), we predict that the presence of foxes per camera day is positively correlated with the local activity index of wolves. (3) Alternatively, if foxes are avoiding wolves, we predict the opposite pattern. For temporal distribution we furthermore expect, if foxes are seeking to minimize detection or encounter rates with wolves, we predict foxes that lives sympatrically with wolves to (4) be more nocturnally active (because it is easier to escape detection when active in the dark) or (5) express a lower diel overlap in activity with wolves (to reduce encounter rates) than foxes that are allopatric to wolves. Finally, we expect, (6) if the presence of wolves does not affect diel activity patterns of foxes, we should expect similar diel activity patterns of foxes in areas where more wolves were present and areas where fewer wolves were present.

Method

Study area

This study is based on data collected as a part of the National Danish Wolf Monitoring Program in Denmark, managed by the National History Museum in Aarhus and Aarhus University, section for Wildlife Ecology Research, with the target of capturing the movement and distribution of wolves in Denmark (Olsen et al., 2021). The data was collected in Western Jutland, in an area that will be referred to as the “Ulfborg territory”. The site contained forest and plantation with primarily coniferous vegetation and open heathland, owned by the Danish government and managed by The Danish Nature Agency. Further information about the research area will not be disclosed because it is sensitive information. Most of mammal species community, detected in the study, consisted of herbivore species; red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), hare (*Lepus europaeus*) and a smaller population of fallow deer (*Dama dama*). Of predator species, foxes were the most abundant species present, followed by badger (*Meles meles*), pine marten (*Martes martes*) and wolves. Furthermore, humans were present in the area with various activities including walking, cycling, horseback riding and driving vehicles.

Using observations from camera traps, scat and tracks, the activity and number of wolves have been closely monitored in the Ulfborg territory. In 2016 the first wolf was observed in the area, and shortly after, there was an established couple and up until 2019, there have been a varying number of wolves (varying from 1-10) in the area (Table 1). In two different periods, there

have been an established couple, that have successfully reproduced (Olsen et al., 2021; Sunde and Olsen, 2018).

Table 1: The seven different wolf periods, number of observations of scat and from camera traps, total number of wolf observations and the number of wolves in each period, estimated by Peter Sunde and status reports of wolves in Denmark (Peter Sunde, pers. comm.).

Time period	Scat samples	Camera traps observations	Total wolf observations	Number of wolves
01-11-2016 – 31-04-2017	11	40	51	2
01-05-2017 – 30-10-2017	20	104	124	10
01-11-2017 – 31-04-2018	78	102	180	8
01-05-2018 – 30-11-2018	23	56	79	1
01-11-2018 – 31-04-2019	56	134	190	2
01-05-2019 – 30-11-2019	63	311	374	8
01-11-2019 – 31-04-2020	130	243	373	7

Data collection

Predators are often elusive species and therefore camera traps are used as a non-invasive way to observe these species (Kucera and Barrett, 2011). Camera traps enable several data to be collected, including abundance, distribution, predator-prey interactions (Keim et al., 2019) and activity patterns (Lashley et al., 2018) like circadian activity patterns (Caravaggi et al., 2018; Ikeda et al., 2016; Thorsen et al., 2019).

The study was done using data from two different datasets (Table 2). Images for dataset A, was collected from a total of 93 camera trap locations managed by a group of volunteers during the period 2016-2020 (Table 2; dataset A). Most observations of a species or human activity (N=10667) were captured by a Bushnell Trophy Cam HD Aggressor (Bushnell, 2017) and a few (N = 2801) with Bushnell Core DS (Bushnell, 2020) and (N = 443) with Reconyx Ultrafire XS8 cameras (Reconyx, 2015). All cameras were activated by a combination of heat and movement. Bushnell cameras had a 0.2 second trigger time and took three pictures and 30 seconds video when triggered during the day and three pictures and 15 second videos during the night, while the Reconyx had a 1.0 sec trigger time, took one picture and a five-minute video, both day and night (Unpublished Camera Protocol). Camera traps were placed following a predefined protocol with the target of capturing wolf activity in the area. They were placed at 80-120 cm above ground, along animal trails, paths, and firebreaks, and were afterwards checked approximately once a month and moved if there was no activity (Kent Olsen, pers. comm.).

The collected images were sorted manually, and data added to a database (see appendix 1 for data selection and data generation). The certainty of the species documented in each observation, was classified using SCALP criteria (Reinhardt et al., 2015), defined using guidelines originally made for monitoring populations of lynx in Europe (Breitenmoser et al., 2006). Observations were classified as C1, C3a, C3b. C1 was given to certain observations with concrete evidence

for the individual to be a specific species. C3a to unconfirmed observations lacking some identification points. C3b to unsure observations, where there is a possibility for the individual to be another species (Thorsen et al., 2019). For analysis SCALP classes C1, C3a and C3b were included. The classes C3a and C3b were included as a previous study by Thorsen et al. (2019) found an underrepresentation of C1 observations during night.

Dataset B included the same camera trap observations of wolves as dataset A and an additional number of camera trap observations collected from a larger area of Ulfborg territory using the same protocol as explained above. The additional camera trap locations have not yet gotten a unique identification number and it is therefore not possible to report the exact number of camera traps for this dataset. The dataset included an additional number of scat observations collected in Ulfborg territory by volunteers involved in the monitoring program and DNA-tested to confirm wolves, using the method described in the report by Thomsen et al. (2020) (Table 2; dataset B).

Table 2: Sample type either camera trap or scat data and the collection period, along with the number of camera placements and number of observations for fox and wolf and human activity (cyclist, man, man + dog, vehicle, and camera control) for the two datasets used in the analysis.

Dataset	Research area	Sampling type	Number of camera placements	Number of observations	Collection period
Dataset A (Wolf monitoring)	Ulfborg territory	Camera trap	51 with fox 89 with human 48 with wolf	879 foxes 5535 humans 658 wolves	10-01-2017 – 05-01-2020
Dataset B (Wolf activity index, WAI)	Ulfborg territory	Camera trap scat		1668 wolf	01-11-2016 – 01-05-2020

Data analysis

The data preparation and analysis were done using R, version 3.6.0 (R Core Team, 2021) and a collection of R-packages in “tidyverse” (Wickham et al., 2019) and the “glmmTMB” package (Magnusson et al., 2020). Additional variables were generated using the open-source geospatial program QGIS, version 3.16.2-Hannover (QGIS.org, 2021).

The season variable divided the year into four seasons and was defined according to daylength, where winter was the three darkest months; November, December and January, spring as February, March and April, summer as May, June and July and fall as August, September, and October.

Habitat variables were made in QGIS using layers containing information about the landscape. The habitat variable estimating distance to the nearest house from a camera trap placement (House distance) was estimated using a linear distance matrix, where the habitat variables estimating distance from a camera trap placement to nearest road (Road distance) and forest (Forest

distance) was found using nearest neighbor relationships. A road was in the data defined as being above 3 meter in width.

The habitat variable containing the mean vegetation height, in a 25-meter buffer zone around a camera trap was found from a Canopy height model (CHM) that was generated by subtracting the Digital Terrain Model (DTM) from the Digital Surface Model (DSM) (obtained from kortforsyningen.dk). A correlation matrix, using Pearson's correlation, of the four variables showed no correlation between variables (all $|r| < 0.2$, appendix 2.1). House distance, Road distance and mean vegetation height were log₁₀ transformed to account for non-normal distribution and forest distance was made into a binary variable, in a forest area or outside a forest area.

Heatmaps describing the activity index for humans and wolves at the different camera placements, were made using kernel density estimation in QGIS (qgistutorials.com, 2021), where the number of points in a location is used to calculate the density, a larger number of points gives a higher heatmap value (QGIS.org, 2020). The output were raster layers with a 10x10 meter resolution. The heatmaps was used as representation of the spatial activity of wolves and the output was sampled for each camera trap placement, they were made using a 1000-meter radius. For the human activity index (HAI), one variable was made containing observations of person, person & dog, cyclist, vehicle, and camera control (Table 2; dataset A).

To represent the activity levels of wolves, a wolf activity index (WAI) was made, using a selection process described in appendix 3. It was made using observations of wolves from camera traps and scat. The data (Table 2; dataset B) was divided into 6-month periods: November-May and May-November (Table 1), accounting for different stages in wolves' reproductive cycle (Castelló, 2018) and a variation in the number of wolves present in the area in different periods, a finer resolution was not possible, because of a too small sample size.

For the WAI, two variables were made from heatmaps. To account for the difference in number of observations in each 6-month period, heatmap values were divided by the number of observations in the period (WAI1). For the second variables (WAI2) to further account for the variation in number of wolves in each period, the value multiplied with the number of wolves. The two wolf activity variables were correlated ($|r| = 0.94$), so WAI2 was excluded from the analysis (appendix 2.2). HAI and WAI1 was log₁₀ transformed to account for non-normal distribution. The active period of foxes in high and low WAI were visualized with observations divided in daytime, twilight and nighttime using the sun angle from the civil twilight definition. A sun angle above 0

degrees was defined as daytime, below -6 degrees as nighttime and between 0 and -6 degrees as twilight (Bikos and Kher, 2021).

Predictions

Spatial distribution

Prediction one (distance to human settlements) was tested using a generalized linear mixed model (GLMM) with a binomial distribution. Data from dataset A was made to represent the presence and absence of each species per camera day including days with zero observations of species. For both foxes and wolves, the null model contained presence or absence of the target species as the response variable, the camera trap placements (CAM) as the random effect and the season variable as a fixed effect. Additional models included one of the habitat variables as an additional fixed effect. A model selection procedure (model selection 1) using Akaike Information Criterion with a correction for small sample sizes (AIC_c) was done for both species (Table 3 & Table 6), selecting the three best models, along with combination of them, to include in another model selection procedure (model selection 2). AIC_c was used as an estimate for relative quality of models in relation to each other, the model with the lowest AIC_c value was regarded as the best model (Burnham et al., 2011).

Prediction two and three (foxes' correlation with wolves), was tested using the same procedure described above for the analysis of prediction one (Table 9).

Temporal distribution

Prediction four and five (diel activity patterns), was tested using an overlap analysis. The analysis was done using the R-packages "overlap" (Meredith et al., 2020). The overlap tool has been made specifically to compare temporal activity patterns between two species (Meredith et al., 2020). It is a non-parametric method, that fits kernel density functions to temporal data using radians by a "probability density function" (Ridout and Linkie, 2009). The method uses D as estimator of density, specifically the estimator $\hat{\Delta}_4$ was used. It was used because it is the most reliable for sample sizes above 50 observations (Meredith et al., 2020; Ridout and Linkie, 2009). If there is a complete overlap in the two species activity patterns $\hat{\Delta}_4 = 1$, and $\hat{\Delta}_4 = 0$ if there is no overlap in the activity pattern (Ridout and Linkie, 2009). The confidence interval was found using 10.000 bootstrap resamples of each species, for stable estimates (Meredith et al., 2020). An overlap analysis was done between wolf and fox observations from dataset A (Table 2), the data was divided into a high and a low dataset using the median value of WAI as intersection (Fig. 7).

Results

Throughout the study period we found 384 observations of foxes and 181 observations of wolves in periods with a high wolf activity index (WAI) and 495 observations of foxes and 61 observations of wolves in periods with a low WAI (Fig. 1).

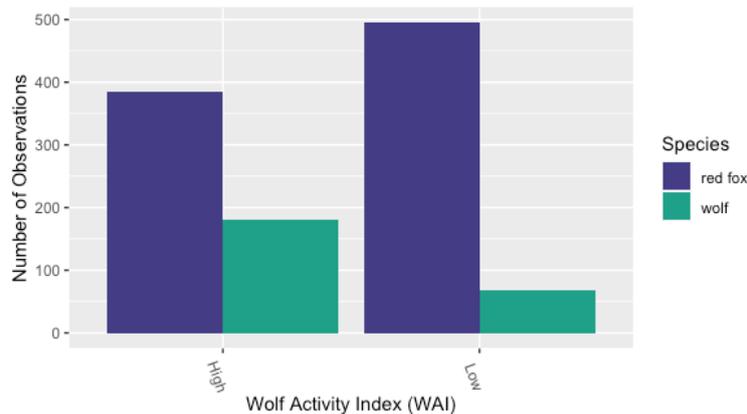


Figure 1: The number of observations of fox (Purple) and wolf (Turquoise) in high wolf activity index (WAI) (left) and low WAI (right).

The distribution of observations between the four seasons showed least observations of foxes in spring (Feb, Mar, Apr) and most observations in summer (May, Jun, Jul). For wolves there were least observations in summer (May, Jun, Jul) and most observations in fall (Aug, Sep, Oct) (Fig. 2; A). The diel distribution of observations of both species showed most observations in the nighttime periods, in both high and low WAI. For foxes, there were fewer observations in both daytime and nighttime in high WAI compared to low WAI. For wolves, there were more daytime observations and less twilight observations in high WAI compared to low WAI (Fig 2; B).

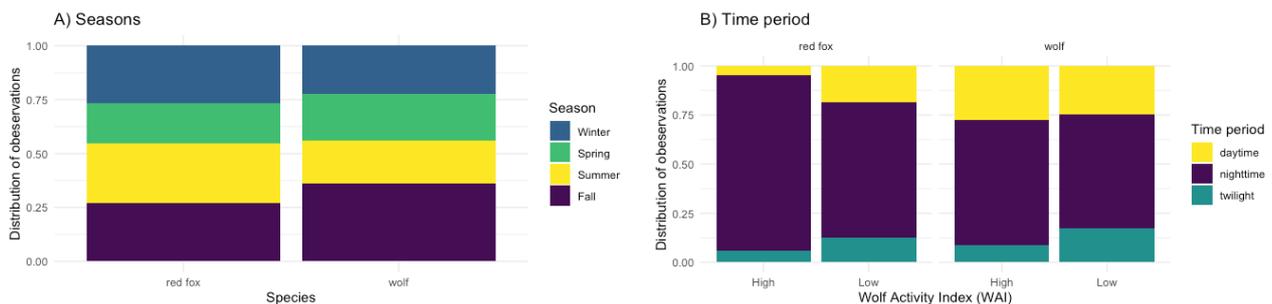


Figure 2: Distribution of observations of wolf and fox A) the distribution of observations of fox (left) and wolf (right) in the four seasons and B) the distribution of observations of fox and wolf in three time periods: daytime (yellow), nighttime (purple) and twilight (turquoise) in high and low WAI.

Most observations of both species were made in the low mean vegetation heights, from 0-2 meter (Fig. 3; A). For fox, most observations were done 600-800 meters from nearest house and most wolves were observed 800-1100 meters from nearest house (Fig. 3; B). Most foxes were observed closest to nearest road and least observations were made furthest from nearest road, for wolves there were most observations 400-600 meters from nearest road and least observations closest to nearest road (Fig. 3; C). Most observations were made in forest areas for both species (Fig. 3; D).

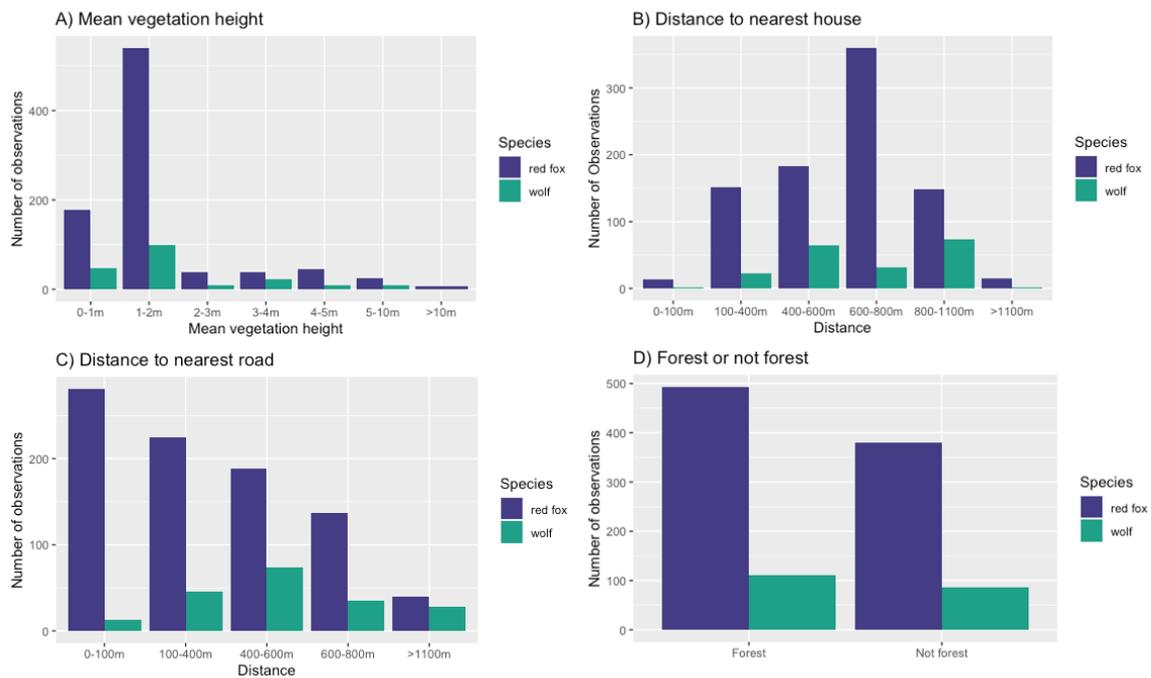


Figure 3: The number of observations of fox (Purple) and wolf (Turquoise), for A) Mean vegetation height, B) Distance to nearest house, C) Distance to nearest road and D) Forest or not forest, where 0 = in forest and 1 = outside forest.

Predictions

Spatial distribution

The analysis for prediction one (distance to human settlement), was for fox done with a model selection between models including House distance, Road distance and Forest distance (Table 3) and a combination of these variables.

Table 3: Results from model selection 1. Models with each habitat variable explaining the presence or absence of fox. AIC_c value indicating which variables that weighed the most in relation to each other. The delta value is the difference between a models AIC_c value and the lowest AIC_c value in the model selection. AIC_c weight, the weight of a model in relation to the other models in the model selection. Fox: the presence or absence of foxes, season: the four seasons, (1|CAM): camera trap placements. The three best models marked in grey.

Model name	AIC_c	delta	AIC_c weight
Fox ~ season + House distance + (1 CAM)	4035.8	0.00	0.853
Fox ~ season + Road distance + (1 CAM)	4041.3	5.51	0.054
Fox ~ season + Forest distance + (1 CAM)	4041.6	5.75	0.048
Fox ~ season + Mean vegetation height + (1 CAM)	4043.0	7.16	0.024
Fox ~ season + (1 CAM)	4043.3	7.42	0.021

Model selection 2 for fox showed that all models including House distance as a predictor weighed most in the analysis and the null model weighing the least. The best model (AIC_c) only included House distance as a predictor variable and weighed 32.9% in the model selection (Table 4). The evidence ratio of the best model was 15.7 times stronger compared to the null model (cf. Burnham et al., 2011). The parameter estimates for the best model, showed a significant negative correlation between the presence of foxes and the House distance variable (Table 5, Fig. 4).

For wolves, model selection 2 was done including mean vegetation height, Forest distance, House distance (Table 6) and a combination of these variables.

Table 4: Results from model selection 2. The three best models from Table 3. That is explaining the presence or absence of fox, a combination of them and the null model. AIC_c value indicating which variables that weighed the most in relation to each other. The delta value is the difference between a models AIC_c value and the lowest AIC_c value in the model selection. AIC_c weight, the weight of a model in relation to the other models in the model selection. Fox: the presence or absence of wolves, season: the four seasons, (1|CAM): camera trap placements. The best model including House distance variable marked in grey.

Model name	AIC_c	delta	AIC_c weight
Fox ~ season + House distance + (1 CAM)	4035.8	0.00	0.329
Fox ~ season + House distance + Forest distance + (1 CAM)	4036.4	0.55	0.250
Fox ~ season + House distance + Road distance + (1 CAM)	4036.6	0.80	0.220
Fox ~ season + House distance + Forest distance + Road distance + (1 CAM)	4037.7	1.83	0.132
Fox ~ season + Road distance + (1 CAM)	4041.3	5.51	0.021
Fox ~ season + Forest distance + Road distance + (1 CAM)	4041.4	5.52	0.021
Fox ~ season + Forest distance + (1 CAM)	4041.6	5.75	0.019
Fox ~ season + (1 CAM)	4043.3	7.42	0.008

Table 5: Parameter estimates for the best model: $Fox \sim season + House\ distance + (I|CAM)$. Signif. codes: 0 '***', 0.001 '**'.

Variable	Estimate	Standard error (SE)	z value	P value	95% CI
Intercept	-3.824	0.254	-15.054	***	(-4.321, -3.326)
Season (Feb, Mar, Apr)	0.589	0.141	4.190	***	(0.314, 0.865)
Season (May, Jun, Jul)	0.121	0.128	0.944		(-0.130, 0.372)
Season (Nov, Dec, Jan)	0.410	0.123	3.246	**	(0.158, 0.641)
House distance	-0.549	0.181	-3.024	**	(-0.904, -0.193)

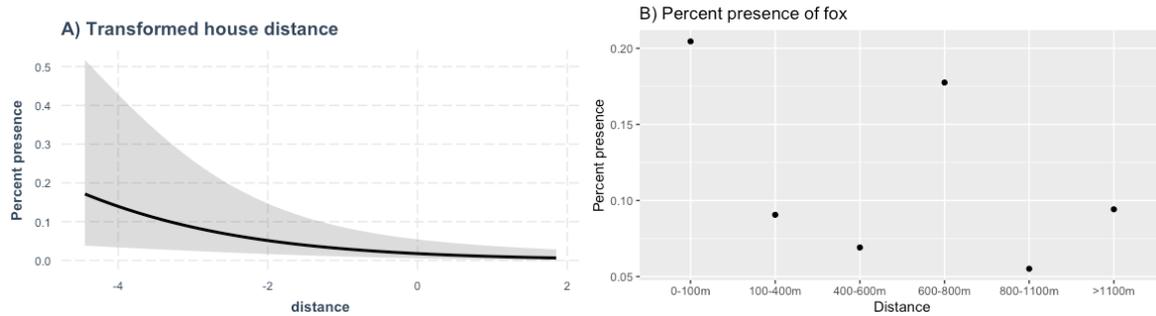


Figure 4: Fox presence A) House distance variable from the best fox model including House distance: $Fox \sim season + House\ distance + (I|CAM)$. With presence or absence of fox along the y-axis and the log10-transformed variables on the x-axis, grey area indicates confidence interval. B) The percent presence of fox in the six different distance classes, with distance to nearest house on the x-axis and the percent presence of fox on the y-axis.

Table 6: Results from model selection 1. Models with each habitat variable explaining the presence or absence of wolves. AIC_c value indicating which variables that weighed the most in relation to each other. The delta value is the difference between a models AIC_c value and the lowest AIC_c value in the model selection. AIC_c weight, the weight of a model in relation to the other models in the model selection. Wolf: the presence or absence of wolves, season: the four seasons, (1|CAM): camera trap placements. The three best models marked in grey.

Model name	AIC_c	delta	AIC_c weight
Wolf ~ season + Mean vegetation height + (1 CAM)	1863.1	0.00	0.593
Wolf ~ season + Forest distance + (1 CAM)	1865.4	2.31	0.187
Wolf ~ season + (1 CAM)	1866.2	3.11	0.125
Wolf ~ season + House distance + (1 CAM)	1868.1	5.01	0.048
Wolf ~ season + Road distance + (1 CAM)	1868.1	5.07	0.047

All models that included mean vegetation height best described the presence of wolves (Table 7). The best model included only mean vegetation height as predictor and weighed 29.6% in the model selection. The evidence ratio for the best model was 4.7 times stronger compared to null model. The best model that included house distance as a predictor, also included mean vegetation height, and weighed 10.9% in the model selection (Table 7) and the evidence ratio was 1.7 times stronger compared to the null model. The parameter estimates for the model showed a significant negative correlation between presence of wolves and mean vegetation height, whereas the effect of house distance, was uninformative (Table 8, Fig. 5).

Table 7: Results from model selection 2. The three best models from Table 6, explaining the presence or absence of wolf, a combination of them and the null model. AIC_c value indicating which variables that weighed the most in relation to each other. The delta value is the difference between a models AIC_c c value and the lowest AIC_c value in the model selection. AIC_c weight, the weight of a model in relation to the other models in the model selection. Wolf: the presence or absence of wolves, season: the four seasons, (1|CAM): camera trap placements. The best model including the house distance variable marked in grey.

Model name	AIC_c	delta	AIC_c weight
Wolf ~ season + mean vegetation height + (1 CAM)	1863.1	0.00	0.296
Wolf ~ season + mean vegetation height + Forest distance + (1 CAM)	1863.2	0.13	0.277
Wolf ~ season + mean vegetation height + House distance + (1 CAM)	1865.1	1.99	0.109
Wolf ~ season + mean vegetation height + Forest distance + House distance + (1 CAM)	1865.2	2.10	0.104
Wolf ~ season + Forest distance + (1 CAM)	1865.4	2.31	0.093
Wolf ~ season + (1 CAM)	1866.2	3.11	0.063
Wolf ~ season + Forest distance + House distance + (1 CAM)	1867.4	4.31	0.034
Wolf ~ season + House distance + (1 CAM)	1868.1	5.01	0.024

Table 8: Parameter estimates for the best model including the house distance variable: wolf ~ season + Mean vegetation height + House distance + (1|CAM). Signif. codes: 0 '***', 0.001 '**'

Variable	Estimate (B)	Standard error (SE)	z value	P value	95% CI
Intercept	-3.849	0.1863	-20.662	***	(-4.214, -3.484)
Season (Feb, Mar, Apr)	0.152	0.2192	0.694		(-0.277, 0.582)
Season (May, Jun, Jul)	-0.341	0.2104	-1.615		(-0.752, 0.073)
Season (Nov, Dec, Jan)	0.113	0.1951	0.581		(-0.269, 0.495)
Mean vegetation height	-0.278	0.132	-2.109	*	(-0.538, -0.021)
House distance	-0.015	0.132	-0.114		(-0.273, 0.243)

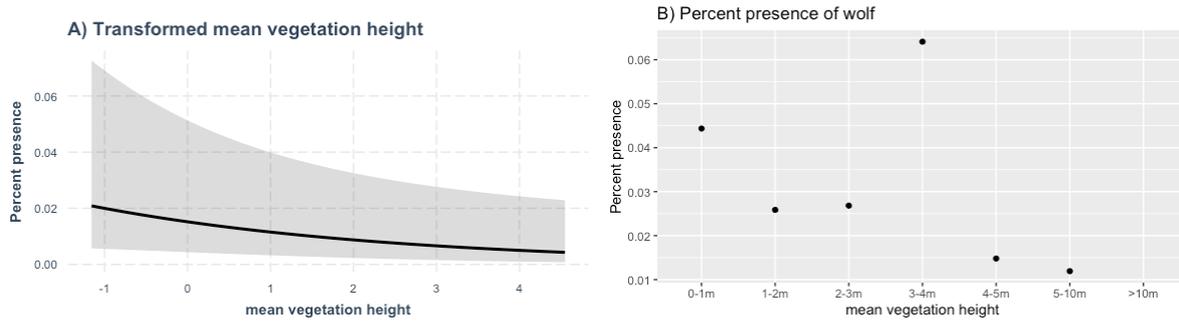


Figure 5: Wolf presence A) the mean vegetation height variable from the best wolf model including house distance: $wolf \sim season + Mean\ vegetation\ height + House\ distance + (1|CAM$. With presence or absence of wolf along y-axis and the log_{10} -transformed variables on the x-axis, grey area indicates confidence interval. B) The percent presence of wolf in the 7 different mean vegetation height classes, with mean vegetation height on the x-axis and the percent presence of wolf on the y-axis.

Model selection 2 was for analysis of prediction two and three (foxes' correlation with wolf activity), was done using the two best variables found in model selection 1 (Table 9), wolf activity index (WAI1) and a combination of them.

Table 9: Results from model selection 1. Models with each variable explaining the presence or absence of fox. AIC_c value indicating which variables that weighed the most in relation to each other. The delta value is the difference between a models AIC_c value and the lowest AIC_c value in the model selection. AIC_c weight, the weight of a model in relation to the other models in the model selection. Fox: the presence or absence of wolves, season: the four seasons, (1|CAM): camera trap placements. WAI1, the wolf activity index. The two best models and the model containing WAI1 marked in grey.

Model name	AIC_c	delta	AIC_c weight
Fox ~ season + mean vegetation height + House distance + (1 CAM)	4036.2	0.00	0.831
Fox ~ season + mean vegetation height + Road distance + (1 CAM)	4041.9	5.75	0.047
Fox ~ season + mean vegetation height + Forest distance + (1 CAM)	4042.3	6.17	0.038
Fox ~ season + mean vegetation height + (1 CAM)	4043.0	6.83	0.027
Fox ~ season + mean vegetation height + wolf number + (1 CAM)	4043.3	7.11	0.024
Fox ~ season + mean vegetation height + human number + (1 CAM)	4044.7	8.49	0.012
Fox ~ season + mean vegetation height + WAI1 + (1 CAM)	4044.9	8.76	0.010
Fox ~ season + mean vegetation height + human activity + (1 CAM)	4045.0	8.80	0.010

The results from model selection 2 showed that a model including only house distance as a variable, best explained the presence or absence of foxes, weighed 35.3 % in the model selection and the evidence ratio was 29.4 times stronger than the null model (Table 10). The best model including WAI1 weighed 15.1 % in the model selection and the evidence ratio was 12.6 times stronger than the null model. Parameter estimates from the best model including the wolf activity variable showed no significant correlation between foxes and wolf activity, a significant negative correlation was found between foxes and house distance (Table 11, Fig. 6).

Table 10: Results from model selection 2. The three best models from Table 9, explaining the presence or absence of fox, a combination of them and the null model. AIC_c value indicating which variables that weighed the most in relation to each other. delta value is the difference between a models AIC_c value and the lowest AIC_c value in the model selection. AIC_c weight, the weight of a model in relation to the other models in the model selection. Fox: the presence or

absence of wolves, season: the four seasons, (1|CAM): camera trap placements. WAI1, the wolf activity index. The best model including the house distance variable marked in grey.

Model name	AIC _c	delta	AIC _c weight
Fox ~ season + mean vegetation height + House distance + (1 CAM)	4036.2	0.00	0.353
Fox ~ season + mean vegetation height + House distance + Forest distance + (1 CAM)	4037.2	1.06	0.208
Fox ~ season + mean vegetation height + House distance + Road distance + (1 CAM)	4037.3	1.16	0.197
Fox ~ season + mean vegetation height + WAI1 + House distance + (1 CAM)	4037.9	1.70	0.151
Fox ~ season + mean vegetation height + Road distance + Forest distance + (1 CAM)	4041.4	5.19	0.026
Fox ~ season + mean vegetation height + Road distance + (1 CAM)	4041.9	5.75	0.020
Fox ~ season + mean vegetation height + Forest distance + (1 CAM)	4042.3	6.17	0.016
Fox ~ season + mean vegetation height + (1 CAM)	4043.0	6.83	0.012
Fox ~ season + mean vegetation height + WAI1 + Road distance + (1 CAM)	4043.9	7.75	0.007
Fox ~ season + mean vegetation height + WAI1 + Forest distance + (1 CAM)	4044.2	8.08	0.006
Fox ~ season + mean vegetation height + WAI1 + (1 CAM)	4044.9	8.76	0.004
Fox ~ season + mean vegetation height + Road distance + House distance + Forest distance + WAI1 + (1 CAM)	4054.9	18.69	0.000

Table 11: Parameter estimates for the best model including WAI: Fox ~ season + mean vegetation height + WAI1 + House distance + (1|CAM). Signif. codes: 0 ‘***’, 0.001 ‘**’.

Variable	Estimate (B)	Standard error (SE)	z value	P value	95% CI
Intercept	-3.721	0.258	-14.399	***	(-4.226, -3.213)
Season (Feb, Mar, Apr)	0.5745	0.141	4.051	***	(0.297, 0.853)
Season (May, Jun, Jul)	0.115	0.130	0.877		(-0.142, 0.371)
Season (Nov, Dec, Jan)	0.3761	0.128	2.932	**	(0.1247, 0.628)
Mean vegetation height	-0.211	0.162	-1.299		(-0.528, 0.107)
WAI1	-0.0433	0.078	-1.552		(-0.197, 0.110)
House distance	-0.541	0.181	-2.985	**	(-0.896, -0.187)

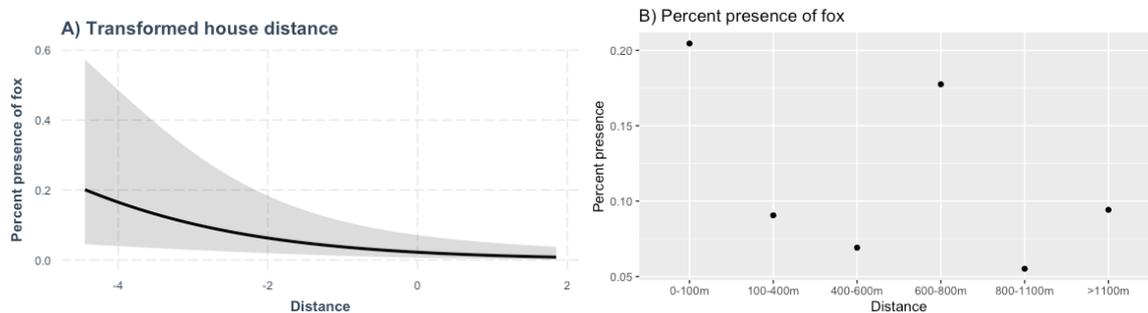


Figure 6: Fox presence A) the house distance variable from the best model including wolf activity index: Fox ~ season + mean vegetation height + WAI1 + House distance + (1|CAM). With presence or absence of fox along the y-axis and the log10-transformed variables on the x-axis, grey area indicates confidence interval. B) The percent presence of fox in the six different distance classes, with distance to nearest house on the x-axis and the percent presence of fox on the y-axis.

Temporal distribution

Overlap analysis testing prediction four and five (difference in noctuality) found an overlap coefficient between foxes and wolves in low WAI of 0.806 (95% confidence interval: 0.708, 0.904; Fig. 7A), and an overlap coefficient between foxes and wolves in high WAI of 0.748 (95% confidence interval: 0.675, 0.821; Fig. 7B). In low WAI periods both species showed nocturnal peaks, with foxes having a small activity peak around 18.00 and wolves a small peak in the twilight period, before and after 06.00. In high WAI periods, fox had an activity peak at 00.00 and wolf had a small activity peak around 09.00. Overlapping confidence interval showed no significant difference between high and low WAI (Fig. 7).

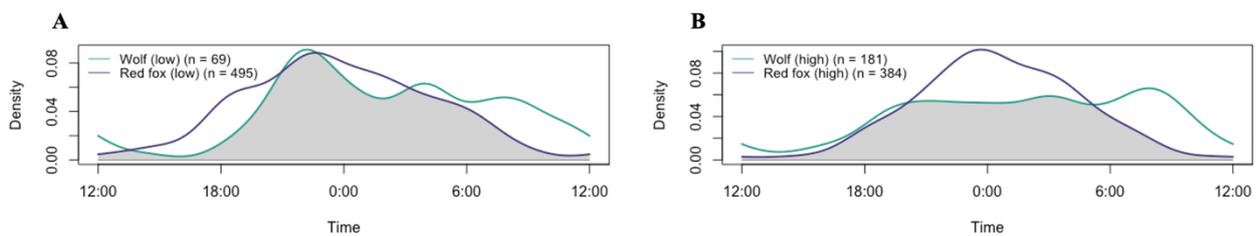


Figure 7: Overlap of daily activity patterns fox (Purple) and wolf (turquoise) in A) low WAI and B) high WAI. Time of day on x-axis and density on y-axis. Note the density scale varies between plots.

Discussion

Synopsis

The distribution of wolves was best explained by mean vegetation height with more wolves being present in low vegetation. The distribution of foxes was best explained by house distance, with more foxes closer to houses and not by the presence or activity of wolves in the area. The temporal overlap of the two species was not significantly different, with nocturnal peaks in activity in both high and low wolf activity index periods.

Spatial distribution

Consistent with our expectation (prediction 1) for foxes, the presence of fox correlated negatively with distance to nearest house, which could be explained by how foxes are documented to be very adaptable in anthropogenic landscapes (Bateman and Fleming, 2012). With their flexible diet (Soe et al., 2017), they can benefit from living near human settlements and utilizing food resources there (Bateman and Fleming, 2012; Hoffmann and Sillero-Zubiri, 2021). No correlation with house distance was found for wolves, but a significant negative correlation with the mean vegetation height was found, which could be explained by wolves using easy routes (e.g., paths, trails, and firebreaks) when moving around the landscape (Ciucci et al., 2003; Zimmermann et al., 2014), as seen in a study from Finland (Gurarie et al., 2011). We also expected to find a significant negative correlation between presence of wolves and distance to nearest road to support this explanation, but the variable Road distance only encompasses roads with a width above 3 meters and therefore did not capture the smaller paths and trails. The results could instead be explained by the study method used to collect this data. Cameras were placed overlooking animal travel routes, paths, and trails, in low vegetation, to maximize species detection and specifically to capture wolves (Reinhardt et al., 2015; Unpublished Camera Protocol), thus more observations would in general be in lower vegetation. Alternatively, could fox correlation with houses indicate that more foxes are using humans as a safe barrier with being near human settlements to avoid risky encounters with wolves, that are elusive and avoiding humans, as it has been documented in other species (Steyaert et al., 2016). However, when expanding the model selection for fox to include wolf activity index (WAI), the results showed no significant correlation between the presence of fox and WAI. This does not support the reasoning that foxes are using houses to avoid wolves (prediction 3). Even though wolves could have a direct effect on foxes via intraguild predation (Palomares and Caro, 1999), which was also observed in Denmark in 2021 by a photographer, our data do not support that foxes are deliberately avoiding wolves. For both variables, that best explained the presence for fox and wolf, the confi-

dence intervals were widespread, which could be an indication of other factors affecting the distribution of the two species and underline the fact that there might be more complex mechanisms driving the distribution of the two species as discussed in other studies (Rossa et al., 2021; Torretta et al., 2016).

Temporal distribution

No significant difference was found between diel activity patterns of fox and wolf with high and low WAI supporting a similar nocturnal diel activity patterns of the two species, consistent with prediction 6. A nocturnal activity pattern of wolves corresponded with results from a previous study on wolves in the area (Thorsen et al., 2019). The results showed a tendency of more nocturnal activity patterns of foxes in periods with high WAI, supporting prediction four. This is corresponding with results from a study showing a temporal partitioning where foxes became more active at night, to utilize travelling routes at times where it was harder to be seen by larger predators (Haswell et al., 2020). Another study found a high temporal overlap between wolf and fox in areas with high wolf activity, which is the opposite of the results of this study (Rossa et al., 2021). And a study by Torretta et al. (2016) found moderate-high overlap in activity patterns between the two species. They propose coexistence is possible because of a temporal segregation in wintertime and a spatial segregation in springtime Torretta et al. (2016), and these seasonal differences would be relevant to examine in future studies to clarify if this could be what is seen in the Ulfborg territory. A previous study on the diel activity patterns of wolves from the same territory found differences in the activity patterns of adult and juvenile wolves (Boe and Kjeldgaard, 2020). Corresponding with knowledge about changing behaviors and activity patterns throughout the life history of species (Castelló, 2018). This could be relevant to distinguish between age-classes in future studies.

Spatiotemporal distribution

While there is an indication that there is a similar diel activity pattern of the two species, the overlap analysis is two-dimensional and is not equipped to considering the spatial distribution of observations. It is therefore not possible to conclude anything from the analysis only, neither is it possible to conclude that foxes are avoiding wolves on a spatial scale. The results indicate that other variables (e.g., House distance) are better at explaining the presence of foxes in an area. If different variables are affecting the habitat selection of the two species and they have a somewhat similar diel activity, it could be an indication of the species being active at the same time, but with a spatial segregation.

This possible spatial segregation, but no temporal segregation does not correspond with results from other studies (Ferretti et al., 2021; Mori et al., 2020). A study found that foxes were not avoiding wolves, in both temporal and spatial scales, they were instead staying close and benefitting from leftover prey (Ferretti et al., 2021). Mori et al. (2020) discussed instead that a dietary partition between the species, where the primary diet of foxes were small mammals, invertebrates, and fruit, may be the reason why a spatiotemporal overlap could be possible. This is supported by Bassi et al. (2018), but Mori et al. (2020) also argued that foxes might benefit from predated on leftover prey from the wolves. To be able to test whether there is an diel activity overlap between foxes and wolves supporting the results from previous studies (Ferretti et al., 2021; Mori et al., 2020; Torretta et al., 2016), there is a need to examine whether there has been a change in the diet composition of foxes after the reappearance of wolves in Denmark. To elaborate on whether foxes present in areas with wolves turn to scavenging more, than foxes in areas with fewer or no wolves present. A study like this could be done by including analysis of stomach content, feces and carcasses killed by wolves.

This study is compiled using wolf-targeted monitoring data, which is where camera traps are being placed in areas where the expectance of finding wolves is high, and is moved after a predefined period, if no observations of wolves is made (Unpublished Camera Protocol). This method might not be adequate to capture species that are not wolves, like foxes, and to study interactions between the species. There are limitations regarding the camera placement and the camera trigger time, that is camera model specific, therefore using different camera models, might yield different results. This study is primarily compiled on data collected by similar camera models, but in the future, when including data from other areas the difference needs to be taken into consideration.

The results might also be influenced by how the date of an observation was determined. An observation day was in this study defined from midnight (00.00) to midnight the following day, but since species living closer to humans have a more nocturnal activity pattern (Haswell et al., 2020). Defining a day by cutting, using noon (12.00) instead of midnight, might better explain the activity patterns of species with a nocturnal activity pattern, in an analysis like this, looking at the presence and absence of a species.

Wider implications

Understanding the shifts in dynamics in the species community after the reappearance of a top predator and the effect on mesopredators is highly relevant to better optimize the conservation ef-

forts, species management and understanding ecosystems changes, especially when studies have found complex interactions between the species (Rossa et al., 2021). These results show little indication of an effect of wolf presence or activity on the distribution of foxes, but to clarify if these results are an indication of a pattern or a one-time occurrence, it is essential to repeat the analysis on data collected in other areas with both species present. It would be interesting to include data from areas where the wolves have been present for a longer period and areas with a larger density of wolves, while also including data on the change in diets of foxes between these areas. This could help explain how foxes have been affected by the reappearance of wolves, after having a longer habituation period to the presence of wolves.

A method to minimize the bias that comes from using data collecting from wolf targeted monitoring, could be compiled by using randomly placed cameras. Cameras placed randomly could be used to acquire observations of a wider range of species with different habitat preferences or foraging styles, to better understand these complex interactions between predatory species.

Conclusion

This study found that it was models containing different variables, that best explained the spatial distribution of fox and wolf. For wolves, mean vegetation height was included in the best model, with more wolves present in low vegetation. For foxes, distance to nearest house was included in the best model with more foxes present closer to human settlements and no correlation between presence or activity levels of wolves and the presence of fox. Indicating a potential spatial segregation not caused by the presence of wolves. Furthermore, the study found an overlap in the temporal distribution of wolf and fox in both time periods with high and low wolf activity levels. The results from this study indicate a temporal overlap and a spatial segregation between fox and wolf in Denmark, that would be highly relevant to study using data from more study sites to understand how the reappearance of wolves have affected the distribution of foxes.

Acknowledgments

I would like to say thank you to several people, without whom this project could not have been completed. First, Rebecca Lyhne for field trips, collaboration and sparring throughout this project. Next a thank you to my supervisors, Jens-Christian Svenning, Peter Sunde and Kent Olsen, for their help, guidance and sparring throughout the project. Thomas and Søren for spending time teaching and showing Rebecca and I how to manage the camera traps during our field trips. Christina Vedel-Smith for her great help with data management and database knowledge. Martin Mayer for help with data analysis. Jens Henrik Jakobsen for letting us see the research area. Oskar for sparring and tolerance during the project. Andreas, Cecilie, Matilde, and Mette for sparring and support.

References

- Bassi, E., Battocchio, D., Marcon, A., Stahlberg, S., Apollonio, M., 2018. Scavenging on ungulate carcasses in a mountain forest area in northern Italy. *Mammal Study* 43, pp. 33–43.
<https://doi.org/10.3106/ms2016-0058>
- Bateman, P.W., Fleming, P.A., 2012. Big city life: Carnivores in urban environments. *J. Zool.* 287, pp. 1–23.
<https://doi.org/10.1111/j.1469-7998.2011.00887.x>
- Berger, K.M., Conner, M.M., 2018. Recolonizing Wolves and Mesopredator Suppression of Coyotes: Impacts on Pronghorn Population Dynamics. *Ecol. Appl.* 18, pp. 599–612.
- Bikos, K., Kher, A., 2021. Twilight, Dawn and Dusk. *timeanddate.com*. URL
<https://www.timeanddate.com/astronomy/different-types-twilight.html> (accessed 29 march 2021).
- Bleicher, S.S., 2017. The landscape of fear conceptual framework: Definition and review of current applications and misuses. *PeerJ* 5, pp. 1–22. <https://doi.org/10.7717/peerj.3772>
- Boe, A.M.B., Kjeldgaard, S.A., 2020. Analyse af danske ulves (*Canis lupus*) aktivitetmønstre og mulige forklaringsvariable. Unpublished work. Aarhus University & Natural History Museum Aarhus.
- Breitenmoser, U., Breitenmoser-Würsten, C., von Arx, M., Zimmermann, F., Ryser, A., Angst, C., Molinari-Jobin, A., Molinari, P., Linnell, J., Siegenthaler, A., Weber, J.-M., 2006. Guidelines for the monitoring of lynx. *Kora Bericht* pp. 1–31.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, pp. 23–35. <https://doi.org/10.1007/s00265-010-1029-6>
- Bushnell, 2020. Instruction Manual - Bushnell CORE and CORE DS.
- Bushnell, 2017. Instruction Manual - Bushnell Trophy Cam HD Agressor.
- Caravaggi, A., Gatta, M., Vallely, M.-C., Hogg, K., Freeman, M., Fadaei, E., Dick, J.T.A., Montgomery, W.I., Reid, N., Tosh, D.G., 2018. Seasonal and predator-prey effects on circadian activity of free-ranging mammals revealed by camera traps. *PeerJ* 6, pp. 1–27. <https://doi.org/10.7717/peerj.5827>
- Carricondo-Sanchez, D., Zimmermann, B., Wabakken, P., Eriksen, A., Milleret, C., Ordiz, A., Sanz-Perez, A., Wikenros, C., 2020. Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features. *Biol. Conserv.* 244, pp. 1–10.
<https://doi.org/10.1016/j.biocon.2020.108514>
- Castelló, J.R., 2018. *Canids of the World*. Princeton University Press, New Jersey.
<https://doi.org/10.2307/j.ctv39x6vm>
- Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balečiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potoečnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* (80-.). 346, pp. 1517–1519.
<https://doi.org/10.1126/science.1257553>
- Ciucci, P., Boitani, L., Francisci, F., Andreoli, G., 1997. Home range, activity and movements of a wolf pack in central Italy. *J. Zool.* 243, pp. 803–819.
- Ciucci, P., Masi, M., Boitani, L., 2003. Winter habitat and travel route selection by wolves in the northern Apennines, Italy. *Ecography* (Cop.). 26, pp. 223–235. <https://doi.org/10.1034/j.1600-0587.2003.03353.x>
- Elmhagen, B., Rushton, S.P., 2007. Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? *Ecol. Lett.* 10, pp. 197–206. <https://doi.org/10.1111/j.1461-0248.2006.01010.x>
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington,

- T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. *Science* (80-). 333, pp. 301–306. <https://doi.org/10.1126/science.1205106>
- Faurby, S., Pedersen, R.Ø., Davis, M., Schowaneck, S.D., Jarvie, S., Antonelli, A., Svenning, J.C., 2020. PHYLACINE 1.2.1: An update to the Phylogenetic Atlas of Mammal Macroecology. <https://doi.org/10.5281/zenodo.3690867>
- Ferretti, F., Pacini, G., Belardi, I., Cate, B.T.E.N., Sensi, M., Oliveira, R., Rossa, M., Burrini, L., Lovari, S., 2021. Recolonizing wolves and opportunistic foxes: Interference or facilitation? *Biol. J. Linn. Soc.* 132, pp. 196–210. <https://doi.org/10.1093/biolinnean/blaa139>
- Gurarie, E., Suutarinen, J., Kojola, I., Ovaskainen, O., 2011. Summer movements, predation and habitat use of wolves in human modified boreal forests. *Oecologia* 165, pp. 891–903. <https://doi.org/10.1007/s00442-010-1883-y>
- Haswell, P.M., Jones, K.A., Kusak, J., Hayward, M.W., 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia* 187, pp. 573–583. <https://doi.org/10.1007/s00442-018-4133-3>
- Haswell, P.M., Kusak, J., Jones, K.A., Hayward, M.W., 2020. Fear of the dark? A mesopredator mitigates large carnivore risk through nocturnality, but humans moderate the interaction. *Behav. Ecol. Sociobiol.* 74, pp. 1–9. <https://doi.org/10.1007/s00265-020-02831-2>
- Hoffmann, M., Sillero-Zubiri, C., 2021. *Vulpes vulpes* (amended version of 2016 assessment). IUCN Red List Threat. Species 2021 e.T23062A193903628. <https://doi.org/https://www.iucnredlist.org/species/23062/193903628>
- Ikedo, T., Uchida, K., Matsuura, Y., Takahashi, H., Yoshida, T., Kaji, K., Koizumi, I., 2016. Seasonal and Diel Activity Patterns of Eight Sympatric Mammals in Northern Japan Revealed by an Intensive Camera-Trap Survey. *PLoS One* 11, pp. 1–16. <https://doi.org/10.1371/journal.pone.0163602>
- Keim, J.L., Lele, S.R., DeWitt, P.D., Fitzpatrick, J.J., Jenni, N.S., 2019. Estimating the intensity of use by interacting predators and prey using camera traps. *J. Anim. Ecol.* 88, pp. 690–701. <https://doi.org/10.1111/1365-2656.12960>
- Kucera, T.E., Barrett, R.H., 2011. Chapter 2 - A History of Camera Trapping, in: *Camera Traps in Animal Ecology: Methods and Analyses*. pp. 9–24. <https://doi.org/10.1007/978-4-431-99495-4>
- Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamailé-Jammes, S., Sand, H., Lone, K., Crowsigt, J.P.G.M., 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R. Soc. B Biol. Sci.* 283, pp. 1-9. <https://doi.org/10.1098/rspb.2016.1625>
- Kuijper, D.P.J., Verwijmeren, M., Churski, M., Zbyryt, A., Schmidt, K., Jedrzejewska, B., Smit, C., 2014. What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS One* 9, pp. 1–12. <https://doi.org/10.1371/journal.pone.0084607>
- Lashley, M.A., Cove, M. V., Chitwood, M.C., Penido, G., Gardner, B., DePerno, C.S., Moorman, C.E., 2018. Estimating wildlife activity curves: comparison of methods and sample size. *Sci. Rep.* 8, pp. 1-11. <https://doi.org/10.1038/s41598-018-22638-6>
- Laundre, J.W., Hernandez, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* 3, pp. 1–7. <https://doi.org/10.2174/1874213001003030001>
- Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions: What are the ecological effects of anti-predator decision-making? *Bioscience* 48, pp. 25–34.
- Madsen, A.B., Andersen, L.W., Sunde, P., 2013. Ulve i Danmark – hvad kan vi forvente? pp. 1-19.
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Brooks, M., 2020. Package ‘glmmTMB,’ Cran.
- Mancinelli, S., Falco, M., Boitani, L., Ciucci, P., 2019. Social, behavioural and temporal components of wolf (*Canis lupus*) responses to anthropogenic landscape features in the central Apennines, Italy. *J. Zool.* 309, pp. 114–124. <https://doi.org/10.1111/jzo.12708>
- Meredith, A.M., Ridout, M., Meredith, M.M., 2020. Package ‘overlap.’
- Mori, E., Bagnato, S., Serroni, P., Sangiuliano, A., Rotondaro, F., Marchianò, V., Cascini, V., Poerio, L., Ferretti, F., 2020. Spatiotemporal mechanisms of coexistence in an European mammal community in a protected area of southern Italy. *J. Zool.* 310, pp. 232–245. <https://doi.org/10.1111/jzo.12743>

- Newsome, T.M., Ripple, W.J., 2015. A continental scale trophic cascade from wolves through coyotes to foxes. *J. Anim. Ecol.* 84, pp. 49–59. <https://doi.org/10.1111/1365-2656.12258>
- Olsen, K., Sunde, P., Vedel-Smith, C., Hansen, M.M., Thomsen, P.F., 2021. Statusrapport fra den national overvågning af ulv (*Canis lupus*) i Danmark - 4. kvartal 2020 - Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, pp. 1-21 – Notat nr. 2021|21.
- Pagh, S., Asferg, T., Madsen, A.B., 2007. Ræv (*Vulpes vulpes*), in: Baagøe, H.J., Thomas S. Jensen (Eds.), *Dansk Pattedyratlas*. Gyldendal, Copenhagen, pp. 176–181.
- Palomares, F., Caro, T.M., 1999. Interspecific Killing among Mammalian Carnivores 153, pp. 492–508.
- Pasanen-Mortensen, M., Elmhagen, B., Lindén, H., Bergström, R., Wallgren, M., van der Velde, Y., Cousins, S.A.O., 2017. The changing contribution of top-down and bottom-up limitation of mesopredators during 220 years of land use and climate change. *J. Anim. Ecol.* 86, pp. 566–576. <https://doi.org/10.1111/1365-2656.12633>
- Pereira, L.M., Owen-Smith, N., Moleón, M., 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra-guild comparisons. *Mamm. Rev.* 44, pp. 44–55. <https://doi.org/10.1111/mam.12005>
- 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, pp. 779–791. <https://doi.org/10.1525/bio.2009.59.9.9>
- QGIS.org, 2021. QGIS Geographic Information System.
- QGIS.org, 2020. 24.1.4.1. Heatmap (kernel density estimation). URL [https://docs.qgis.org/3.16/en/docs/user_manual/processing_algs/qgis/interpolation.html?highlight=kernel density estimation#heatmap-kernel-density-estimation](https://docs.qgis.org/3.16/en/docs/user_manual/processing_algs/qgis/interpolation.html?highlight=kernel%20density%20estimation#heatmap-kernel-density-estimation) (accessed 24 april 2021).
- qgistutorials.com, 2021. Creating Heatmaps (QGIS3). URL https://www.qgistutorials.com/en/docs/3/creating_heatmaps.html (accessed 20 april 2021).
- R Core Team, 2021. R: A language and environment for statistical computing (Version 3.6.0). R Found. Stat. Comput.
- Reconyx, 2015. Instruction Manual - Reconyx UltraFire XS8.
- Reinhardt, I., Kluth, G., Nowak, S., Mysłajek, R.W., 2015. Standards for the monitoring of the Central European wolf population in Germany and Poland, Bfn-Skripten, pp. 1-46.
- Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* 14, pp. 322–337. <https://doi.org/10.1198/jabes.2009.08038>
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* (80-.). 343, pp. 1–13. <https://doi.org/10.1126/science.1241484>
- Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecol. Lett.* 12, pp. 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Rossa, M., Lovari, S., Ferretti, F., 2021. Spatiotemporal patterns of wolf, mesocarnivores and prey in a Mediterranean area. *Behav. Ecol. Sociobiol.* 75, pp. 1-32. <https://doi.org/10.1007/s00265-020-02956-4>
- Sivy, K.J., Pozzanghera, C.B., Colson, K.E., Mumma, M.A., Prugh, L.R., 2018. Apex predators and the facilitation of resource partitioning among mesopredators. *Oikos* 127, pp. 607–621. <https://doi.org/10.1111/oik.04647>
- Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H., Haskell, J.P., 2003. Body mass of late quaternary mammals. *Ecology* 84, pp. 3403–3403. <https://doi.org/10.1890/02-9003>
- Soe, E., Davison, J., Süld, K., Valdmann, H., Laurimaa, L., Saarma, U., 2017. Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox *Vulpes vulpes*: a quantitative review. *Mamm. Rev.* 47, pp. 198–211. <https://doi.org/10.1111/mam.12092>
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M., Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2, pp. 75–92. <https://doi.org/10.1111/j.1523-1739.1988.tb00337.x>
- Steyaert, S.M.J.G., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J.E., Zedrosser, A., 2016. Human shields mediate sexual conflict in a top predator. *Proc. R. Soc. B Biol. Sci.* 283, pp. 1-7,

- <https://doi.org/10.1098/rspb.2016.0906>
- Sunde, P., Olsen, K., 2018. Ulve (*Canis lupus*) i Danmark 2012-2017 Oversigt og analyse af tilgængelig bestandsinformation - DCE – Nationalt Center for Miljø og Energi, pp. 1-7, <https://doi.org/10.13140/RG.2.2.24365.18403>
- Thomsen, P.F., Hansen, M.M., Olsen, K., Sunde, P., 2020. Genetiske analysemetoder i den nationale overvågning af ulv (*Canis lupus*) i Danmark. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, pp. 1-10 – Notat nr. 2020|43
- Thorsen, H., Olsen, K., Sunde, P., 2019. Danske ulves (*Canis lupus lupus*) døgnaktivitets- mønster studeret med brug af vildtkameraer. *Flora og Fauna* 125, pp. 1–11.
- Torretta, E., Serafini, M., Puopolo, F., Schenone, L., 2016. Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (N-W Italy). *Acta Ethol.* 19, pp. 123–132. <https://doi.org/10.1007/s10211-015-0231-y>
- Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J., Shanas, U., 2015. What is an apex predator? *Oikos* 124, pp. 1453–1461. <https://doi.org/10.1111/oik.01977>
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Golemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. *J. Open Source Softw.* 4, 1686. <https://doi.org/10.21105/joss.01686>
- Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., Liberg, O., 2014. Behavioral responses of wolves to roads: Scale-dependent ambivalence. *Behav. Ecol.* 25, pp.1353–1364. <https://doi.org/10.1093/beheco/aru134>

Appendix 1 – Data selection and data generation

1.1 Data selection

The data generation process started with the selection of camera trap placements (CTP). The camera trap placements with the longest continued time-period between 2017-19 was prioritized, from the most spatially distributed placements in the research area as possible. Especially three CTP were prioritized, because they were, according to the volunteers, hotspot placements, with activity from many different species.

1.2 Data generation

Following a deletion process of pictures and videos without a species present, often caused by faulty misfires because of shadows, plants moving or problems with the camera, the observations were added to a database using Microsoft Access, following a manual. Each CTP has a unique name, and each series of pictures between two camera control sessions is collected in a separate folder as a survey series. During a camera control session, the camera is checked for mistakes, problems with time and date and whether any misfires have occurred because of moving vegetation.

An observation is classified as a collection of pictures of one species taken by a camera during a five-minute period, but if more than one species is present, an additional observation is made and *overlapping observations* is added as a comment. It is noted down whether the camera control is seen in the beginning and end of each survey series, to check if the camera ran out of power or had other problems during the collection period.

For each observation added to the database a list of information is included from the pictures and video. For observations including a human is only the time, night or day, number of individuals and the activity noted down (vehicle, cyclist, person, person with dog, horseback rider).

- Time of observation
- Species or species group (e.g., ungulate sp. or mustelid sp.)
- How certain the observer is on the classification using SCALP-criteria explained in the text.
- Day or night, decided based on whether the observation is black/white or in color
- Number of individuals (one, group or female with offspring)
- If it is a countable observation, defined as an observation of a species done with more than one hour of the last observation of the same species, to account for whether the same individuals are just hanging out in front of the camera
- Age and sex, if possible, for the specific species

- The behavior of the individual based on a behavioral definition chart or ethogram from the manual

Behavior	Definition
Vigilance	Standing still with its head held parallel to body or higher, looking around and/or twitching the ears. Hares can also press their body close to the ground
Foraging	Includes grazing, browsing, carnivores with prey/ looking for prey.
Walking	Walking without eating, getting from A to B (skridt/trav)
Running	Quick movement in the observation, running from/to something (gallop).
Sudden rush	When an animal went from standing still to running – demand more than one picture or a video for this definition
Sniffing/explorer	Sniffing to scent source, animal have its head near the ground or objects without chewing or eating
Other behavior	All other behavior which isn't included in mentioned behaviors
Social behavior (all interactions)	Social interaction between animals, touching/rubbing heads, aggression/fighting, social play, mating
Marking	Marking with urine, scent canals and/or scratching/rubbing on the ground or on/at threes.
Checking camera	Walking towards camera, sniffing it

Appendix 1, 2: Ethogram table obtained from the unpublished manual, used to decide an individual's behavior. The categories are modified from behaviors defined in (Kuijper et al., 2014) ("What cues do ungulates use to assess predation risk in dense temperate forest?").

Appendix 2 – Additional tables

2.1 – Pearson's correlation of variables from Table 3 and Table 6

	House distance	Road distance	Forest distance	Mean vegetation height
House distance	1	0.235	0.081	0.125
Road distance	0.235	1	-0.093	0.196
Forest distance	0.081	-0.093	1	-0.145
Mean vegetation height	0.125	0.196	-0.145	1

Appendix 2, 1: Pearson's correlation test of the four habitat variables used in Table 3 and Table 6.

2.2 – Pearson's correlation of variables used in Table 10.

	Human activity	Mean vegetation height	House distance	Road distance	Forest distance	wolf activity / number of observations	(wolf activity / number of observations) * number
Human activity	1	0.212	-0.181	-0.241	-0.036	0.093	0.105
Mean vegetation height	0.212	1	0.125	0.196	-0.145	-0.026	0.045
House distance	-0.181	0.125	1	0.235	0.081	-0.372	-0.271
Road distance	-0.241	0.196	0.235	1	-0.093	0.151	0.134
Forest distance	-0.036	-0.145	0.081	-0.093	1	-0.021	-0.009
Wolf activity / number of observations	0.093	-0.026	-0.372	0.151	-0.021	1	0.942
(wolf activity / number of observations) * number	0.105	0.045	-0.271	0.134	-0.009	0.942	1

Appendix 2, 2: Pearson's correlation test of variables from Table 10. Correlated variables in grey.

Appendix 3 – QGIS work

3.1 Heatmaps of wolf activity

The heatmap work done in QGIS, included several steps before the final method was found.

To represent the variation in wolf activity most precisely, we decided to include more than just camera trap (CT) observations. We wanted to also include confirmed scat samples from Ulfborg territory, and we wanted to divide the data into 3-month or 6-month periods, to get a better representation of wolves use of the territory. We tested whether it would be feasible to combine the two observation types for the analysis and divide the data in smaller periods, by creating heatmaps for each observation type in 6-month periods, extracting the values to each of our camera traps in dataset A and did a Pearson’s correlation matrix. For both CT and scat observations separately in a 6-month, there were gaps in the distribution of observations, which meant that there were NA observations in the heatmap-values, to be able to do a correlation matrix, NA values was substituted with a 0. There were so few observations in the winter period between 16-17, that they could not be included in the correlation matrix at all (appendix 3.2). The correlation matrix showed correlation between the two observation types, and they were therefore combined (appendix 3.3). A visual presentation of each 6-month period with the combined observation types (appendix 3.4) and human activity (appendix 3.5) was made.

3.2: Correlation matrix two observation type

Pearson’s correlation matrix of camera trap and scat data from each 6-month period.

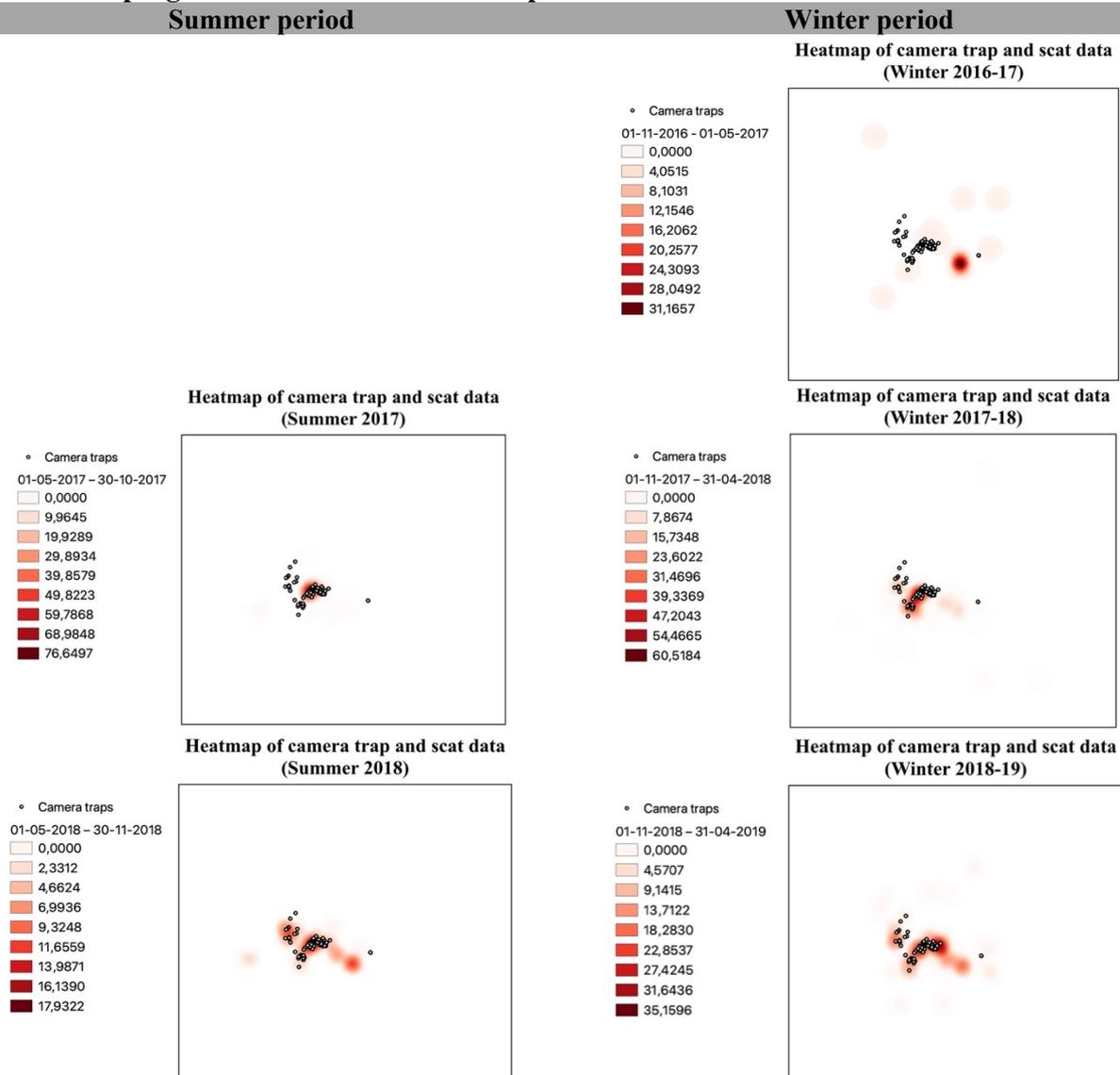
	Summer 2018 CT	Winter 2018-2019 CT	Summer 2019 CT	Winter 2019-2020 CT	Summer 2018 scat	Winter 2018-2019 scat	Summer 2019 scat	Winter 2019-2020 scat	Summer 2017 CT	Winter 2017-2018 CT	Summer 2017 scat	Winter 2017-2018 scat
Summer 2018 CT	1	0.526	-0.316	0.015	0.463	-0.211	-0.498	-0.1837	0.7685	0.4929	0.651	0.710
Winter 2018-19 CT	0.526	1	0.274	0.724	0.695	0.598	0.002	0.547	0.692	0.226	0.722	0.646
Summer 2019 CT	-0.316	0.274	1	0.600	0.109	0.614	0.906	0.810	0.089	-0.673	0.211	-0.166
Winter 2019-20 CT	0.015	0.724	0.600	1	0.431	0.816	0.401	0.863	0.237	-0.264	0.346	0.039
Summer 2018 scat	0.463	0.695	0.109	0.431	1	0.606	-0.107	0.486	0.815	0.493	0.840	0.777
Winter 2018-19 scat	-0.211	0.598	0.614	0.816	0.606	1	0.411	0.886	0.260	-0.137	0.421	0.162
Summer 2019 scat	-0.498	0.002	0.906	0.401	-0.109	0.411	1	0.622	-0.151	-0.664	-0.057	-0.343
Winter 2019-20 scat	-0.184	0.547	0.810	0.863	0.486	0.886	0.622	1	0.278	-0.420	0.413	0.010
Summer 2017 CT	0.769	0.692	0.089	0.237	0.815	0.260	-0.151	0.278	1	0.355	0.973	0.876
Winter 2017-18 CT	0.493	0.226	-0.673	-0.264	0.493	-0.137	-0.664	-0.420	0.355	1	0.257	0.684
Summer 2017 scat	0.651	0.722	0.211	0.345	0.840	0.421	-0.057	0.413	0.973	0.257	1	0.825
Winter 2017-18 scat	0.710	0.646	-0.166	0.039	0.777	0.162	-0.343	0.010	0.876	0.684	0.825	1

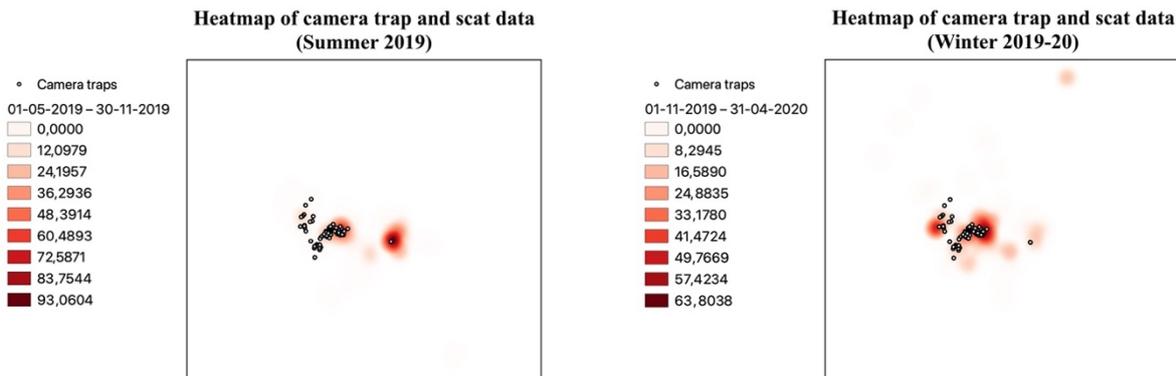
3.3: Correlation matrix for combined observations in 6-months periods

Pearson's correlation matrix of combined camera trap and scat data from each 6-month period.

	Summer 2017	Winter 2017-18	Summer 2018	Winter 2018-19	Summer 2019	Winter 2019-20
Summer 2017	1	0.814	0.846	0.641	0.085	0.275
Winter 2017-18	0.814	1	0.787	0.515	-0.288	-0.033
Summer 2018	0.846	0.787	1	0.487	-0.270	0.064
Winter 2018-19	0.641	0.515	0.487	1	0.371	0.798
Summer 2019	0.085	-0.288	-0.270	0.371	1	0.675
Winter 2019-20	0.275	-0.033	0.064	0.798	0.675	1

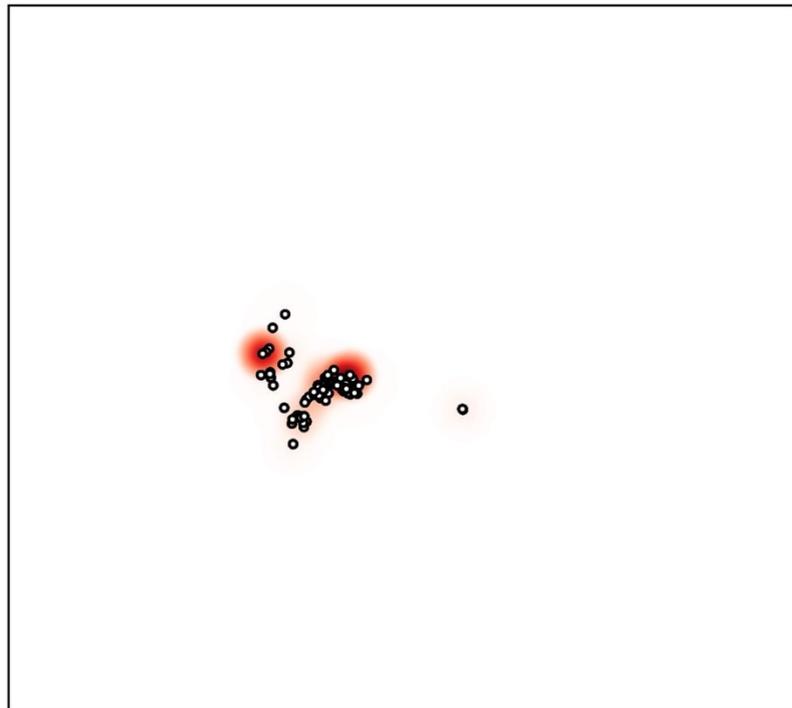
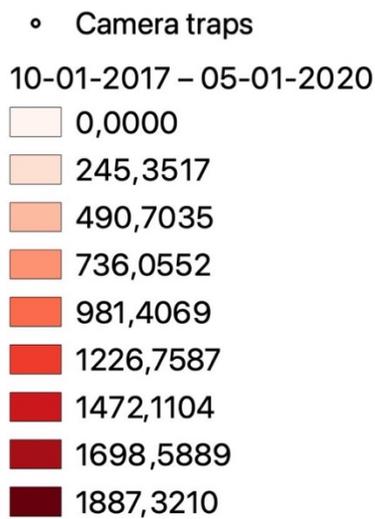
3.4: Heatmap figure of winter and summer periods





3.5: Figure of human activity heatmap

Heatmap of human activity (2016-2020)



Appendix 4 – R code

Will be provided in a zip folder.