Faculty of Applied Ecology, Agricultural Sciences and Biotechnology (A-EAB)

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PhD Thesis

Determinant factors for mesocarnivore distribution patterns along a gradient of anthropogenic influence

Phd in Applied Ecology

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“…

To survive
we'd all turn thief

and rascal, or so says the fox,
with her coat of an elegant scoundrel,
her white knife of a smile,
who knows just where she's going:

to steal something
that doesn't belong to her -
some chicken, or one more chance,
or other life.”

© Margaret Atwood

From ‘*Morning in the Burned House*’

Preface

This was a hard one. When I started, I thought that the effort put on this against the time since the beginning would be very much like a type III functional response. Heck, no. It was a type I tending to infinity. It was worth it after all.

Who to start thanking for it? Probably is best to start with the people who made possible for me to set a foot on Evenstad in the first place. Maybe they do not remember, but Barbara Zimmerman and Lucrezia Gorini, international coordinators at the time, managed to turn the right knobs to allow me to stay at Evenstad with an internship that was not meant for universities. Thank you!

Next came Morten Odden, and he stayed there for the following years. What can I say? I think no one has ever put so much faith on me knowing me just barely. As a boss, as a supervisor, and as a friend, he always bet for me. And there were so many things. There was Byttingarna, there were family restaurants in India, there were burger joints in Australia. Huge thanks to you.

Many thanks to all the students and field workers I have had under my wing these years. I had so many good moments with you guys… and so many headaches… Sometimes I felt like Papa Smurf, bringing wisdom to his little smurfs, sometimes like the father of a bunch of wretched teenagers, and sometimes like the United Nations, trying to handle so many different nationalities. But it was a lot of fun.

Thanks to all the people I have been working with in the field over these years. Abi Tamin Vanak, Abhijeet Kulkarni and the Indian crew made me feel so welcomed in such a distant place. I had so many good moments riding through the field with Abhimanyu Lele. And a very special thanks to Bosse Soderberg, who made my visits to Sweden so enjoyable. You are a wonderful person.

Huge thanks to my comrades in arms, current and past fellow PhD students. It has been really nice working side by side with you. Madhu Chetri, Zea Walton, Degitu Borecha, Cicik Udayana, of course Marcel Shcrivjers (I will exchange one of my printed thesis for you lichen book), everyone that has been there and those that just started. I can assure you there is a light at the end of the tunnel, what I am not sure yet is about what lies ahead… Those that managed to go through, Obeyd Mahenya, Nuria Fandos, Torffin Jahren, I feel you now. Of course many thanks to Kaja Johnsen, who helped me with the translation of my abstract into Viking. And a special thanks to Cyril Milleret, who has been more than a friend. He has been a reviewer, and a really hard one. In spite of that, you are a very special friend.

Thank you to all the stuff and to the Evenstad community. That family feeling turned Evenstad from the home away from home to the home I was away from. Special thanks to Olivier Devineau, my statistics guru and supporting friend.

Saying that this would have been impossible without having Rocío Cano by my side is simply understating it. I would not be here and I would not be who I am if it was not for her. This last period of my Phd unleashed my monster within. She stoically tamed it. I am officially starting a religion worshiping her. I love you Rocío.

If this religion will worship Rocío, she will be standing right next to my parents. And this next bit comes in Spanish.

Una de las principales fuentes de energía que me han mantenido en pie tan lejos de mi tierra ha sido la perspectiva de una buena lumbre, un brasero y una copa de mistela. De llegar a la cueva en un día de calor. De la familia alrededor de un buen arroz o una lata de cordero. De una noche vieja con veinte personas con la misma sangre. Y es que la familia tira mucho. Os quiero a todos. Pero quiero más a mi padre y a mi madre, qué le vamos a hacer. No estaría aquí si no fuera por mi padre, que me enseñó las recompensas del trabajo duro, y sobre todo me enseñó a amar todo bicho viviente. Todo eso te lo debo a ti. Tampoco estaría aquí si no fuese por mi madre, que me dio el amor a la lectura, a crear y a ver el lado bueno de las cosas. Todo eso te lo debo a ti. Buen trabajo a los dos. Os quiero.

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Sammendrag

Økning i den menneskelige befolkningen og klimaforandringer kan påvirke utbredelsen, sammensetning, og bevegelsesmønster hos viltlevende dyr, og endre ulike arters realiserte nisje. Effekten av disse endringene på arter med en bred nisje er vanskelig å forutsi. Dette gjelder først og fremst arter som er hovedsakelig generalister, slik som de mellomstore predatorene. Med tanke på deres sentrale posisjon i næringsnettet, kan endringer i populasjonen påvirke både høyere og lavere trofiske nivåer. Det er derfor veldig viktig å forstå hvordan disse artene responderer på disse endringene. I denne avhandlingen har jeg studert rødrev *Vulpes vulpes* og Indisk rev *Vulpes bengalensis*, som typiske mellomstore predatorer, i en gradient av menneskelig påvirkning. Hovedmålet mitt var å identifisere de viktigste faktorene som påvirker utbredelse og bevegelsesmønster, og hvordan disse faktorene påvirker hverandre. Jeg undersøkte hvordan abiotiske faktorer påvirket byttedyrtilgangens effekt på utbredelsen av rødrev i områder med liten menneskelig påvirkning. I mer befolkede områder så jeg på hvordan menneskelig aktivitet påvirker oppdagbarheten av rødrev, og smitte av sykdommen skabb. I områder med høy menneskelig tetthet så jeg på hvordan mennesker påvirket habitatbruk og interaksjoner mellom Indisk rev og andre mellomstore predatorer i området. Jeg fant ut at menneskeskapte ressurser, enten gjennom en økt tilgang til åtsler eller gjennom en økt tilgang til menneskemat, er en av de viktigste menneskeskapte faktorene som påvirker mellomstore predatorer. En økt tilgang til kadaver av hjortevilt eller slakteavfall som en konsekvens av tamreindrift og jakt, kan øke tilstedeværelsen av rødrev i habitat med lav ressurstilgang eller øke oppdagbarheten i mer urbane områder. Samtidig kan en økt tilgang til menneskeskapte ressurser øke faren for smitte av skabb hos rødrev, og tiltrekke seg andre arter av mellomstore predatorer, slik som sjakal og jungle cat. Videre fant jeg ut at graden av å spesialiserer seg innen et habitat er viktig for å predikere hvordan en art responderer på menneskelig tilstedeværelse. For eksempel vil tap av habitat og tilstedeværelsen av arter assosiert med mennesker (f.eks. hunder) påvirke habitatbruk hos den habitatspesialiserende Indisk reven negativt. I motsetning til dette var mer opportunistiske arter i området positivt påvirket av menneskelig tilstedeværelse. For å konkludere så ser det ut som at mennesker kan ha både en positiv og en negativ effekt på mellomstore predatorer, og deres tilstedeværelse og påvirkning bør vurderes som en del av økosystemet, selv i uforstyrrede habitater med lav ressurstilgang.

Abstract

Human expansion and climate change may influence the distribution, community structure, and activity patterns of wildlife and alter the realized niche of the species. The response of species with a wide niche breath to these changes may be diverse and difficult to predict. This is the case of predominantly generalized species like mesocarnivores. Given the central position in the food web of these species, changes in their populations may influence upper and lower trophic levels. Therefore, understanding their responses is of crucial importance. In this thesis, I studied the red fox *Vulpes vulpes* and the Indian fox *Vulpes bengalensis* as representative of the mesocarnivore community, in a gradient of anthropogenic influence. My main goal was to identify the main factors determining their distribution and activity patterns and investigate how these factors interacted with each other. I studied how the abiotic factors affected the influence of prey availability on the distribution of red foxes in marginal habitats of low human impact. In more developed areas, I studied how human activity influenced the detectability of red foxes and the transmission of a wildlife disease, the sarcoptic mange. In highly human dominated areas, I studied how the influence of humans affected the habitat use and the interspecific interactions of Indian foxes. I found that human subsidization of mesocarnivores, through an increased availability of carcasses or through an increased access to anthropogenic food, is one of the most important human-driven factors affecting mesocarnivores. An increased availability of ungulate carcasses or hunting remains consequence of the herding of semidomestic reindeers and hunting activity may increase the presence of red foxes in marginal habitat or increase their detectability in more developed areas. Likewise, an increased access to anthropogenic food may facilitate the transmission of sarcoptic mange in red foxes and attract other mesocarnivore species like jackals *Canis aureus* and jungle cats *Felis chaus*. Furthermore, I found that the degree of habitat specialization is important when predicting the response of a species to human influence. For example, habitat loss and the presence of species associated with humans (e.g. domestic dog) affected negatively the habitat use of Indian fox, which showed some habitat specialization. In contrast, more opportunistic species of that assemblage were positively affected by human presence. In conclusion, humans may have a positive or negative effect on mesocarnivore species and their influence should be considered intrinsic in the ecosystems even in apparently undisturbed marginal habitats.

Key words:

Vulpes vulpes, Vulpes bengalensis, distribution, activity patterns, human impact, mesocarnivore, wildlife disease, interspecific interactions, detectability, food subsidization.

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List of publications

This thesis is based on the following original publications and manuscripts:

I. Spatial and temporal variation in the distribution and abundance of red foxes in the tundra and taiga of northern Sweden. Carricondo-Sanchez, D., Samelius, G., Odden, M., & Willebrand, T. (2016). *European Journal of Wildlife Research, 62*(2), 211-218. doi:10.1007/s10344-016-0995-z

II. Seasonal variation in detection probability of red foxes along an environmental gradient in southern Norway. Carricondo-Sanchez, D., Odden, M., Devineau, O., Cano-Martinez, R., Linnell, J.D.C., & Odden, J. Manuscript.

III. The range of the mange: Spatiotemporal patterns of sarcoptic mange in red foxes (*Vulpes vulpes*) as revealed by camera trapping. Carricondo-Sanchez, D., Odden, M., Linnell, J. D. C., & Odden, J. (2017). *PLoS One, 12*(4). doi:10.1371/journal.pone.0176200

IV. Co-occurrence of meso-carnivores in a human dominated landscape in Maharashtra, India. Carricondo-Sanchez, D., Odden, M, Kulkami, A., & Vanak, A.T. Manuscript.

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1. Introduction

1.1. Niche concept and the distribution of species

The range of abiotic conditions and food resources that a species requires to survive and reproduce is called the fundamental niche (Hutchinson, 1957). However, a species may not be able to express its fundamental niche because interspecific interactions such as predation or competition may limit its expansion and use of the resources (Hutchinson, 1957; Malanson, Westman, & Yan, 1992). The part of the fundamental niche that a species is limited to use is called the realized niche (Hutchinson, 1957), and the study of the factors that influence it often aims to predict the outcomes of conservation and restoration actions (Guisan & Zimmermann, 2000; Margules & Pressey, 2000).

Changes in predation pressure or competition over resources may alter the realized niche of a species (Elbroch, Lendrum, Newby, Quigley, & Thompson, 2015). Furthermore, other biotic interactions such as facilitation may contribute to expand it (Bruno, Stachowicz, & Bertness, 2003). Alterations in the realized niche of a species may be manifested as changes in its geographic distribution or activity pattern as they are correlated with the former (Guisan & Zimmermann, 2000; Ilse & Hellgren, 1995; Soberon, 2007).

Human expansion and climate change may influence the distribution, community structure, and activity patterns of wildlife (Benitez-Lopez, Alkemade, & Verweij, 2010; Walther et al., 2002). Geographical ranges of many species have contracted (Laliberte & Ripple, 2004; Parmesan, 2006), some species have changed their behavior due to human interference (Frid & Dill, 2002), and human activity have altered wildlife community structures (Oro, Genovart, Tavecchia, Fowler, & Martinez-Abrain, 2013; Ruiz-Capillas, Mata, & Malo, 2013).

The response to environmental alterations by species with a narrow niche breath (i.e. specialized species) may be straightforward and easier to anticipate. However, species with a wide niche breadth (i.e. generalist species) have a higher plasticity that allow them to adapt rapidly to these changes in a variety of ways, and therefore, their response is less predictable. Mesocarnivores are typically described as generalist species. Given the role of these species in the ecosystem, changes in their distribution and activity patterns may influence other components of the ecosystem. Hence, understanding the consequences of these changes is of crucial importance.

1.2. Mesocarnivores in ecosystems

What is a mesocarnivore?

In recent years, scientists have paid increased attention to the study of mesocarnivore communities. A search of 'mesocarnivore' (and derivates, e.g. meso-carnivore, mesopredator or meso-predator) in the Web Of Science reveals that the term was first mentioned as far back as 1995 (Goodrich & Buskirk, 1995). However, the use of the term has incremented exponentially during the last decade (Fig 1).

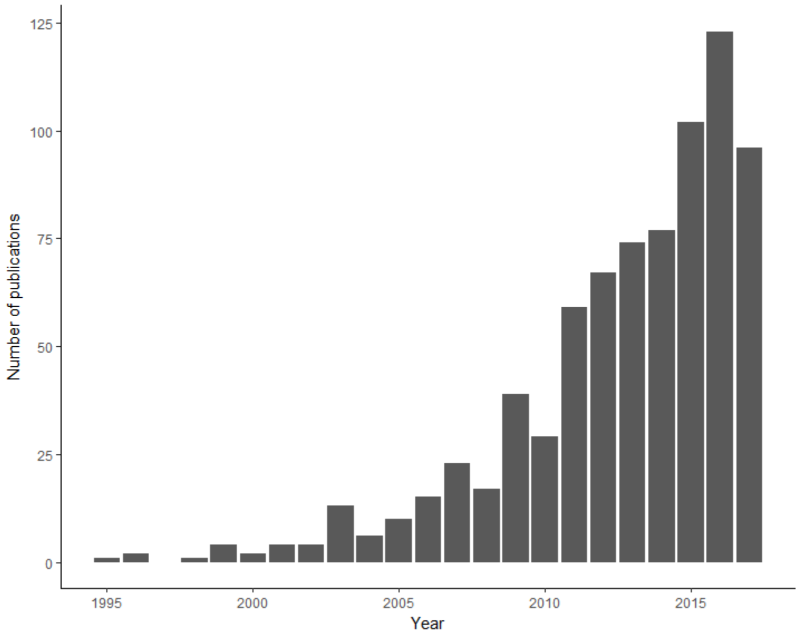

Figure 1. Histogram depicting the number of publications per year based on the search of "(mesocarnivore$ OR (meso-carnivore$ OR (mesopredator$ OR meso-predator$)))" in Web of Science accessed the 23th of October, 2017.

This increase was probably a result of an emerging realization of the important role of mesopredator communities in the ecosystems and the responsibility of humans in the recent changes experienced by these species. Anthropogenic food subsidization, hunting, habitat alteration or climate change are some examples of the human driven factors affecting aspects of these species such as distribution, abundance or activity patterns (Elmhagen et al., 2017; T. M. Newsome et al., 2015; Prugh et al., 2009; Ritchie & Johnson, 2009).

In spite of the escalation in popularity of the term, there is not a clear consensus of its definition. For example, Roemer, Gompper, and Van Valkenburgh (2009) referred to mesocarnivores as small or and medium species with a body weight lower than 15 kilograms. According to their diets, Van Valkenburgh (2007) defined mesocarnivores as carnivores with a diet consisting of about 50 to 70% of meat, and the rest composed of invertebrate material (e.g. plants, fungi, insects). In terms of their position in the trophic pyramid, they can be defined as predators that are at a lower position than apex predators, thus adding an ecosystem-specific dimension to the definition (Prugh et al., 2009; Ritchie & Johnson, 2009). In this context, mesocarnivores can sometimes take the role of the apex predator. Such is the case in otters (*Lontra canadensis*) in freshwater systems (Gittleman & Gompper, 2005) or coyotes (*Canis latrans*) in ecosystems absent of larger predators (Crooks & Soule, 1999). For the purpose of this thesis, I will regard a carnivore species or a community as mesocarnivore if it occupies an intermediate position in the food web.

From specialists to generalists

Mesocarnivores range from specialist predators to generalists and facultative predators. Some species like weasels (*Mustela nivalis*) and stoats (*Mustela erminea*) base their diet almost solely on rodents (Jedrzejewski & Jedrzejewska, 1993). However, more common are the cases where a marked generalist character govern the feeding behavior of the mesocarnivore. Examples of this are the raccoon dog (*Nyctereutes procyonoides*) or the pine marten (*Martes martes*), which are considered true generalist species (Jedrzejewski, Zalewski, & Jedrzejewska, 1993; Kauhala, Laukkanen, & von Rege, 1998). In some cases, a single species can display different levels of opportunism in different parts of its distribution range. Badgers (*Meles meles*), for instance, are considered to be overall food generalist (Roper, 1994). However, in some parts of Britain or certain habitat types in Spain, the badger can act as a specialist predator of earthworms (Kruuk & Parish, 1981; Virgos et al., 2004). Moreover, in some species, whether an individual is prone to exhibit specialist or generalist behaviors depends on prey availability. Genets (*Genetta genetta*), for example, although regarded as specialist predators of wood mice (*Apodemus sylvaticus*) in the Balearic islands, vary their diet seasonally and in different islands depending on prey availability (Clevenger, 1995). In northern ecosystems where seasonality is pronounced and the abundance of microtine rodents fluctuate among years, the diet of red foxes (*Vulpes vulpes*) varies according the availability of this prey (Jedrzejewski & Jedrzejewska, 1992).

Role and importance in ecosystems

The wide niche breadth of mesocarnivores allow them to influence different species in different trophic levels in the ecosystems. One of the main functions of the mesocarnivore community is the top down control of prey species. For example, experimental removal of predators in western Finland manifested an additive effect of the mesocarnivore community on the densities of small rodents (Korpimaki & Norrdahl, 1998). In some carnivore assemblages, mesocarnivores may also reduce the abundances of smaller competitors. A reduction of island foxes in Santa Cruz and Santa Rosa islands due to an increased predation by golden eagles (*Aquila chrysaetos*) led to an increase in its inferior competitor, the island spotted skunk (*Spilogale gracilis amphiala*) (Roemer, Donlan, & Courchamp, 2002). A good example of effects on both prey and competitor took place during the outbreak of sarcoptic mange on red foxes in Fennoscandia in the decades of the 1970s and 1980s. The outbreak reduced the red fox population by 90% in some areas. The population decline was followed by an increase in several prey species such as the carpercaillie

(*Tetrao urogallus*), black grouse (*Tetrao tetrix*), and mountain hares (*Lepus timidus*), and an increase in a competitor predator, the pine marten (*Martes martes*) (E. R. Lindström, Brainerd, Helldin, & Overskaug, 1995).

The indirect effect of mesocarnivores on other trophic levels is less clear. According to the cascading effects concept, an increase in the abundance of a predator can lead to a reduced herbivory and therefore an increase in the abundance of the primary producers (Hairston, Smith, & Slobodkin, 1960). In relatively simple linear trophic models consisting of a predator, a prey, and a primary producer species, this relationship is more apparent, and the removal of the predator may trigger a trophic cascade (Ripple et al., 2014). For example, the reduction of sea otters (*Enhydra lutis*) abundance by killer whale predation in Alaska led to an increase in sea urchin biomass. In turn, the overgrazing by sea urchins resulted in a loss of kelp forests (Estes, Tinker, Williams, & Doak, 1998). Another example arose when the introduction of Artic fox in the Aleutian archipelago indirectly altered the vegetation community by reducing the seabird community that transferred nutrients to the soil (Croll, Maron, Estes, Danner, & Byrd, 2005). Adding compositional complexity will weaken this effect, for instance when a predator species is replaced by another within a carnivore assemblage composed of several competitive species (Gompper, Lesmeister, Ray, Malcolm, & Kays, 2016).

Abiotic factors may also influence the top-down effects of the mesocarnivores in the ecosystem. Fluctuations in the climate, for instance, may lead to an increase in the bottom-up effects on the consumers by an increase in the primary producers. The increase might shadow, to some extent, the top-down effect of mesocarnivores (Ims & Fuglei, 2005; Meserve, Kelt, Milstead, & Gutierrez, 2003; Norrdahl, Klemola, Korpimaki, & Koivula, 2002). Likewise, other factors such as snow conditions may affect the predator directly and reduce the top-down effect by decreasing predation pressure (Barton & Zalewski, 2007).

Beyond top-down effects on the prey species, mesocarnivores have other important roles in the ecosystems. For example, they can function as seed dispersers (Willson, 1993). This dispersion can occur either by direct consumption of fruits (Koike, Morimoto, Goto, Kozakai, & Yamazaki, 2008), or by secondary seed dispersal (i.e. by consumption of the primary seed disperser) (Hamalainen et al., 2017). Certainly, mesocarnivores can transport seeds longer distances than other dispersers such as passerine birds (Jordano, Garcia, Godoy, & Garcia-Castano, 2007).

More importantly, mesocarnivores may play an important role in disease dynamics. Wildlife diseases are an increasing problem due to the threat they represent to wild and domestic species, livestock, and humans (Daszak, Cunningham, & Hyatt, 2000; Gortazar, Ferroglio, Hofle, Frolich, & Vicente, 2007). Midsized carnivores are susceptible and in many cases reservoirs of zoonotic diseases like sarcoptic mange or parvo-, rabies and distemper viruses (PRD) among others (Bornstein, 2001; Laurenson et al., 1998; Nel, Jacobs, Jaftha, & Meredith, 1997). The threat of these zoonoses lies in the potential spillover, and cross-species transmission (Kolodziej-Sobocinska, Zalewski, & Kowalczyk, 2014; Nel et al., 1997). Mesocarnivores can also play a role in the dynamic of other diseases by controlling populations of intermediate host (Levi, Kilpatrick, Mangel, & Wilmers, 2012).

Because of the wide diversity of roles that the mesocarnivore community play in ecosystems, the understanding of the mechanisms that govern their distribution patterns is of crucial importance. Moreover, given our direct or indirect responsibility in the alteration of these roles, humans have a responsibility towards a sound management of these species.

1.3. Factors affecting the distribution and activity patterns of mesocarnivores.

Some factors shape the fundamental and realized niche of mesopredatores and consequently affect their distribution and activity patterns.

Importance of prey, the landscape, and other abiotic factors

The abundance or the distribution of a natural prey species may affect the distribution and movement patterns of a mesocarnivore (Burton, Sam, Balangtaa, & Brashares, 2012; Mortelliti & Boitani, 2008; Soykan & Sabo, 2009). Likewise, the distribution of other allochthonous food resources such as marine subsidies can be an important factor influencing the presence of the carnivore (Killengreen et al., 2011; Rose & Polis, 1998).

The structure of the landscape is also important to explain the distribution of the species. For example, mesocarnivores can select their habitat according to their potential to offer shelter and avoid larger predators (Mangas, Lozano, Cabezas-Diaz, & Virgos, 2008). The size of the habitat patch or the connectivity between patches are also important in the distribution and expansion of mesocarnivores (Andren, 1994).

Moreover, some abiotic factors affecting the landscape will also affect the distribution, abundance or activity patterns of mesocarnivores including snow conditions (Pozzanghera, Sivy, Lindberg, & Prugh, 2016; Thibault & Ouellet, 2005), distance to a water source, or temperature (Cuyckens, Perovic, & Cristobal, 2015).

Importance of intraguild interactions

Interactions between different species of the carnivore guild may affect the spatiotemporal distribution of mesocarnivores. Common ones are interference competition, exploitative competition or intraguild predation (Palomares & Caro, 1999). In order to avoid these interactions, the subordinate competitor may alter its distribution or activity patterns by spatial niche partitioning (Berger & Gese, 2007; Hersteinsson & Macdonald, 1992) or by temporal niche partitioning (Carothers & Jaksic, 1984; Monterroso, Alves, & Ferreras, 2014).

Importance of diseases

Zoonosis affecting wildlife often have a strong impact on the host species. For example, outbreaks can severely reduce the abundance and alter the population age structure of the species (McCallum et al., 2007; Mörner, 1992), or cause local extinctions (Ginsberg, Mace, & Albon, 1995). At the individual scale, wildlife diseases may cause a detriment of the body condition of the host (Newey, Thirgood, & Hudson, 2004; Newman, Baker, & Harris, 2002). In mesocarnivores, a detriment in the body condition might lead to a reduced hunting success and thus, to alterations in the movement and activity patterns (Todd, Gunson, & Samuel, 1981).

1.4. Human impact and changes in mesocarnivore communities

The influence of humans in the distribution, community structure or behavior of the wildlife species increases with human expansion (Benitez-Lopez et al., 2010; Walther et al., 2002). The shape and direction of these effects, however, will vary markedly among wildlife species. For example, habitat fragmentation can affect different species positively or negatively (Fahrig, 2003). Whereas generalist species can be favored by some degree of habitat fragmentation (Andren, 1994), fragmentation may affect negatively other species (i.e. Cougar (*Puma concolor*)) (Beier, 1995). This variety of responses of wildlife to the influence of humans is mirrored in the mesocarnivore community and hinge on the species, the population or the community affected. Although all the effects derived from human activity are somehow interrelated and nested within each other, we can distinguish five different types of impact:

Anthropogenic subsidization

Subsidization of wildlife species by anthropogenic food can have consequences for wildlife at the individual, population, and ecosystem levels (Oro et al., 2013). Given their role in the ecosystems, subsidization in predator species is particularly dire (Gompper & Vanak, 2008; T. M. Newsome et al., 2015). The availability of human waste, hunting remains or livestock can alter traits of predators by changing movement patterns and home range sizes (Bino et al., 2010; Newsome, Garbe, Wilson, & Gehrt, 2015), increasing abundances (Fedriani, Fuller, & Sauvajot, 2001) or altering interspecies interactions (Fernandez-Olalla et al., 2012). Intensive farming, for example, can subsidize and increase the abundance of mesocarnivores, which in turn, will increase the pressure on the prey (Shapira, Sultan, & Shanas, 2008).

Habitat alteration

Loss and fragmentations of the natural habitat caused by agriculture expansion and urban development are threats for wildlife species (Saunders, Hobbs, & Margules, 1991). In general, the size of the habitat patch and the connectivity between suitable habitats are positively associated with the presence of mesocarnivores (Andren, 1994). However, mesocarnivores show species-specific responses to habitat fragmentation (Gehring & Swihart, 2003). For example, habitat fragmentation may involve a loss of the natural habitat of the mesocarnivore, and thus, influence negatively the species by isolating populations (Dharmarajan, Beasley, Fike, & Rhodes, 2014). Conversely, fragmentation can also contribute to the creation of edge habitat, which can be preferred by some mesocarnivores as they offer cover and food requirements (Magrini et al., 2009; Salek, Kreisinger, Sedlacek, & Albrecht, 2010). Nevertheless, although in some cases some degree of fragmentation can favor the species, surpassing certain levels can be detrimental (Caryl, Quine, & Park, 2012). Habitat fragmentation and habitat loss produce heterogeneity in the landscape. The preference of a homogeneous or a rather heterogeneous landscape might depend on the degree of habitat specialization and how mobile is each species (Gehring & Swihart, 2003).

Direct interference

The direct presence of humans (e.g. hikers, cyclist, dog walking, etc.) in areas utilized by wildlife may affect the activity patterns of the resident species (Steven, Pickering, & Castley, 2011; Taylor & Knight, 2003). This is especially true regarding species sensitive to human disturbance like carnivores (George & Crooks, 2006; Woodroffe, 2000). The persistence of this human presence over time might lead to either the extinction of a species in that location or the recolonization of a previously absent species (Rota et al., 2016; Schuette, Wagner, Wagner, & Creel, 2013).

Likewise, the impact of human urbanization and expansion of human infrastructures (e.g. roads, water canals, power lines) affect the presence of mesocarnivores in different ways depending on the susceptibility of the species (Ordenana et al., 2010; Ruiz-Capillas et al., 2013; Wang, Allen, & Wilmers, 2015). At a community level, human interference with wildlife and exurban expansion can also alter interspecific interactions (Rota et al., 2016; Wang et al., 2015).

Associated species

Frequently, native mesocarnivore communities have to coexist with species associated with humans such as domestic dogs and cats (Gehring & Swihart, 2003). Such interactions may have negative consequences for the mesopredator (Hughes & Macdonald, 2013; Vanak & Gompper, 2009). Studies have shown how domestic dogs interact with mesocarnivores as competitors (Butler, du Toit, & Bingham, 2004; Silva-Rodriguez, Ortega-Solis, & Jimenez, 2010), prey (Butler et al., 2004), predators (Campos, Esteves, Ferraz, Crawshaw, & Verdade, 2007), or by modifying their behavior through fear and interference (Vanak, Thaker, & Gompper, 2009). In other cases, domestic dogs can act as reservoirs of infectious diseases for the mesocarnivore community and therefore, represent a source of contagion for those species (Cleaveland et al., 2000).

Mesocarnivore release

The additive effect of all these factors can ultimately lead to the partial or total eradication of a species from certain areas of its natural range. For example, populations of large predators have experienced a reduction of their natural distribution worldwide mainly due to human development (Laliberte & Ripple, 2004; Morrison, Sechrest, Dinerstein, Wilcove, & Lamoreux, 2007). The removal of a top-down control over the mesocarnivore community in an ecosystem can trigger an increase in its abundance. This is a well-studied phenomenon called mesopredator release (Prugh et al., 2009; Ritchie & Johnson, 2009). For instance, areas in Australia where dingoes (*Canis lupus dingo*) were less abundant had higher densities of mesocarnivore prey, suggesting that dingoes kept red fox and cat populations low (Johnson, Isaac, & Fisher, 2007). Likewise, the control of smaller carnivores by coyotes in fragmented landscapes in California, reduced the predation pressure over birds species (Crooks & Soule, 1999).

1.5. *Vulpes* genera as a case of study

In this thesis, I use the genus *Vulpes* as a representative of the mesocarnivore community. This genus comprises eleven species distributed worldwide except for South America and Antarctica. In most of its range, the species of this genus are part of the mesocarnivore trophic level in their ecosystems (Sillero-Zubiri, Hoffmann, & Macdonald, 2004). Specifically, I focus this thesis on the red fox (*Vulpes vulpes*) and the Indian fox (*Vulpes bengalensis*).

The red fox has the largest distribution of carnivores worldwide (Lariviere & Pasitschniak-Arts, 1996). This large geographic range is a consequence of a generalist character that makes the red fox thrive in contrasting habitats like marginal natural areas or urban habitats highly influenced by the human presence (Macdonald & Reynolds, 2004). Moreover, red foxes feed opportunistically on different food sources that range from invertebrates, mammals, birds and fruits to carrion and anthropogenic food (Cagnacci, Lovari, & Meriggi, 2003; Macdonald & Reynolds, 2004; Plumer, Davison, & Saarma, 2014).

Contrary to the red fox, the Indian fox range is restricted to the Indian subcontinent (Gompper & Vanak, 2006). Regarding habitat use, Indian foxes prefer grassland and open scrub forest avoiding areas of dense vegetation, deserts and steep slopes (Johnsingh & Jhala, 2004). Nevertheless, they are somewhat tolerant to human disturbance and can be found close to villages or agriculture land (Gompper & Vanak, 2006). Similar to red foxes, Indian foxes are opportunistic feeders with a diet consisting mainly of insects, small rodents and small birds and their eggs (Johnsingh & Jhala, 2004).

2. Objectives

The variety of responses of the mesocarnivore community to the influence of humans and other factors is a reflection of their predominant generalist character. This peculiarity makes the study of these species challenging. The aim of this thesis is to investigate the responses of mesocarnivores to different conditions by studying a representative mesocarnivore genus, the *Vulpes* genus (particularly red fox and Indian fox). Specifically, this thesis will investigate **how the factors affecting the distribution and activity patterns of mesopredators interact with each other in a gradient of anthropogenic influence.** For that, I will address the following questions:

Is the influence of prey availability on the distribution of red fox affected by abiotic factors? The habitat use of red fox is, to a large extent, determined by prey availability (Cavallini & Lovari, 1991; Halpin & Bissonette, 1988). Nevertheless, abiotic factors also have an important role in the distribution of foxes (Barton & Zalewski, 2007; Halpin & Bissonette, 1988). In the first chapter, I investigate the interactive effect of prey availability and abiotic factors on the distribution of red fox in a marginal habitat (i.e. low quality habitat (Kawecki, 2008)) with a low level of anthropogenic disturbances.

Are the seasonal changes in the detectability of foxes influenced by human activity? Barton and Zalewski (2007) showed that winter severity is an important factor limiting densities of red foxes in Eurasia. Furthermore, activity patterns of red foxes are likely to vary across seasons (Cavallini & Lovari, 1991). Because the detection probability of a species is a function of its abundance and activity (i.e. movement rates, length of activity periods), changes in these components should also be reflected in the detectability of the species. In chapter two, I study the effect of seasonality in the detection probabilities of red foxes and investigate how this effect varies in a gradient of habitat productivity and human influence.

Are the distribution patterns of a wildlife disease influenced by human activity? Human populated areas can act as hotspot for wildlife diseases that ultimately can affect the distribution of mesocarnivores (Williams, Yuill, Artois, Fischer, & Haigh, 2002). In the third chapter, I examine the factors determining the distribution of sarcoptic mange in red foxes. Additionally, I depict the dynamic of sarcoptic mange outbreaks and its relationship with human population distributions.

Do humans influence the habitat use and the interactions between species in the mesocarnivore community? Interspecific interactions in the community affect the space use and the temporal activity of the mesocarnivores (Palomares & Caro, 1999; Ritchie & Johnson, 2009). In the fourth chapter, I study how intraspecific interactions shape the habitat use and activity patterns of a mesocarnivore assemblage in a heavily human dominated landscape in India.

3. Material and methods

3.1. Study areas, the anthropogenic gradient

The study areas represent a gradient of anthropogenic influence that consist of: (a) an area of marginal habitat in the northern Swedish tundra with low human impact, (b) an area dominated by boreal forest in south eastern Norway, with a moderate human influence, and (c) an area composed of highly human dominated landscapes in central India.

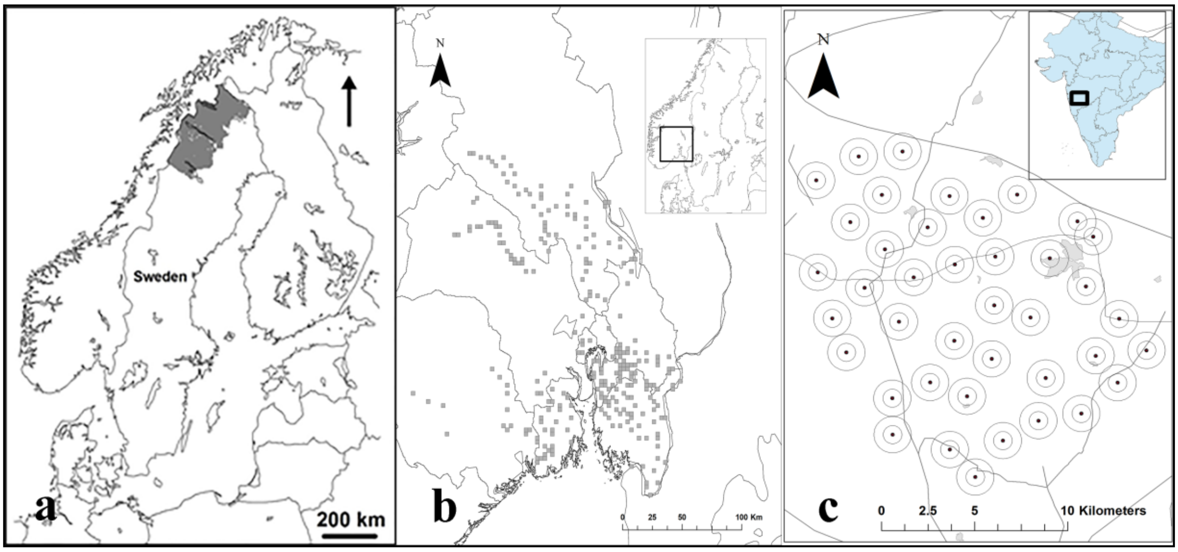

Figure 2. Locations of the different studies depicting a) Paper I study area in Northern Sweden highlighted in grey, b) Papers II and III study area in South Norway where the gray cells represent the 10km^2 grids where the cameras were located, and c) Paper IV study area in central India where dots are camera sites and circles depict buffer areas around the sites.

The study of the effect of prey availability and abiotic factors in the red fox distribution (**Paper I**) was conducted in northern Sweden (Fig 2a). The study area covered 65375 km^2 consisting mainly of open tundra, mountain birch *(Betulla pubescens tortuosa)* forest, and mixed boreal conifer forest. The population density was 0.33 inhabitants per km^2 (Statistics Sweden, www.scb.se), mainly concentrated in four townships. The herding of semi-domestic reindeer is extensive in the area.

I studied the seasonal variation in the detectability of red foxes and the effect of diseases on their distribution (**Paper II and III**) in southeast Norway (Fig 2b).

This study area extended for approximately 18000 km^2 covering parts of the counties of Oslo, Akershus, and Østfold. The mean population density was 34 inhabitants per km^2 (Statistics Norway, www.ssb.no). The study area covered an environmental gradient that ranged from suburban areas and fragmented forest with an agriculture matrix in the south to landscapes dominated by alpine areas and boreal forest in the north.

The study of the interactions within the mesocarnivore community (**Paper IV**) was carried out in a highly human dominated landscape of Maharashtra, India (Fig 2c). The study area covered 230 km^2 including several villages that belonged to the municipalities of Baramati and Daund, with 397 and 380 inhabitants per km^2 respectively (www.census2011.com). The area consisted of a matrix of sugarcane fields, seasonal crops, communal grazing land, small villages, and forestry plantations.

3.2. Data collection

Snow tracking

To study the effect of prey density and abiotic factors (**Paper I**), the presence and abundance of red fox and prey species (i.e. mountain hare, tetraonid species, small rodents, and ungulates) was monitored from 1974 to 1985 in 2080 sampling blocks of 25 km^2 in northern Sweden (Fig 2a). All the areas accessible with snow mobile in each sampling block was thoroughly searched (5.56 ± 0.10 km per sampling block) to detect signs of the focus species. Sampling blocks were monitored once every year. Average snow depth per sampling block was recorded and mean altitude was extracted from the National Land Survey of Sweden (www.lantmateriet.se). Additionally, I created an index of species richness defined as the number of different potential prey species in the sampling block.

Camera trapping in Norway

I used camera trapping data to study the effect of seasonality on the detectability (**Paper II**) and the role of diseases in the distribution (**Paper III**) of red foxes in southeast Norway (Fig 2b). Overall, I obtained data from 305 cameras traps covering the full extent of the study area (Fig 2b). The cameras were active from winter 2010/2011 to summer 2015.

To investigate the seasonal detection probabilities of foxes (**Paper II**), I used camera trapping data from December 2011 to December 2014 in order to obtain a balanced data across the years. I divided the year in three seasons according the red fox biology (Fig 3) and calculated the detectability of foxes defined as the daily probability of detecting a red fox per camera and season. I used variables related to human activity as potential predictors of the activity of foxes. I extracted agriculture areas and buildings from the NT50 map of Norway and populations densities from Statistics Norway (www.ssb.no). Then, I calculated their planar kernel densities with a bandwidth of the diameter of an average red fox home range in Scandinavia (95% MCP = 26 ± 6.7 km^2) (Walton, Samelius, Odden, & Willebrand, 2017). I also calculated the distance from the cameras to the closest urban area and the number of moose and red deer culled per square kilometer (www.ssb.no).

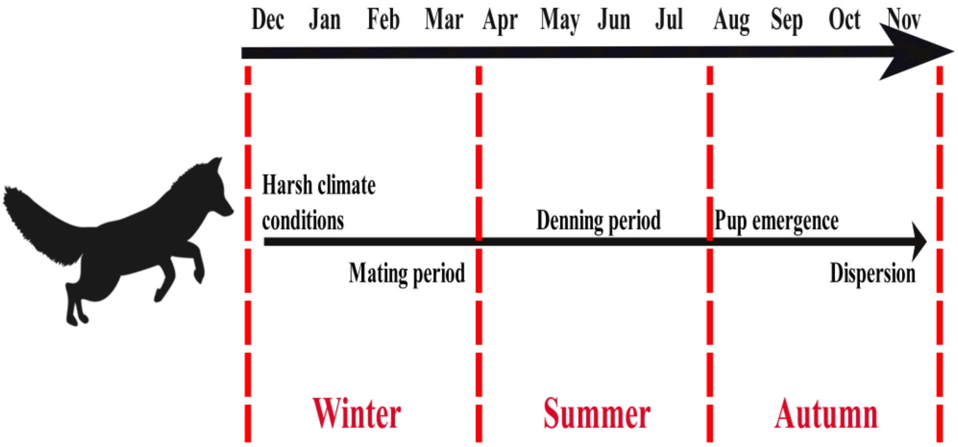

Figure 3. Justification of the three seasons defined according the biology of red fox for the study of the variations in red fox detections.

In order to explore the factors associated with the occurrence of sarcoptic mange in red foxes (**Paper III**), red fox photographic events were visually checked for lesions compatible with sarcoptic mange such as alopecia in the lower back and the tail of the fox (Fig. 4) (Oleaga et al., 2011). I used each red fox event as a Bernoulli trial of a binomial process (i.e. presence or absence of mange-compatible lesion). I overlaid a grid of 10 km^2 square cells on the study area in order to group cameras too close together and defined two seasons per year; i.e. winter, from October to March (roughly the months with snow cover), and summer from April to September (snow free months). From each 10 km^2 grid I extracted the proportion of agricultural land, and human settlements from the Vegetation Map of Norway (Johansen, 2009), and the mean population density from Statistics Norway (www.ssb.no). In addition, I used the number of months since the beginning of the study, the frequency of red fox events per day and camera, the season and the area.

Figure 4. An example of two camera trapped red foxes with mange-compatible lesions.

Camera trapping in India

For the study of the interspecific interactions among mesocarnivores (**Paper IV**), I used a camera trap design in a human dominated land in Maharashtra, India (Fig 2c). To record the activity of Indian fox, jungle cat (*Felis chaus*), jackals (*Canis aureus*) and domestic dogs (*Canis familiaris*), I set up 40 camera trap locations spaced two kilometers apart from each other to ensure that the whole area was covered (Fig 2c). I used one camera trap per site that was active from dusk until dawn for six consecutive nights. The data obtained was transformed into binary detection histories for each species and site (e.g. y_{si} = 100101; species *s* was detected in location *i* at least once during the first, third and sixth trapping nights). I extracted habitat variables using buffers of 1000m, 500m, and 100m around each camera site in order to investigate different scales of habitat selection of each species. To obtain the variables of interest I digitized satellite imagery of the study area. Then I extracted the coverage of forestry plantations, agriculture land, fallow land, and human settlements from each buffer size as variables of interest. Furthermore, I calculated the length of tarmac roads and irrigation canals in each buffer size. Additionally, I investigated the temporal interactions of the species following two approaches. (1) I created density curves of activity for each of the study species by calculating the kernel densities of the radian times of the camera-trapping events and calculated the coefficients of overlap for each pair of density curves (Ridout & Linkie, 2009). (2) I investigated the temporal interactions with dogs by calculating the Avoidance-Attraction Ratios (AARs) as the ratios of T2 intervals over T1 intervals (Parsons et al., 2016). T1 intervals are the time span between the detection of the target species and the posterior detection of a dog and, T2 intervals are the time span between the detection of a dog and the posterior detection of the target species.

3.3. Data analyses

Red fox distribution

To study the distribution of red foxes in relation to prey availability and abiotic factors (**Paper I**), we fitted 17 candidate logistic mixed effects models (GLMM). The set of candidate models included models with different combinations of presence of the main prey (i.e. small rodents) and presence of the alternative prey species (i.e. mountain hare, tetraonid species, and ungulates), models with the index of species richness, and models with snow depth and altitude interacting with the other variables. The continuous variables (i.e. altitude and snow depth) were standardized by $(x_i - \bar{X})/(2 \times SD)$ (Gelman & Hill, 2007). I ranked the models according to their fit to the data by using the Akaike's information criterion (AIC) and considered models within two AIC units to be of similar quality (Anderson, Burnham, & White, 1998).

Detectability rates

I investigated the seasonal variations in the detectability of foxes (**Paper II**) by fitting the daily detection probabilities to a set of regression models. Given the nature of the data (proportion data with an excess of zeroes), I used zero-inflated beta regressions in a Bayesian framework. Zero-inflated models take into account and model the excess of zeroes. To do so, these models assume that there is a process that originates only zeros and another process that originates zero and non-zero data (Martin et al., 2005). This way, a zero in the data means either that the species is not present (only zeroes process) or that it was present but the camera failed to detect it (zeroes and non-zero process). I built a set of 26 candidate models by considering ecologically meaningful combinations of variables and interactions between the variables and the season. I then used the Left-one-out cross correlation values (hereafter LOO) as a model selection method (Vehtari, Gelman, & Gabry, 2016).

Occurrence of sarcoptic mange

I used generalized linear mixed models in a Bayesian framework to study the factors affecting the occurrence of sarcoptic mange in red foxes (**Papers III**). I fitted a candidate list of nine models created by combining the variables of interest and interactions between them. Again, LOO values were used to carry out model selection. Additionally, in order to detect potential spatiotemporal cluster of the disease, I used the Kulldorff algorithm (Kulldorff, 1997) based on a Bernouilli probability. The Kulldorff algorithm takes into account failures and successes of the Bernoulli process and analyze them in three-dimensional cylindrical windows that move across the study area. The height and the base of these windows are flexible and represent the time and the space respectively.

Spatial interactions

I studied the spatial interactions among the species of the mesocarnivore community in India (**Paper IV**) by using a Bayesian multispecies occupancy model (Rota et al., 2016). This model is a generalization of the single-species occupancy model (MacKenzie et al., 2002) to include two or more interacting species. In this model, the direction of the interaction between each pair of species reveal any spatial avoidance or association between them.

4. Prey availability, abiotic effects and distribution (Paper I)

Previous studies have shown the importance of prey availability in the distribution of red foxes (Angelstam, Lindstrom, & Widen, 1984; Hersteinsson & Macdonald, 1992; E. Lindström, Angelstam, Widen, & Andren, 1987). This is in conformity with the results from **Paper I**, which show the importance of the availability of small rodents, tetraonid species, and ungulates. However**,** the results also show that this importance varies with snow depth and altitude (Table 1).

Table 1. Best model coefficients explaining the distribution of red foxes in northern Sweden in 1974 to 1985 and 95% confident intervals.

Model coefficients		
	Estimates	95% CI
Intercept	0.081	(-0.062, 0.225)
Rodents	0.707	(0.511, 0.904)
Hares	1.116	(0.968, 1.264)
Tetraonids	1.208	(1.064, 1.352)
Ungulates	0.375	(0.246, 0.504)
SnowDepth	0.244	(0.007, 0.482)
Altitude	-0.071	(-0.293, 0.150)
Hares:SnowDepth	-0.467	(-0.73, -0.206)
Tetraonids:SnowDepth	-0.218	(-0.481, 0.046)
Ungulates:SnowDepth	0.265	(0.022, 0.508)
Hares:Altitude	0.398	(0.118, 0.679)
Tetraonids:Altitude	-0.147	(-0.387, 0.092)
Ungulates:Altitude	0.137	(-0.095, 0.370)

The effect of the presence of ungulates (i.e. moose and reindeer) in the distribution of foxes is of special interest. Since foxes do not prey on these species, in my study, the effect of ungulates is probably a reflection of the dependency of red foxes on carrion during shortages of the main prey (i.e. small rodents). The likely origin of these carcasses is natural death, inanition under harsh winter conditions, predation, and human hunting (Saether, Andersen, Hjeljord, & Heim, 1996; Tveraa, Fauchald, Henaug, & Yoccoz, 2003). The linkage between the availability of carcasses and red fox occurrence has been previously documented (Cagnacci et al., 2003; Henden, Stien, Bardsen, Yoccoz, & Ims, 2014; Needham, Odden, Lundstadsveen, & Wegge, 2014). Here I show that this relationship varies with snow depth so that the importance of carcasses for red fox distribution increases with deeper snow (Table 1). A possible reason for this is that it is probably difficult to hunt live prey, especially small rodents, when the snow is deep. Under these conditions, it is probably easier for the red fox to rely on carcasses.

Likewise, the effect of other alternative species also interacted with abiotic factors. This was the case for mountain hares (*Lepus lepus*). Hares represent another important alternative prey for the red fox in Scandinavia (Danell & Hornfeldt, 1987; E. R. Lindström et al., 1994), but the results from **Paper I** revealed that the effect of hares on red fox occurrence varied with altitude and snow depth. The magnitude of the effect of hares decreased with snow depth and increased with altitude. Deep snow makes moving, and thus hunting, more difficult for the red fox. Therefore, other food resources like carcasses might be preferred in those conditions. Further, altitude was a surrogate for habitat composition in the analyses. In consequence, an increase in altitude entailed an increase in tundra landscape. Hares may be more exposed in the open landscape and thus, easier to detect and catch.

These results suggest that the increase of large ungulates like moose and reindeer in many areas of Scandinavia (Cederlund, Lovari, & Meriggi, 1996; Ims et al., 2007) may benefit red foxes. Furthermore, an increase in the availability of carcasses during the winter when other prey is scarce could stabilize the temporal dynamics of red fox populations in Scandinavia. Additionally, I show the importance of taking into account the interactions between prey availability and abiotic factors in order to predict the distribution and the dynamics of this mesocarnivore.

5. Seasonality and detectability (Paper II)

Some human activities vary among seasons (e.g. hiking, hunting, seeding season). Therefore, the influence of humans on the abundance and activity of red foxes may differ seasonally. Likewise, a strong seasonality involving harsh winter periods may negatively affect red fox densities (Barton & Zalewski, 2007). These changes should be reflected in the detection probabilities of red foxes as it is a function of the abundance and activity of the species (Royle & Nichols, 2003).

The best ranked zero-inflated model explaining the seasonal variation in the red fox detection probabilities revealed that the highest detectability occurred in the winter, whereas summer and autumn detectability remained low across the years (Fig. 5a). This is in accordance with the peaks reported in red fox hunting bag counts in Scandinavia (Stubbe, 1980). This peak is probably a consequence of high activity of foxes during the mating season and longer activity periods during long winter nights. Moreover, red foxes may forage more actively during periods of low availability of food.

However, the seasonal differences decreased towards northern latitudes (Fig. 5b). This decrease followed a productivity gradient that ranged from high productivity landscapes in the south, to low productivity areas dominated by boreal forest and alpine landscapes in the north. The severity of winter conditions in marginal alpine areas in the north when food is less available may affect red fox survival (Barton & Zalewski, 2007), and hence, reduce winter detection probabilities.

The availability of hunting remains had a possitive effect in red fox detection probabilities during the autumn (Fig. 5c). The peak number of moose culled during the hunting season (25th September to 23th of December) occurs in the months of October and November, and therefore, the number of hunting remains available for the red fox is larger during that period. Foxes are attracted to the remains and cache surplus food (Sklepkovych & Montevecchi, 1996). This may increase their activity, and consequently, increase the detection probability in that period.

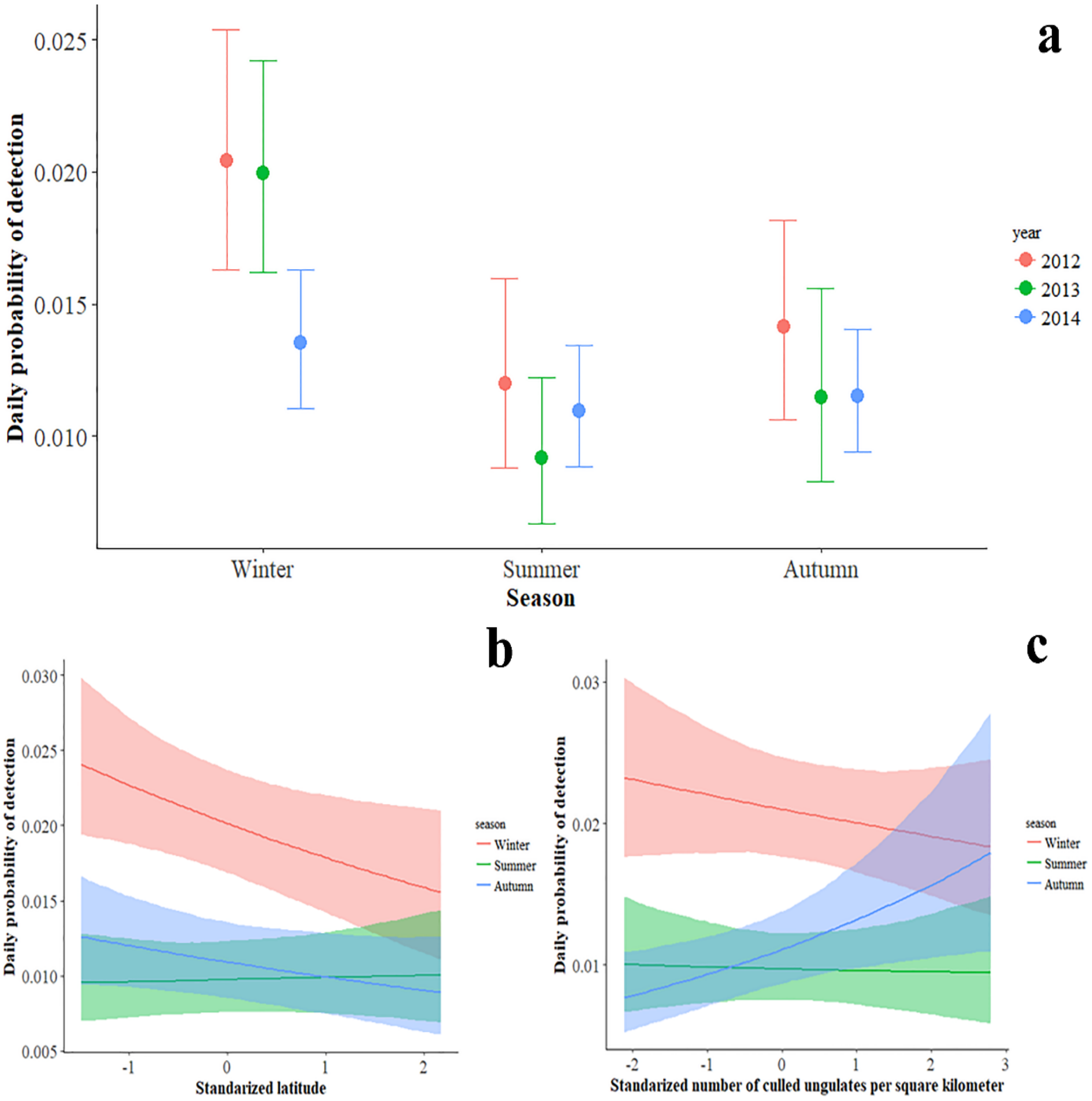

Figure 5. a) Boxplot of the variation in detection probability of red foxes each season and year of the study period. b) Marginal effect of latitude in detection probability of red foxes each season. c) Marginal effect of hunting (number of big ungulates culled/km^2) each season.

I did not detect an effect of agriculture density or human settlements in the detectability of foxes; even though it has been previously shown that these variables affect other aspects of red foxes (Killengreen et al., 2011; Walton et al., 2017). Hence, although these factors may affect red fox abundance or distribution, they may not be reflected in fox detection probabilities. A possible cause of this dissociation is that activity patterns of foxes may be altered in human-dominated areas. They may use natural patches, where the cameras were placed, mainly for shelter and resting, and forage more actively in the neighboring agriculture and periurban areas. This cause of dissociation has been suggested for white tail deer (Parsons et al., 2017) and for pumas and bobcats in urbanized areas (Lewis et al., 2015).

Here I show how detection probabilities of a mesocarnivore vary seasonally and along a gradient of environmental productivity. The results show that different human-related factors affect the detectability of red foxes through changes in their abundance and activity patterns. Further human development might affect relatively undisturbed population from marginal areas.

6. Role of diseases (Paper III)

Zoonotic diseases like sarcoptic mange can alter the host populations in different ways. For example, by increasing mortality rates (Uraguchi, Ueno, Iijima, & Saitoh, 2014), or altering movements when surviving individuals colonize the vacant territories of the deceased (Potts, Harris, & Giuggioli, 2013). The results of **Paper III** suggest that humans mediate the manner in which sarcoptic mange affects a host population. The two best ranked model according to its LOO value included the interaction between season and distance to settlement, revealing that red foxes infected with sarcoptic mange occurred more frequently closer to human settlement than healthy ones during the winter (Table 2). This result suggest that anthropogenic resources may affect the development of the disease.

Table 2. Parameter estimates form the best model explaining the presence of red foxes with mange-compatible lesions in southeastern Norway.

	Estimate	**l-95% CRI**	**u-95% CRI**	**$\hat{R}$**
Intercept	-3.90	-5.74	-1.86	1
Time	-0.04	-0.11	-0.01	1
Dist_Settle	-0.14	-0.88	0.54	1
SeasonW	0.14	-0.78	1.69	1
Dist_Settle:SeasonW	-0.62	-1.24	-0.03	1
Grid_id(sd(Intercept))	2.14	1.60	2.86	1
Time period(sd(Intercept))	0.77	0.13	2.36	1

l-CRI and u-CRI refer to 95% lower- and upper credible intervals, and $\hat{R}$ refer to Gelman and Rubin´s converge diagnosis.

Additionally, the clusters detected by the spatiotemporal scan analysis (Figure 4) suggested that the dynamics of sarcoptic mange in red foxes was characterized by small-localized outbreaks that disappeared after a time. Moreover, the sites included in the cluster with the highest likelihood were located closer to human settlements than the rest of the sites.

Two, not mutually exclusive, mechanisms can explain the high frequency of mange cases close to human settlements. A poor body condition due to advanced states of sarcoptic mange (Balestrieri et al., 2006; Oleaga et al., 2011; Simpson, Johnson, & Carver, 2016) may undermine the ability of the host to hunt live prey or locate and fight for carrion. Hence, the infected individual may approach human settlements in order to forage for easily accessible food resources. This has been previously reported for coyotes with a deteriorated body condition due to sarcoptic mange (Todd et al., 1981). Furthermore, Balestrieri et al. (2006), suggested that infected animals coming closer to villages searching for easy food sources may bias the apparent disease prevalence in road kills.

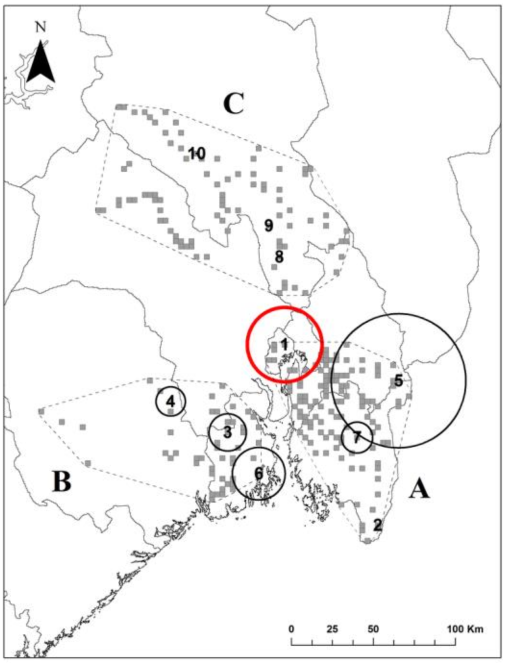

Figure 4. Geographic distribution of significant clusters of red foxes potentially infected with sarcoptic mange identified by scan analysis. The circles define the size of the clusters and the numbers refer to the ranking position of each cluster according to its likelihood ratio. The red circle represents the cluster with the highest likelihood ratio.

A second mechanism explaining this phenomenon may be related to the transmission dynamic of the disease. Although I discarded a density dependent transmission (the analyses did not detect a higher abundance of foxes close to settlements), a frequency dependent transmission due to an increased contact rate by an increased overlap between home ranges cannot be ruled out (Devenish-Nelson, Richards, Harris, Soulsbury, & Stephens, 2014).

Regardless of the mechanism, the results show that human activity can influence the dynamic of sarcoptic mange in red foxes. Moreover, outbreaks close to human settlements might increase the risk of infection of domestic animals, livestock or other wildlife (Kolodziej-Sobocinska et al., 2014).

7. Community interactions (Paper IV)

In **Paper IV** I studied the intraguild interactions among four sympatric species (i.e. Indian fox, jackal, jungle cat, and domestic dog) in a mesocarnivore assemblage in a highly human dominated landscape of central India. The results revealed the existence of spatial niche partitioning between Indian fox and jackals (Fig. 5). In contrast, the rest of the species overlapped in their habitat use. Assemblages of sympatric mesocarnivores in which a smaller member is displaced have been described previously (Lesmeister, Nielsen, Schauber, & Hellgren, 2015).

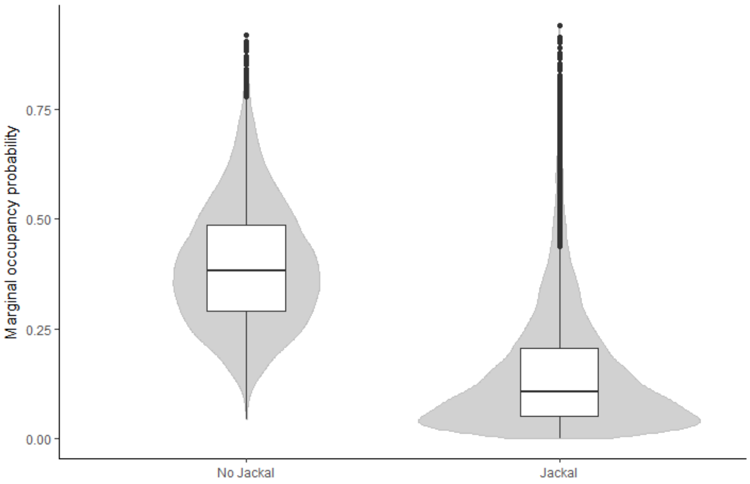

Figure 5. Posterior distributions of the marginal occupancy probability of Indan fox conditional on the presence or absence of Jackal

The spatial partitioning between foxes and jackals was probably a consequence of the differences in their habitat use. Foxes avoided human settlements and were positively associated with forest patches and with the mean size of habitat patch (i.e. habitat homogeneity, Fig. 6). Jackals, on the other hand, where positively associated with settlements. Indian foxes showed the most specialized habitat use among the study species. Consequently, the spatial segregation between Indian fox and jackals in this assemblage is in agreement with Soto and Palomares (2015) who showed that some degree of habitat specialization favored spatial niche partitioning. On the contrary, jungle cats and dogs showed fewer associations with the different factors than the other studied species, and thus seemed more generalist. For example, they did not show clear associations with habitat except for a positive correlation with the presence of human settlements at the finest scale. The association with human settlements was also manifested in jackals. This pattern is possibly a result of a dependency of these three species on human food resources (Jaeger, Haque, Sultana, & Bruggers, 2007; Nowell & Jackson, 1996).

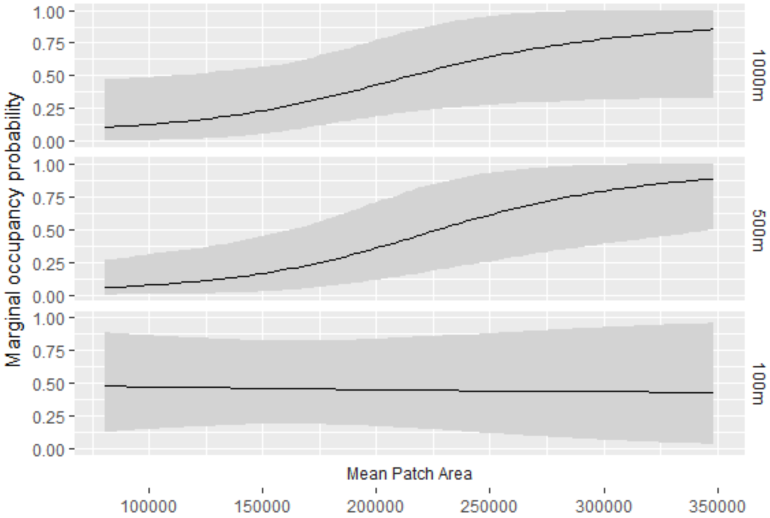

Figure 6. Mean patch habitat area (i.e. habitat homogeneity) effect on the habitat use of Indian foxes at three buffer sizes. Solid lines represent the general trend and the shaded area the 95% credible interval.

Although Indian foxes overlapped spatially with dogs, the results showed temporal niche partitioning between these two species. The detectability of foxes decreased with an increase in dogs detected per trapping night, the AARs showed longer time intervals to the detection of Indian foxes after a dog was detected (T2 intervals > T1 intervals), and the kernel density plots of activity revealed peaks of Indian fox activity when dog activity was lowest (Fig. 7). Vanak et al. (2009) already described some avoidance of dogs by Indian foxes showing that the latter reduced the visits to food trays that were exposed to dog odor. The other species did not manifest clear patterns suggesting spatial niche partitioning with dogs (Fig. 7). Avoidance behavior among species with similar body size might not be as marked. Intraguild killing, for example, is less likely among species with similar body size (Palomares & Caro, 1999).

The results suggest that species with some degree of habitat specialization might be more sensitive to human influence than the more generalist ones. In this mesocarnivore assemblage, the presence of humans may benefit jungle cats and jackals through food subsidization, but it may affect Indian foxes negatively through loss and fragmentation of habitats and by interactions with domestic dogs.

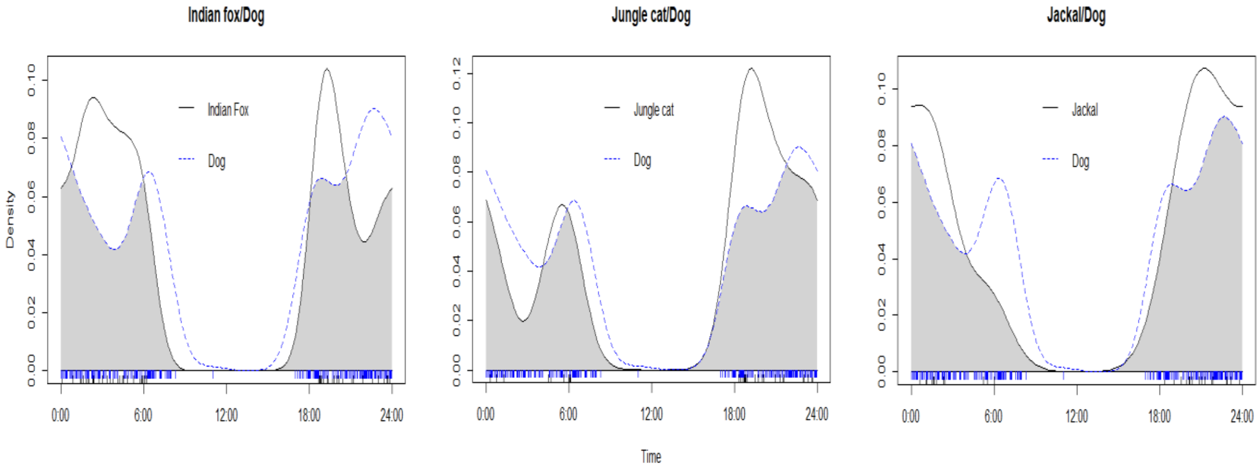

Figure 7. Activity kernel density plots of the activity of Indian fox, jungle cat and jackal with domestic dog. Ticks along the y axis represent the actual observations for each of the species.

8. Conclusions

This thesis investigated determinant factors for the distribution and activity patterns of mesocarnivores and how they interacted with each other along a gradient of anthropogenic influence. The results confirm the complexity of the responses of mesocarnivores to different influential factors and reveal the important role of humans in shaping the distribution and activity patterns of these species.

The results suggest that the management of large ungulates can act as a strong influential factor for mesocarnivores. The association of red fox winter distribution with the presence of ungulates (Paper I) is most probably an indication of the dependence of foxes on carcasses in areas of deep snow where other prey species are less available. Further, hunting of large ungulates as a source of hunting remains was also an important factor increasing the detectability of foxes during autumn (Paper II), when the number of culled individuals was higher. This suggest that reindeer herding and moose hunting have a profound impact in the ecology of foxes through subsidization during periods when other resources are less available, which is in accordance with previous research (Henden et al., 2014; Killengreen et al., 2011; Needham et al., 2014). Interestingly, here I show that this is true not only for developed areas where the impact of humans is more apparent (Paper II), but also in marginal alpine habitats where the influence of humans is relatively low (Paper I). Moreover, the availability of hunting remains probably affects other mesocarnivores, like the pine marten, that can benefit from an alternative food source during periods of low availability of prey (Jedrzejewski et al., 1993; Wikenros, Stahlberg, & Sand, 2014).

A similarly important factor affecting mesocarnivore distribution and activity is the proximity to human settlements, probably due to the accessibility to anthropogenic food (e.g. waste). This importance was manifested in the analyses in the associations between jackals, jungle cats and dogs with human settlements (Paper IV). Moreover, red foxes infected with sarcoptic mange occurred close to settlements more often than healthy ones during the winter (Paper III). In addition, I speculated that a possible explanation for the disassociation between the detectability of red foxes and some human related variables was a change in the activity patterns of this species in developed areas (Paper II).

In general, the results suggest the importance of subsidization of mesocarnivores by humans either through an increased availability of carcasses or through access to anthropogenic food. Indeed, food-subsidizing mesocarnivores can affect their distribution and activity patterns (Paper I and Paper II), their habitat use (Paper IV), and can have important implications in disease transmission (Paper III). In this context, humans may have a role as facilitators of mesocarnivores, and therefore, expanding the realized niche of these species (Bruno et al., 2003). My results support the conclusion from T. M. Newsome et al. (2015) in claiming that the availability of anthropogenic food and hunting remains for mesocarnivores should be managed and somehow restricted.

My results also suggest that the degree of habitat specialization is an important aspect when predicting the response of a particular species to human influence. Whereas generalist species can easily adapt and often be favored by the addition of supplementary anthropogenic resources, species with a higher degree of specialization can be affected negatively by the result of human activities. As shown in this thesis (Paper I, II, and III), red fox is an example of the former. It can adapt and take advantage of the human influence in the ecosystem that it inhabits. Other examples of this are jackals and jungle cats in highly human dominated landscapes (Paper IV). On the contrary, human activities resulting in habitat loss and fragmentation or the introduction of species associated with humans (e.g. domestic dog) might affect negatively species showing some degree of habitat specialization like the Indian fox (Paper IV). My results on the susceptibility to human impact of species with some degree of habitat specialization confirm what has already been shown in other species (e.g. bird species (Devictor, Julliard, & Jiguet, 2008), invertebrates (With & Crist, 1995)).

This study revealed other important factors to take into account in future management actions. For example, I showed that during the winter, snow depth and altitude (a proxy for habitat) affected the influence of alternative prey on red foxes in marginal habitats (Paper I). This has important implications for the management of small game species as predation pressure from foxes may vary in different habitats and conditions. Further, I showed that species interactions within a carnivore guild are important for the habitat use of each of the members, especially in assemblages with species of very different body sizes. These intraguild interactions can lead to spatial niche partitioning (e.g. Indian fox and Jackal; Paper IV) or temporal niche partitioning (e.g. Indian fox and dog; Paper IV). Management actions directed to the conservation of a mesocarnivore or to its natural habitat might affect the intraguild interactions within the carnivore assemblage. Hence, these actions must take into account the relationships among the community members in order to predict the potential responses of non-target species.

In conclusion, humans may have a positive (e.g. facilitation through anthropogenic food subsidization) or negative (e.g. human interference, alteration of the intraguild interactions) effect on mesocarnivore species. These effects may alter the realized niche of the species by expanding or reducing it. Humans should be no longer considered external agents affecting the ecosystems. On the contrary, my results suggest that the effect of humans is intrinsic in the ecosystems even in apparently undisturbed marginal habitats.

9. Future perspectives

In this thesis, I show the importance of anthropogenic subsidies in the distribution and activity patterns of mesocarnivores. However, I did not study the effect of subsidization directly. Future research should focus in the design of experimental studies delving into the effects of human subsidization of mesocarnivores. There has been interesting approaches in this matter. For example, Henden et al. (2014) carried out a quasi-experiment placing camera traps in areas with different reindeer densities and found that carnivore occupancy increased with reindeer counts. Bino et al. (2010) manipulated the waste disposal in several villages to observe the numerical and spatial response of red foxes. Experimental or quasi-experimental approaches testing the effect of subsidization both in human dominated and undisturbed areas might reveal the influence of anthropogenic food sources in other aspects of mesocarnivores like their dynamics. For example, in Paper I, I speculated that an increase in the availability of carcasses could attenuate the interannual fluctuations in the Scandinavian red fox; such experiments could test for this hypothesis.

The study of the detection probability of red foxes (Paper II) raised interesting questions about the possible impact of humans in the activity patterns of this species. For example, I did not detect an association with agriculture density, urban areas, or extra urban settlements; however, I argued that different daily activity patterns in developed areas could affect the detections probabilities of red foxes and thus, conceal the effect of human-related variables. Behavioral approaches, like the study of the temporal dynamics of the species (used in Paper IV), are gaining popularity (Frey, Fisher, Burton, & Volpe, 2017). Comparing daily activity patterns of populations influenced by human subsidization against marginal populations could reveal the impact of humans in the behavior of mesocarnivores.

10. References

Anderson, D. R., Burnham, K. P., & White, G. C. (1998). Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. *Journal of Applied Statistics, 25*(2), 263-282.

Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat - a review. *Oikos, 71*(3), 355-366. doi:10.2307/3545823

Angelstam, P., Lindstrom, E., & Widen, P. (1984). Role of predation in short-term population fluctuations of some birds and mammals in fennoscandia. *Oecologia, 62*(2), 199-208. doi:10.1007/bf00379014

Balestrieri, A., Remonti, L., Ferrari, N., Ferrari, A., Lo Valvo, T., Robetto, S., & Orusa, R. (2006). Sarcoptic mange in wild carnivores and its co-occurrence with parasitic helminths in the Western Italian Alps. *European Journal of Wildlife Research, 52*(3), 196-201. doi:10.1007/s10344-006-0036-4

Barton, K. A., & Zalewski, A. (2007). Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography, 16*(3), 281-289. doi:10.1111/j.1466-8238.2007.00299.x

Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management, 59*(2), 228-237. doi:10.2307/3808935

Benitez-Lopez, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation, 143*(6), 1307-1316. doi:10.1016/j.biocon.2010.02.009

Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology, 76*(6), 1075-1085. doi:10.1111/j.1365-2656.2007.01287.x

Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D., & Kark, S. (2010). Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology, 47*(6), 1262-1271. doi:10.1111/j.1365-2664.2010.01882.x

Bornstein, S., Mörner, T., Samuel, W.M. (2001). Sarcoptes scabiei and sarcoptic mange. In W. M. Samuel, Pybus, M.J., Kocan, A.A. (Ed.), *Parasitic*

Diseases of Wild Mammals. (2nd ed ed., pp. 107–119). Ames: Iowa State University Press.

Bruno, J. F., Stachowicz, J. J., & Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution, 18*(3), 119-125. doi:10.1016/s0169-5347(02)00045-9

Burton, A. C., Sam, M. K., Balangtaa, C., & Brashares, J. S. (2012). Hierarchical Multi-Species Modeling of Carnivore Responses to Hunting, Habitat and Prey in a West African Protected Area. *PLoS One, 7*(5). doi:10.1371/journal.pone.0038007

Butler, J. R. A., du Toit, J. T., & Bingham, J. (2004). Free-ranging domestic dogs (Canis familiaris) as predators and prey in rural Zimbabwe: threats of competition and disease to large wild carnivores. *Biological Conservation, 115*(3), 369-378. doi:10.1016/s0006-3207(03)00152-6

Cagnacci, F., Lovari, S., & Meriggi, A. (2003). Carrion dependence and food habits of the red fox in an Alpine area. *Italian Journal of Zoology, 70*(1), 31-38.

Campos, C. B., Esteves, C. F., Ferraz, K., Crawshaw, P. G., & Verdade, L. M. (2007). Diet of free-ranging cats and dogs in a suburban and rural environment, south-eastern Brazil. *Journal of Zoology, 273*(1), 14-20. doi:10.1111/j.1469-7998.2007.00291.x

Carothers, J. H., & Jaksic, F. M. (1984). Time as a niche difference - the role of interference competition. *Oikos, 42*(3), 403-406. doi:10.2307/3544413

Caryl, F. M., Quine, C. P., & Park, K. J. (2012). Martens in the matrix: the importance of nonforested habitats for forest carnivores in fragmented landscapes. *Journal of Mammalogy, 93*(2), 464-474. doi:10.1644/11-mamm-a-149.1

Cavallini, P., & Lovari, S. (1991). Environmental-factors influencing the use of habitat in the red fox, vulpes-vulpes. *Journal of Zoology, 223*, 323-339.

Cederlund, G., Lovari, S., & Meriggi, A. (1996). Trends in the moose-forest system in Fennoscandia, with special reference to Sweden. In R. M. DeGraaf & R. I. Miller (Eds.), *Conservation of faunal diversity in forested landscapes.* (pp. 265:281). London: Chapman & Hall.

Cleaveland, S., Appel, M. G. J., Chalmers, W. S. K., Chillingworth, C., Kaare, M., & Dye, C. (2000). Serological and demographic evidence for domestic dogs as a source of canine distemper virus infection for Serengeti wildlife. *Veterinary Microbiology, 72*(3-4), 217-227. doi:10.1016/s0378-1135(99)00207-2

Clevenger, A. P. (1995). Seasonality and relationships of food resource use of martes-martes, genetta-genetta and felis-catus in the balearic-islands. *Revue D Ecologie-La Terre Et La Vie, 50*(2), 109-131.

Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., & Byrd, G. V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science, 307*(5717), 1959-1961. doi:10.1126/science.1108485

Crooks, K. R., & Soule, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature, 400*(6744), 563-566. doi:10.1038/23028

Cuyckens, G. A. E., Perovic, P. G., & Cristobal, L. (2015). How are wetlands and biological interactions related to carnivore distributions at high altitude? *Journal of Arid Environments, 115*, 14-18. doi:10.1016/j.jaridenv.2014.12.009

Danell, K., & Hornfeldt, B. (1987). Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. *Oecologia, 73*(4), 533-536. doi:10.1007/bf00379412

Daszak, P., Cunningham, A. A., & Hyatt, A. D. (2000). Wildlife ecology - Emerging infectious diseases of wildlife - Threats to biodiversity and human health. *Science, 287*(5452), 443-449. doi:10.1126/science.287.5452.443

Devenish-Nelson, E. S., Richards, S. A., Harris, S., Soulsbury, C., & Stephens, P. A. (2014). Demonstrating frequency-dependent transmission of sarcoptic mange in red foxes. *Biology Letters, 10*(10). doi:10.1098/rsbl.2014.0524

Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos, 117*(4), 507-514. doi:10.1111/j.2008.0030-1299.16215.x

Dharmarajan, G., Beasley, J. C., Fike, J. A., & Rhodes, O. E. (2014). Effects of landscape, demographic and behavioral factors on kin structure: testing ecological predictions in a mesopredator with high dispersal capability. *Animal Conservation, 17*(3), 225-234. doi:10.1111/acv.12086

Elbroch, L. M., Lendrum, P. E., Newby, J., Quigley, H., & Thompson, D. J. (2015). Recolonizing wolves influence the realized niche of resident cougars. *Zoological Studies, 54*, 11. doi:10.1186/s40555-015-0122-y

Elmhagen, B., Berteaux, D., Burgess, R. M., Ehrich, D., Gallant, D., Henttonen, H., . . . Angerbjorn, A. (2017). Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Research, 36*. doi:10.1080/17518369.2017.1319109

Estes, J. A., Tinker, M. T., Williams, T. M., & Doak, D. F. (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science, 282*(5388), 473-476. doi:10.1126/science.282.5388.473

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics, 34*, 487-515. doi:10.1146/annurev.ecolsys.34.011802.132419

Fedriani, J. M., Fuller, T. K., & Sauvajot, R. M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography, 24*(3), 325-331. doi:10.1034/j.1600-0587.2001.240310.x

Fernandez-Olalla, M., Martinez-Abrain, A., Canut, J., Garcia-Ferre, D., Afonso, I., & Gonzalez, L. M. (2012). Assessing different management scenarios to reverse the declining trend of a relict capercaillie population: A modelling approach within an adaptive management framework. *Biological Conservation, 148*(1), 79-87. doi:10.1016/j.biocon.2012.01.047

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 Sensing in Ecology and Conservation, 3*(3), 123-132. doi:10.1002/rse2.60

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology, 6*(1).

Gehring, T. M., & Swihart, R. K. (2003). Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. *Biological Conservation, 109*(2), 283-295. doi:10.1016/s0006-3207(02)00156-8

Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models.* . Cambridge: Cambridge University Press.

George, S. L., & Crooks, K. R. (2006). Recreation and large mammal activity in an urban nature reserve. *Biological Conservation, 133*(1), 107-117. doi:10.1016/j.biocon.2006.05.024

Ginsberg, J. R., Mace, G. M., & Albon, S. (1995). Local extinction in a small and declining population - wild dogs in the serengeti. *Proceedings of the Royal Society B-Biological Sciences, 262*(1364), 221-228. doi:10.1098/rspb.1995.0199

Gittleman, J., & Gompper, M. (2005). Plight of predators: The importance of carnivores for understanding patterns of biodiversity and extinction risk. In P. Barbosa & I. Castellanos (Eds.), *The Ecology of Predator-Prey Interactions* (pp. 370-388). Oxford (United Kingdom): Oxford University Press.

Gompper, M. E., Lesmeister, D. B., Ray, J. C., Malcolm, J. R., & Kays, R. (2016). Differential Habitat Use or Intraguild Interactions: What Structures a Carnivore Community? *PLoS One, 11*(1). doi:10.1371/journal.pone.0146055

Gompper, M. E., & Vanak, A. T. (2006). Vulpes bengalensis. *Mammalian Species*(795), 1:5.

Gompper, M. E., & Vanak, A. T. (2008). Subsidized predators, landscapes of fear and disarticulated carnivore communities. *Animal Conservation, 11*(1), 13-14. doi:10.1111/j.1469-1795.2008.00160.x

Goodrich, J. M., & Buskirk, S. W. (1995). Control of abundant native vertebrates for conservation of endangered species. *Conservation Biology, 9*(6), 1357-1364. doi:10.1046/j.1523-1739.1995.09061357.x

Gortazar, C., Ferroglio, E., Hofle, U., Frolich, K., & Vicente, J. (2007). Diseases shared between wildlife and livestock: a European perspective. *European Journal of Wildlife Research, 53*(4), 241-256. doi:10.1007/s10344-007-0098-y

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling, 135*(2-3), 147-186. doi:10.1016/s0304-3800(00)00354-9

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist, 94*(879), 421-425.

Halpin, M. A., & Bissonette, J. A. (1988). Influence of snow depth on prey availability and habitat use by red fox. *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 66*(3), 587-592. doi:10.1139/z88-086

Hamalainen, A., Broadley, K., Droghini, A., Haines, J. A., Lamb, C. T., Boutin, S., & Gilbert, S. (2017). The ecological significance of secondary seed dispersal by carnivores. *Ecosphere, 8*(2), 16. doi:10.1002/ecs2.1685

Henden, J. A., Stien, A., Bardsen, B. J., Yoccoz, N. G., & Ims, R. A. (2014). Community-wide mesocarnivore response to partial ungulate migration. *Journal of Applied Ecology, 51*(6), 1525-1533. doi:10.1111/1365-2664.12328

Hersteinsson, P., & Macdonald, D. W. (1992). Interspecific competition and the geographical-distribution of red and arctic foxes Vulpes-vulpes and Alopex-lagopus. *Oikos, 64*(3), 505-515. doi:10.2307/3545168

Hughes, J., & Macdonald, D. W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation, 157*, 341-351. doi:10.1016/j.biocon.2012.07.005

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symp, 22*, 415-427.

Ilse, L. M., & Hellgren, E. C. (1995). Resource partitioning in sympatric populations of collared peccaries and feral hogs in southern texas. *Journal of Mammalogy, 76*(3), 784-799. doi:10.2307/1382747

Ims, R. A., & Fuglei, E. (2005). Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience, 55*(4), 311-322. doi:10.1641/0006-3568(2005)055[0311:ticite]2.0.co;2

Ims, R. A., Yoccoz, N. G., Brathen, K. A., Fauchald, P., Tveraa, T., & Hausner, V. (2007). Can reindeer overabundance cause a trophic cascade? *Ecosystems, 10*(4), 607-622. doi:10.1007/s10021-007-9060-9

Jaeger, M. M., Haque, E., Sultana, P., & Bruggers, R. L. (2007). Daytime cover, diet and space-use of golden jackals (Canis aureus) in agro-ecosystems of Bangladesh. *Mammalia, 71*(1-2), 1-10. doi:10.1515/mamm.2007.016

Jedrzejewski, W., & Jedrzejewska, B. (1992). Foraging and diet of the red fox vulpes-vulpes in relation to variable food resources in bialowieza-national-park, Poland. *Ecography, 15*(2), 212-220. doi:10.1111/j.1600-0587.1992.tb00027.x

Jedrzejewski, W., & Jedrzejewska, B. (1993). Predation on rodents in bialowieza primeval forest, Poland. *Ecography, 16*(1), 47-64. doi:10.1111/j.1600-0587.1993.tb00058.x

Jedrzejewski, W., Zalewski, A., & Jedrzejewska, B. (1993). Foraging by pine marten martes martes in relation to food resources in Bialowieza national-park, Poland. *Acta Theriologica, 38*(4), 405-426.

Johansen, B. (2009). Vegetasjonskart for Norge basert på Landsat TM/ETM+ data. *Norut-Tromsø Rapport 4/2009. 86 s*.

Johnsingh, A. J. T., & Jhala, Y. V. (2004). Indian fox *Vulpes bengalensis*. In C. Sillero-Zubiri, M. Hoffmann, & D. W. Macdonald (Eds.), *Canids: Foxes, Wolves, Jackals* *and Dogs. Status Survey and Conservation Action Plan* (pp. 219-222). Gland, Switzerland and Cambridge, Uk.: IUCN/SCC Canid Specialist Group.

Johnson, C. N., Isaac, J. L., & Fisher, D. O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B-Biological Sciences, 274*(1608), 341-346. doi:10.1098/rspb.2006.3711

Jordano, P., Garcia, C., Godoy, J. A., & Garcia-Castano, J. L. (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America, 104*(9), 3278-3282. doi:10.1073/pnas.0606793104

Kauhala, K., Laukkanen, P., & von Rege, I. (1998). Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. *Ecography, 21*(5), 457-463. doi:10.1111/j.1600-0587.1998.tb00436.x

Kawecki, T. J. (2008). Adaptation to Marginal Habitats *Annual Review of Ecology Evolution and Systematics* (Vol. 39, pp. 321-342). Palo Alto: Annual Reviews.

Killengreen, S. T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N. G., & Ims, R. A. (2011). The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. *Journal of Animal Ecology, 80*(5), 1049-1060. doi:10.1111/j.1365-2656.2011.01840.x

Koike, S., Morimoto, H., Goto, Y., Kozakai, C., & Yamazaki, K. (2008). Frugivory of carnivores and seed dispersal of fleshy fruits in cool-temperate deciduous forests. *Journal of Forest Research, 13*(4), 215-222. doi:10.1007/s10310-008-0069-5

Kolodziej-Sobocinska, M., Zalewski, A., & Kowalczyk, R. (2014). Sarcoptic mange vulnerability in carnivores of the BiaowieA1/4a Primeval Forest, Poland: underlying determinant factors. *Ecological Research, 29*(2), 237-244. doi:10.1007/s11284-013-1118-x

Korpimaki, E., & Norrdahl, K. (1998). Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology, 79*(7), 2448-2455. doi:10.1890/0012-9658(1998)079[2448:eroprt]2.0.co;2

Kruuk, H., & Parish, T. (1981). Feeding specialization of the european badger meles-meles in scotland. *Journal of Animal Ecology, 50*(3), 773-788. doi:10.2307/4136

Kulldorff, M. (1997). A spatial scan statistic. *Communications in Statistics-Theory and Methods, 26*(6), 1481-1496. doi:10.1080/03610929708831995

Laliberte, A. S., & Ripple, W. J. (2004). Range contractions of North American carnivores and ungulates. *Bioscience, 54*(2), 123-138. doi:10.1641/0006-3568(2004)054[0123:rconac]2.0.co;2

Lariviere, S., & Pasitschniak-Arts, M. (1996). Vulpes vulpes. *Mammalian Species*(537), 1:11.

Laurenson, K., Sillero-Zubiri, C., Thompson, H., Shiferaw, F., Thirgood, S., & Malcolm, J. (1998). Disease as a threat to endangered species: Ethiopian wolves, domestic dogs and canine pathogens. *Animal Conservation, 1*(4), 273-280. doi:10.1111/j.1469-1795.1998.tb00038.x

Lesmeister, D. B., Nielsen, C. K., Schauber, E. M., & Hellgren, E. C. (2015). Spatial and Temporal Structure of a Mesocarnivore Guild in Midwestern North America. *Wildlife Monographs, 191*(1), 1-61. doi:10.1002/wmon.1015

Levi, T., Kilpatrick, A. M., Mangel, M., & Wilmers, C. C. (2012). Deer, predators, and the emergence of Lyme disease. *Proceedings of the National Academy of Sciences of the United States of America, 109*(27), 10942-10947. doi:10.1073/pnas.1204536109

Lewis, J. S., Logan, K. A., Alldredge, M. W., Bailey, L. L., VandeWoude, S., & Crooks, K. R. (2015). The effects of urbanization on population density, occupancy, and detection probability of wild felids. *Ecological Applications, 25*(7), 1880-1895. doi:10.1890/14-1664.1

Lindström, E., Angelstam, P., Widen, P., & Andren, H. (1987). Do predators synchronize vole and grouse fluctuations? An experiment. *Oikos, 48*(2), 121-124. doi:10.2307/3565847

Lindström, E. R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., . . . Swenson, J. E. (1994). Disease reveals the predator - sarcoptic mange, red fox predation, and prey populations. *Ecology, 75*(4), 1042-1049. doi:10.2307/1939428

Lindström, E. R., Brainerd, S. M., Helldin, J. O., & Overskaug, K. (1995). Pine marten red fox interactions - a case of intraguild predation. *Annales Zoologici Fennici, 32*(1), 123-130.

Macdonald, D. W., & Reynolds, J. C. (2004). Red fox Vulpes vulpes. In C. Sillero-Zubiri, M. hoffmann, & D. W. Macdonald (Eds.), *Canids: Foxes, Wolves, Jackals and Dogs* (pp. 129:135). Gland, Switzerland and Cambridge, UK.: IUCN/SSC Canid Specialist Group.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology, 83*(8), 2248-2255. doi:10.2307/3072056

Magrini, C., Manzo, E., Zapponi, L., Angelici, F. M., Boitani, L., & Cento, M. (2009). Weasel Mustela nivalis spatial ranging behaviour and habitat selection in agricultural landscape. *Acta Theriologica, 54*(2), 137-146. doi:10.1007/bf03193169

Malanson, G. P., Westman, W. E., & Yan, Y. L. (1992). Realized versus fundamental niche functions in a model of chaparral response to climatic-change. *Ecological Modelling, 64*(4), 261-277. doi:10.1016/0304-3800(92)90026-b

Mangas, J. G., Lozano, J., Cabezas-Diaz, S., & Virgos, E. (2008). The priority value of scrubland habitats for carnivore conservation in Mediterranean ecosystems. *Biodiversity and Conservation, 17*(1), 43-51. doi:10.1007/s10531-007-9229-8

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature, 405*(6783), 243-253. doi:10.1038/35012251

Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., . . . Possingham, H. P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters, 8*(11), 1235-1246. doi:10.1111/j.1461-0248.2005.00826.x

McCallum, H., Tompkins, D. M., Jones, M., Lachish, S., Marvanek, S., Lazenby, B., . . . Hawkins, C. E. (2007). Distribution and impacts of Tasmanian devil facial tumor disease. *Ecohealth, 4*(3), 318-325. doi:10.1007/s10393-007-0118-0

Meserve, P. L., Kelt, D. A., Milstead, W. B., & Gutierrez, J. R. (2003). Thirteen years of shifting top-down and bottom-up control. *Bioscience, 53*(7), 633-646. doi:10.1641/0006-3568(2003)053[0633:tyosta]2.0.co;2

Monterroso, P., Alves, P. C., & Ferreras, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. *Behavioral Ecology and Sociobiology, 68*(9), 1403-1417. doi:10.1007/s00265-014-1748-1

Mörner, T. (1992). Sarcoptic mange in Swedish wildlife. *Rev. sci. tech. Off. int. Epiz., 11*(4), 1115-1121.

Morrison, J. C., Sechrest, W., Dinerstein, E., Wilcove, D. S., & Lamoreux, J. F. (2007). Persistence of large mammal faunas as indicators of global human impacts. *Journal of Mammalogy, 88*(6), 1363-1380. doi:10.1644/06-mamm-a-124r2.1

Mortelliti, A., & Boitani, L. (2008). Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes. *Landscape Ecology, 23*(3), 285-298. doi:10.1007/s10980-007-9182-7

Needham, R., Odden, M., Lundstadsveen, S. K., & Wegge, P. (2014). Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. *Acta Theriologica, 59*(3), 391-398. doi:10.1007/s13364-014-0188-7

Nel, L., Jacobs, J., Jaftha, J., & Meredith, C. (1997). Natural spillover of a distinctly Canidae-associated biotype of rabies virus into an expanded wildlife host range in southern Africa. *Virus Genes, 15*(1), 79-82. doi:10.1023/a:1007979502754

Newey, S., Thirgood, S. J., & Hudson, P. J. (2004). Do parasite burdens in spring influence condition and fecundity of female mountain hares Lepus timidus? *Wildlife Biology, 10*(3), 171-176.

Newman, T. J., Baker, P. J., & Harris, S. (2002). Nutritional condition and survival of red foxes with sarcoptic mange. *Canadian Journal of Zoology-Revue Canadienne De Zoologie, 80*(1), 154-161. doi:10.1139/z01-216

Newsome, S. D., Garbe, H. M., Wilson, E. C., & Gehrt, S. D. (2015). Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia, 178*(1), 115-128. doi:10.1007/s00442-014-3205-2

Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., & Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography, 24*(1), 1-11. doi:10.1111/geb.12236

Norrdahl, K., Klemola, T., Korpimaki, E., & Koivula, M. (2002). Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos, 99*(3), 419-430. doi:10.1034/j.1600-0706.2002.12025.x

Nowell, K., & Jackson, P. (1996). Jungle Cat, *Felis chaus* Schreber, 1777. In K. Nowell & P. Jackson (Eds.), *Wild Cats. Status survey and conservation action plan.*

(pp. 83-85): IUCN Publications Services Unit.

Oleaga, A., Casais, R., Balseiro, A., Espi, A., Llaneza, L., Hartasanchez, A., & Gortazar, C. (2011). New techniques for an old disease: Sarcoptic mange in the Iberian wolf. *Veterinary Parasitology, 181*(2-4), 255-266. doi:10.1016/j.vetpar.2011.04.036

Ordenana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., . . . Van Vuren, D. H. (2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy, 91*(6), 1322-1331. doi:10.1644/09-mamm-a-312.1

Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S., & Martinez-Abrain, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters, 16*(12), 1501-1514. doi:10.1111/ele.12187

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *American Naturalist, 153*(5), 492-508. doi:10.1086/303189

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics, 37*, 637-669. doi:10.1146/annurev.ecolsys.37.091305.110100

Parsons, A. W., Bland, C., Forrester, T., Baker-Whatton, M. C., Schuttler, S. G., McShea, W. J., . . . Kays, R. (2016). The ecological impact of humans and dogs on wildlife in protected areas in eastern North America. *Biological Conservation, 203*, 75-88. doi:10.1016/j.biocon.2016.09.001

Parsons, A. W., Forrester, T., McShea, W. J., Baker-Whatton, M. C., Millspaugh, J. J., & Kays, R. (2017). Do occupancy or detection rates from camera traps reflect deer density? *Journal of Mammalogy, Advance online publication*. doi:10.1093/jmammal/gyx128

Plumer, L., Davison, J., & Saarma, U. (2014). Rapid Urbanization of Red Foxes in Estonia: Distribution, Behaviour, Attacks on Domestic Animals, and Health-Risks Related to Zoonotic Diseases. *PLoS One, 9*(12). doi:10.1371/journal.pone.0115124

Potts, J. R., Harris, S., & Giuggioli, L. (2013). Quantifying Behavioral Changes in Territorial Animals Caused by Sudden Population Declines. *American Naturalist, 182*(3), E73-E82. doi:10.1086/671260

Pozzanghera, C. B., Sivy, K. J., Lindberg, M. S., & Prugh, L. R. (2016). Variable effects of snow conditions across boreal mesocarnivore species. *Canadian Journal of Zoology, 94*(10), 697-705. doi:10.1139/cjz-2016-0050

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The Rise of the Mesopredator. *Bioscience, 59*(9), 779-791. doi:10.1525/bio.2009.59.9.9

Ridout, M. S., & Linkie, M. (2009). Estimating Overlap of Daily Activity Patterns From Camera Trap Data. *Journal of Agricultural Biological and Environmental Statistics, 14*(3), 322-337. doi:10.1198/jabes.2009.08038

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., . . . Wirsing, A. J. (2014). Status and Ecological Effects of the World's Largest Carnivores. *Science, 343*(6167), 151-+. doi:10.1126/science.1241484

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters, 12*(9), 982-998. doi:10.1111/j.1461-0248.2009.01347.x

Roemer, G. W., Donlan, C. J., & Courchamp, F. (2002). Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences of the United States of America, 99*(2), 791-796. doi:10.1073/pnas.012422499

Roemer, G. W., Gompper, M. E., & Van Valkenburgh, B. (2009). The Ecological Role of the Mammalian Mesocarnivore. *Bioscience, 59*(2), 165-173. doi:10.1525/bio.2009.59.2.9

Roper, T. J. (1994). The european badger meles-meles - food specialist or generalist. *Journal of Zoology, 234*, 437-452.

Rose, M. D., & Polis, G. A. (1998). The distribution and abundance of coyotes: The effects of allochthonous food subsidies from the sea. *Ecology, 79*(3), 998-1007. doi:10.1890/0012-9658(1998)079[0998:tdaaoc]2.0.co;2

Rota, C. T., Ferreira, M. A. R., Kays, R. W., Forrester, T. D., Kalies, E. L., McShea, W. J., . . . Millspaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution, 7*(10), 1164-1173. doi:10.1111/2041-210x.12587

Royle, J. A., & Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology, 84*(3), 777-790. doi:10.1890/0012-9658(2003)084[0777:eafrpa]2.0.co;2

Ruiz-Capillas, P., Mata, C., & Malo, J. E. (2013). Community Response of Mammalian Predators and Their Prey to Motorways: Implications for Predator-Prey Dynamics. *Ecosystems, 16*(4), 617-626. doi:10.1007/s10021-013-9634-7

Saether, B. E., Andersen, R., Hjeljord, O., & Heim, M. (1996). Ecological correlates of regional variation in life history of the moose Alces alces. *Ecology, 77*(5), 1493-1500. doi:10.2307/2265546

Salek, M., Kreisinger, J., Sedlacek, F., & Albrecht, T. (2010). Do prey densities determine preferences of mammalian predators for habitat edges in an agricultural landscape? *Landscape and Urban Planning, 98*(2), 86-91. doi:10.1016/j.landurbplan.2010.07.013

Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation - a review. *Conservation Biology, 5*(1), 18-32. doi:10.1111/j.1523-1739.1991.tb00384.x

Schuette, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation, 158*, 301-312. doi:10.1016/j.biocon.2012.08.008

Shapira, I., Sultan, H., & Shanas, U. (2008). Agricultural farming alters predator-prey interactions in nearby natural habitats. *Animal Conservation, 11*(1), 1-8. doi:10.1111/j.1469-1795.2007.00145.x

Sillero-Zubiri, C., Hoffmann, M., & Macdonald, D. W. (2004). *Canids: Foxes, Wolves, Jackals and Dogs*: IUCN/SSC Canid Specialist Group.

Silva-Rodriguez, E. A., Ortega-Solis, G. R., & Jimenez, J. E. (2010). Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-dominated landscape in southern Chile. *Austral Ecology, 35*(7), 765-777. doi:10.1111/j.1442-9993.2009.02083.x

Simpson, K., Johnson, C. N., & Carver, S. (2016). Sarcoptes scabiei: The Mange Mite with Mighty Effects on the Common Wombat (Vombatus ursinus). *PLoS One, 11*(3). doi:10.1371/journal.pone.0149749

Sklepkovych, B. O., & Montevecchi, W. A. (1996). Food availability and food hoarding behaviour by red and arctic foxes. *Arctic, 49*(3), 228-234.

Soberon, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters, 10*(12), 1115-1123. doi:10.1111/j.1461-0248.2007.01107.x

Soto, C., & Palomares, F. (2015). Coexistence of sympatric carnivores in relatively homogeneous Mediterranean landscapes: functional importance of habitat segregation at the fine-scale level. *Oecologia, 179*(1), 223-235. doi:10.1007/s00442-015-3311-9

Soykan, C. U., & Sabo, J. L. (2009). Spatiotemporal food web dynamics along a desert riparian-upland transition. *Ecography, 32*(2), 354-368. doi:10.1111/j.1600-0587.2008.05615.x

Steven, R., Pickering, C., & Castley, J. G. (2011). A review of the impacts of nature based recreation on birds. *Journal of Environmental Management, 92*(10), 2287-2294. doi:10.1016/j.jenvman.2011.05.005

Stubbe, M. (1980). Population ecology of the Red Fox *Vulpes vulpes* (L., 1758) in the G.D.R. In E. Zimen (Ed.), *The red fox. Symposium on behaviour and ecology.* (pp. 71-96): The Hague-Boston-London.

Taylor, A. R., & Knight, R. L. (2003). Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications, 13*(4), 951-963. doi:10.1890/1051-0761(2003)13[951:wrtraa]2.0.co;2

Thibault, I., & Ouellet, J. P. (2005). Hunting behaviour of eastern coyotes in relation to vegetation cover, snow conditions, and hare distribution. *Ecoscience, 12*(4), 466-475. doi:10.2980/i1195-6860-12-4-466.1

Todd, A., Gunson, J., & Samuel, W. (1981). Sarcoptic mange: an important disease in coyotes and wolves of Albertya, Canada. *Worldwide Furbearer Conference Proceedings, Frostburg, Maryland.*, 706-729.

Tveraa, T., Fauchald, P., Henaug, C., & Yoccoz, N. G. (2003). An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. *Oecologia, 137*(3), 370-376. doi:10.1007/s00442-003-1373-6

Uraguchi, K., Ueno, M., Iijima, H., & Saitoh, T. (2014). Demographic Analyses of a Fox Population Suffering From Sarcoptic Mange. *Journal of Wildlife Management, 78*(8), 1356-1371. doi:10.1002/jwmg.794

Van Valkenburgh, B. (2007). Deja vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology, 47*(1), 147-163. doi:10.1093/icb/icm016

Vanak, A. T., & Gompper, M. E. (2009). Dogs Canis familiaris as carnivores: their role and function in intraguild competition. *Mammal Review, 39*(4), 265-283. doi:10.1111/j.1365-2907.2009.00148.x

Vanak, A. T., Thaker, M., & Gompper, M. E. (2009). Experimental examination of behavioural interactions between free-ranging wild and domestic canids. *Behavioral Ecology and Sociobiology, 64*(2), 279-287. doi:10.1007/s00265-009-0845-z

Vehtari, A., Gelman, A., & Gabry, J. (2016). Practical bayesian model evaluation using leave-one-out cross-validation and WAIC. *arXiv:1507.04544v5 [stat.CO]*.

Virgos, E., Mangas, J. G., Blanco-Aguiar, J. A., Garrote, G., Almagro, N., & Viso, R. P. (2004). Food habits of European badgers (Meles meles) along an altitudinal gradient of Mediterranean environments: a field test of the earthworm specialization hypothesis. *Canadian Journal of Zoology, 82*(1), 41-51. doi:10.1139/z03-205

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., . . . Bairlein, F. (2002). Ecological responses to recent climate change. *Nature, 416*(6879), 389-395. doi:10.1038/416389a

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

Wang, Y. W., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation, 190*, 23-33. doi:10.1016/j.biocon.2015.05.007

Wikenros, C., Stahlberg, S., & Sand, H. (2014). Feeding under high risk of intraguild predation: vigilance patterns of two medium-sized generalist predators. *Journal of Mammalogy, 95*(4), 862-870. doi:10.1644/13-mamm-a-125

Williams, E. S., Yuill, T., Artois, M., Fischer, J., & Haigh, S. A. (2002). Emerging infectious diseases in wildlife. *Revue Scientifique Et Technique De L Office International Des Epizooties, 21*(1), 139-157.

Willson, M. F. (1993). Mammals as seed-dispersal mutualists in north-america. *Oikos, 67*(1), 159-176. doi:10.2307/3545106

With, K. A., & Crist, T. O. (1995). Critical thresholds in species responses to landscape structure. *Ecology, 76*(8), 2446-2459. doi:10.2307/2265819

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation, 3*, 165-173. doi:10.1017/s136794300000086x

Paper I

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ORIGINAL ARTICLE

Spatial and temporal variation in the distribution and abundance of red foxes in the tundra and taiga of northern Sweden

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Abstract Variation in the distribution and abundance of animals in space and time are key concepts of population ecology. We studied these variations in a population of red foxes (*Vulpes vulpes*) in the tundra and taiga of northern Sweden. We analysed 12 years (1974–1985) of snow tracking data from a large area of 65,375 km^2. Specifically, we evaluated to what extent the distribution of red foxes was explained by the presence of prey and how this interacted with snow depth and altitude. We also tested for temporal linear trends in the distribution and abundance of red foxes during the study period. The distribution of red foxes was explained by the presence of rodents, hares, tetraonid species, and ungulates (i.e. carcasses). Snow depth had a negative effect on the impact of small prey on the distribution of the red foxes, whereas it had a positive effect on the impact of ungulates. The influence of hares increased with altitude. Neither distribution nor abundance of red foxes showed a positive or negative linear trend, suggesting a stable population in northern Sweden during our study. This study showed that the distribution of red foxes was not only influenced by the presence of their main prey (rodents), but also by interactions between alternative prey, altitude, and snow depth. This study also emphasizes the importance of ungulate carcasses for red foxes and for wildlife management.

Keywords *Vulpes vulpes* · Carcass · Snow depth · Temporal trends · Alternative prey

Introduction

Understanding how the distribution and abundance of animals vary in space and time is one of the main aims of ecology (Begon et al. 1996). The need for this knowledge is increasingly important today when human alteration of habitats and environmental changes are strongly affecting the majority of ecosystems worldwide (Walther et al. 2002). Food abundance and competition for resources are key determinants for the distribution of organisms (Osenberg and Mittelbach 1996; Persson et al. 1996) although several studies show that the mechanisms governing spatial and temporal variation in these distributions often are complex even in relatively simple food webs (e.g. Krebs et al. 1995; Post et al. 2000).

In recent years, much attention has been focused on top-down effects on the abundance and distribution of mesopredators due to the previous decline and recent return of apex predator populations, e.g. mesopredator release (Courchamp et al. 1999; Prugh et al. 2009; Ritchie and Johnson 2009). However, bottom-up effects mediated by changes in food availability may also affect mesopredator abundance and distribution (Ritchie and Johnson 2009). Increased human population densities and habitat fragmentation may provide new food resources and alter prey abundance, respectively (Kurki et al. 1998; Fahrig 2003).

The red fox (*Vulpes vulpes* Linnaeus, 1758) has one of the largest natural distributions of all mammals (Zimen 1980). It preys on a wide range of animal species and feed

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opportunistically on food resources such as berries and human garbage (Hartova-Nentvichova et al. 2010; Rosalino et al. 2010; Dell'Arte et al. 2007). The red fox occupies highly contrasting habitats (Lariviere and Pasitschniak-Arts 1996), and its distribution and abundance are determined to a large extent by food availability (Barton and Zalewski 2007; Rosalino et al. 2010; Gallant et al. 2012). In Scandinavia, the main prey of the red fox is microtine rodents (Lindström et al. 1987). Consequently, the production of young in Scandinavia is known to follow the 3–4 year cycle of rodents (Englund 1970; Lindström 1989; Lindström et al. 1994). During periods of low availability of main prey, the red fox includes a larger proportion of alternative food resources in its diet, including small game (Angelstam et al. 1984; Lindström et al. 1987) or ungulate carcasses (Jedrzejewski and Jedrzejewska 1992; Selås and Vik 2006; Killengreen et al. 2011). Recent studies have shown that moose carcasses are a main part of the winter diet of the red fox (Needham et al. 2014) and that red fox occupancy increases with higher densities of reindeer in the area (Henden et al. 2014).

The red fox population in Scandinavia increased rapidly from the 1940s to the 1970s (Selås and Vik 2006). This increase was probably facilitated by reduced harvest, absence of large carnivores, and increased food availability (Selås and Vik 2006; Elmhagen and Rushton 2007). The latter may have been caused by both direct and indirect human influences; an increase on human living standards providing more garbage (Killengreen et al. 2011), carcasses, and slaughter remains from increased ungulate populations including semi-domesticated reindeer (Ims et al. 2007; Angerbjörn et al. 2013) and increased abundance of rodents as a result of increased clear-cutting in forestry (Michal and Rafal 2014).

It has been suggested that the increase in the red fox abundance resulted in an expansion to higher altitudes and more northern latitudes since the early twentieth century (Hersteinsson and Macdonald 1992; Post et al. 2009; Killengreen et al. 2011). The overabundance of semi-domestic reindeer in northern Norway (Ims et al. 2007) has probably provided red foxes with carcasses as an important food resource during winter (Henden et al. 2010; Killengreen et al. 2011). Moreover, a warmer climate and an increase in primary production would ultimately lead to higher prey availability (Hersteinsson et al. 1989; Hersteinsson and Macdonald 1992). On the other hand, red foxes were already reported to breed in the open tundra in the first half of the twentieth century (Lönnberg 1926). It is thus unclear if the increased number of red foxes in the tundra is due to range expansion, or if it mirrored a general increase in abundance throughout Fennoscandia.

An increase in the red fox abundance may lead to elevated predation rates which may affect the structure and function of the ecosystem (Lindström et al. 1987, 1994; Danell and Hornfeldt 1987). For example, the densities of mountain hare (*Lepus timidus*), black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*) have increased in periods when the abundance of red foxes was reduced through control or disease (Lindström et al. 1987, 1994; Marcström et al. 1988; Smedshaug et al. 1999). Furthermore, Kjellander and Nordström (2003) found a negative correlation between the number of red fox litters and the ratio of roe deer fawns per doe.

Another example of the ecological impact of an increase in the red fox abundance is the case of the Scandinavian arctic fox (*Vulpes lagopus*). The arctic fox population in Scandinavia experienced a decline due to an intensive harvesting during the first part of the twentieth century (Lönnberg 1926) and has since not recovered. This has been partially attributed to competitive exclusion by red foxes (Hersteinsson and Macdonald 1992; Killengreen et al. 2007; Selås and Vik 2007; Henden et al. 2009) and therefore lethal control of red foxes has been used in experimental management in the tundra region (Angerbjörn et al. 2013). Despite the importance of red foxes and their anticipated positive response to climate change, information on the distribution and population trends of red foxes in the tundra and taiga region of northern Scandinavia is very limited.

The main objective of our study was to investigate how the distribution of red foxes varied in space in relation to the presence of main prey and alternative food resources and to depict the relationships between these bottom up effects, altitude and snow depth. We also investigated the relationship between the red fox distribution and prey species richness. In order to examine factors affecting the distribution of red foxes, we analysed snow tracking data on distribution and abundance of various wildlife species collected during 12 years in the tundra and taiga region of northern Sweden. Additionally, we also examined the relationship between linear temporal trends and altitude in the distribution and relative abundance of this red fox population.

Methods

Study area

This study was part of a monitoring program for the tundra and taiga area in the northernmost county (Norrbotten) in Sweden from 1974 to 1985 (Fig. 1). The data collection was conducted by the Swedish Environmental Protection Agency (SEPA). The study area (65,375 km^2) had a human population density of 0.33 people per km^2 (Statistics Sweden (SCB) 2015) with ca. 5 % of the area covered by human settlements and consisted of four townships. There are several large national parks (5932 km^2) situated in the study area, and most of the land (ca. 42,000 km^2) is managed by the state. Traditional semi-domestic reindeer herding by the indigenous Sami people is extensive in the study area.

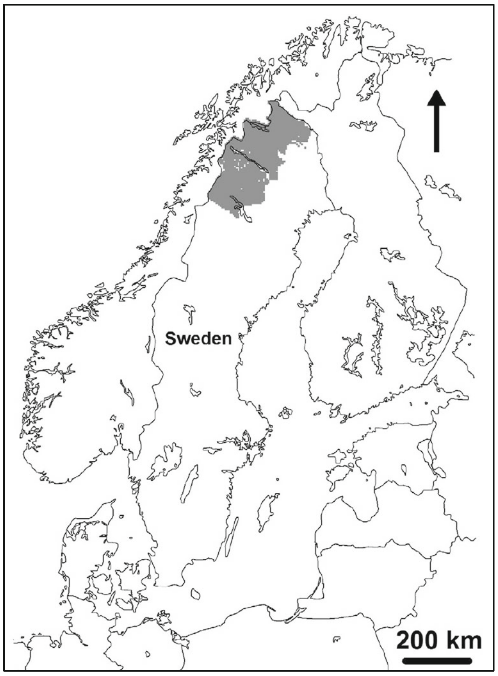

Fig. 1 The location and extent of the study area in northern Sweden where mammals and birds were monitored from 1974 to 1985

The landscape can be divided into three main categories: (1) treeless open tundra with limited vegetation, (2) mountain birch (*Betulla pubescens tortuosa*) forest, and (3) mixed boreal conifer forest dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The tree line in the study area is approximately 950 masl in the southern part and about 600 masl in the northern part. The highest peaks are about 2100 masl and more than 200 glaciers can be found in the area. Potential prey species for the red fox in the study area included mountain hare, red squirrel (*Sciurus vulgaris*), black grouse, capercaillie, hazel grouse (*Bonasa bonasia*), willow grouse (*Lagopus lagopus*), rock ptarmigan (*Lagopus muta*), and small rodents, which consisted of bank vole (*Myodes glareolus*), northern red-backed vole (*Myodes rutilus*), field vole (*Microtus agrestis*), tundra vole (*Microtus oeconomus*), grey-sided vole (*Myodes rufocanus*), water vole (*Arvicola amphibius*), and Norwegian lemming (*Lemmus lemmus*). Large carnivores present in the area included brown bears (*Ursus arctos*), wolverines (*Gulo gulo*), Eurasian lynx (*Lynx lynx*), wolves (*Canis lupus*), and golden eagles (*Aquila chrysaetos*).

Monitoring the abundance and distribution of mammals and birds

The study area consisted of 2080 squared sampling blocks of 25 km^2 that followed the Swedish map grid (RT90) on 5 × 5 km intersections. The distribution and abundance of red foxes and potential prey species were monitored by recording the number of signs per species observed per sampling block. In each block, all signs of mammals and birds were recorded in areas that were accessible with snow mobiles. These signs included tracks in the snow, observations of animals, nesting sites, scats and signs of foraging. Observers attempted to scan and drive the whole study block and would scan the area with binoculars from natural observation points (e.g. knolls or ridges). The length driven within an area was dependent on the degree of tree cover and boulders obstructing the line of sight (5.56 ± 0.10 km per block in average). All tracks were registered as independent tracks unless further investigation showed otherwise. For example, observers followed the tracks in cases when they were uncertain if it was from one or two animals to check if tracks joined up or if two animals had walked in the same track. Snow depth, snow condition, cloud cover, wind and temperature data were also measured in the field. Sampling blocks were monitored once per year from January to May plus a second visit to sampling blocks where bears, wolverines, lynx and wolves had been detected. The same two observers would travel through the same areas, mostly following the same route.

Wind and precipitation can make it difficult to read tracks on the snow. Hence, we only included data collected during periods when favourable conditions of wind, precipitation and snow allowed for the detection of rodent tracks. We used box plots to identify outlayers and removed four observations with values higher than 100 times the average. The resulting data set consisted of 9984 surveys of the 2080 different sampling blocks. Among these blocks, 1195 were visited three or more years (lack of snow and severe weather prevented full coverage in all years).

Environmental data

We calculated the proportion of boreal forest and alpine tundra for each sampling block by using the Intersect function in ArcGis 9.3 (ESRI 2009) where we used a 1:250,000 map from the National Land Survey of Sweden as input data. We calculated mean elevation for each block by using the Zonal Statistics function in ArcGIS 9.3 where we used elevation data from the National Land Survey of Sweden as input data (the resolution of input data was 50 m).

Statistical analysis

Distribution of red foxes

We used model selection to assess how the distribution (presence/absence per sampling block) of red foxes varied in relation to the presence of potential prey species. For this, we fitted logistic mixed effect models by using the function ‘glmer’ in the R package lme4 (Bates et al. 2014; R Development Core Team 2012). We derived a set of 17 candidate models constituted by models with different combinations of the main prey and alternative prey species as explanatory variables, models with an index of prey species richness (number of prey species present in the sampling block), and models with snow depth and altitude interacting in different combinations with the variables listed above. All candidate models included sampling block ID as a random effect for the intercept to control for repeated measures. We were interested in explaining the variations in the data rather than obtaining a strong predicting power and therefore we included models that contained up to 14 explanatory variables. We used variation around the grand mean as a *null model* (i.e. model with no explanatory variables) of no effect of neither of the variables examined. We used Akaike's information criterion (AIC) to rank models and considered models within two AIC units to be of similar quality (Anderson et al. 1998).

Prey species categories were mountain hares, tetraonid species (i.e. black grouse, capercaillie, hazel grouse, willow ptarmigan and rock ptarmigan), small rodents and ungulates (i.e. moose and reindeer as a source of carcasses). The index of species richness was defined as the number of different potential prey species present in the sampling block (i.e. small rodent, mountain hare, black grouse, capercaillie, hazel grouse, willow- and rock ptarmigans, moose and reindeer). We standardized altitude and snow depth variables by using the following equation: $\left(x_i - \overline{X}\right)/(2 \times \mathrm{SD})$ (Gelman and Hill 2007). Altitude was highly correlated with both the proportion of boreal forest (Pearson's $r = -0.75$, $p < 0.001$) and the proportion of tundra ($r = 0.84$, $p < 0.001$). Thus, the variable altitude represented both altitude and habitat composition and we excluded proportion of forest and tundra variables from the models. We checked for collinearity of the explanatory variables, and we found no correlation between any of them.

Temporal trends

When examining for temporal trends in the red fox distribution and relative abundance (average number of signs per sampling block), we restricted the analysis to only include sampling blocks that had been monitored six or more years ($n = 756$ sampling blocks). These blocks were surveyed a total of 6142 times.

We examined temporal trends in the red fox distribution and abundance by using mixed effect models (R Development Core Team 2012). In order to assess the relationship between the linear temporal trends and altitude, we defined three altitude categories by dividing the total altitude range, from 299 to 1419 masl, into three zones of 373.3 m altitude range each, i.e. "low altitude" (<672.5 masl, $n = 3693$ surveys of 452 sampling blocks), "medium altitude" (672.5–1016.1 masl, $n = 1832$ surveys of 224 sampling blocks) and "high altitude" (>1016.1 masl, $n = 617$ surveys of 80 sampling blocks). The altitude categories contained different proportions of boreal forest and tundra (low altitude: 61.51 % boreal forest, 13.10 % tundra; medium altitude: 16.35 % boreal forest, 74.80 % tundra; high altitude: 1.18 % boreal forest, 95.5 % tundra). Both models included sampling block ID as a random effect for the intercept to control for repeated measures.

Results

Distribution of red foxes

Red foxes were present in the majority of the study area in all years. On average, red fox signs were found in 84.29 % (±0.36 S.E.) of the sampling blocks in each year. Hare signs were present in 63.60 % (±0.50 S.E.) of the sampling blocks, rodents in 17.53 % (±0.38 S.E.), tetraonid species in 81.72 % (±0.39 S.E.) and ungulates in 54.18 % (±0.49 S.E.). The model in which the red fox distribution was explained by the species richness index was 170.23 AIC units away from the top model. Instead, the presence of rodents, hares, tetraonids and ungulates was important to explain the distribution of red foxes as indicated by these variables being included in the best models that accounted for 62 % of the overall model fit (Table 1). When excluding the main prey (i.e. rodents), the model showed a delta AIC of 69.57. The best model presented a marginal R^2 of 0.40 (see Nakagawa and Schielzeth 2013). The presence of hares, tetraonid species and ungulates as alternative prey had highly positive effects on the distribution of red foxes (Table 2). These variables interacted with snow depth and altitude in different ways. The interaction with altitude was positive for hares. The confidence intervals of the interaction with altitude for large ungulates and for tetraonids included zero and the effect was therefore inconclusive. The best model also showed a negative interaction with snow depth for hares and a less pronounced positive interaction between snow depth and ungulates. The interaction between tetraonids and snow depth included zero in the confidence intervals, and hence, we were uncertain of its effect (Table 2).

Temporal trends

The presence and number of signs of red foxes per sampling block varied among years (Fig. 2). However, there was no positive or negative linear temporal trend in these variables during the study period (Table 3). Similarly, there was no positive or negative linear temporal trend in any of the different altitude categories neither for the distribution nor the relative abundance of red foxes in the study area (Table 3).

Table 1 Top ranked models explaining the distribution (presence/absence of signs per sampling block) of red foxes in northern Sweden in 1974 to 1985

	Distribution model	K	ΔAIC	AICWt	LL
mod.1	Rodents + (hares + tetraonids + ungulates) * snow depth + (hares + tetraonids + ungulates) * altitude	14	0.00	0.62	−3788.97
mod.2	Rodents + ungulates + (hares + tetraonids) * snow depth + (hare + tetraonids) * altitude	12	2.04	0.22	−3792.00

The table shows model candidates, number of parameters in the model (K), difference in the Akaike's information criterion (ΔAIC), model weights (AICWt), and negative likelihood (LL). Sampling block ID was included as a random effect in all the models

Discussion

The close association between the distributions of red foxes and prey species observed in our study is in accordance with previous findings (Angelstam et al. 1984; Lindström et al. 1987; Hersteinsson and Macdonald 1992). Halpin and Bissonette (1988) found that snow depth affected habitat use of red foxes by shifting the availability of the prey species. However, we show that the magnitude of the effects of different prey categories on the distribution of red fox also depends on altitude and snow depth. This demonstrates that several interacting factors must be taken into account in order to predict the distribution of red foxes, and not only prey abundance or presence.

Ungulates as a source of carcasses have been shown to be a significant part of the diet of red foxes during the winter period or during low density phases in the rodent cycle (Jedrzejewski and Jedrzejewska 1992; Cagnacci et al. 2003; Killengreen et al. 2011; Needham et al. 2014). In our study, we show that the presence of ungulates also affects the spatial distribution of the red fox. Henden et al. (2014) recently showed that the occupancy of the community of scavengers, including the red fox, was higher where the density of reindeer was larger. Selås and Vik (2006) also found a positive correlation between the increase of red fox hunting bags and the increase of ungulate numbers in Norway. During the 12 years of our study, the population of moose experienced a dramatic increase in northern Sweden (Cederlund and Bergstrom 1996). Similarly, the reindeer population in our study area increased markedly and peaked in 1990 (Moen and Danell 2003). Accordingly, the availability of carcasses for the red fox probably increased. The origin of these carcasses possibly was death by disease, inanition under harsh winter conditions, human hunting and predation (Saether et al. 1996; Lavsund et al. 2003; Tveraa et al. 2003). Our results show that the importance of carcasses for the distribution of red foxes interacted with altitude and snow depth. This importance increased as snow depth increased. It is probably easier for the red fox to feed on carcasses rather than on live prey in areas where deep snow makes moving, and therefore hunting, difficult (see Lindström 1983). Also, our study shows that the interaction of altitude with the availability of carcasses was important for the distribution of red foxes. However, the confidence interval included zero, and hence, we are uncertain of the impact of this effect. Given the habitat use of moose and reindeer, the effect of this interaction could represent a bias towards the use of carcasses of one of these species. Nonetheless, the second ranked model in the model selection process differed from the

Table 2 Best model coefficients explaining the distribution of red foxes in northern Sweden in 1974 to 1985 and 95 % confident intervals

Model coefficients		
	Estimates	95 % CI
Intercept	0.081	(−0.062, 0.225)
Rodents	0.707	(0.511, 0.904)
Hares	1.116	(0.968, 1.264)
Tetraonids	1.208	(1.064, 1.352)
Ungulates	0.375	(0.246, 0.504)
Snow depth	0.244	(0.007, 0.482)
Altitude	−0.071	(−0.293, 0.150)
Hares:snow depth	−0.467	(−0.73, −0.206)
Tetraonids:snow depth	−0.218	(−0.481, 0.046)
Ungulates:snow depth	0.265	(0.022, 0.508)
Hares:altitude	0.398	(0.118, 0.679)
Tetraonids:altitude	−0.147	(−0.387, 0.092)
Ungulates:altitude	0.137	(−0.095, 0.370)

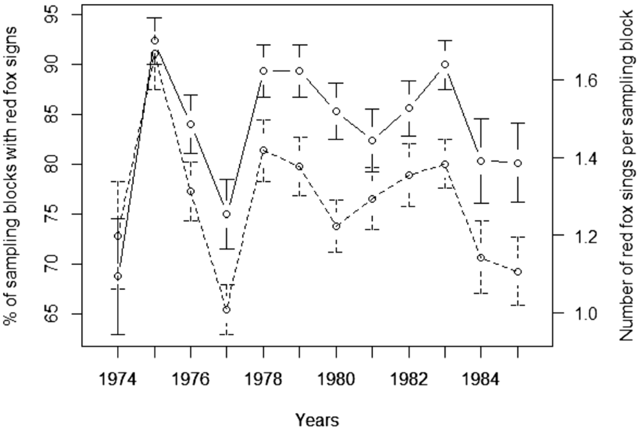

Fig. 2 Annual variation in % of sampling blocks with red fox signs ± 95 % CI (*solid line*) and average number of signs of red fox per sampling block ± 95 % CI (*dash line*) in northern Sweden during the study period

Table 3 Generalized linear mixed model coefficients for the analysis of linear temporal trends in red fox distribution and abundance and 95 % confident intervals

	Presence of red fox signs		Number of red fox signs	
	Estimate	95 % CI	Estimate	95 % CI
(Intercept)	−5.493	(−106.424, 100.989)	16.358	(−35.884, 68.469)
Year	0.003	(−0.050, 0.054)	−0.008	(−0.03, 0.018)
Low altitude	−44.986	(−166.495, 74.353)	3.305	(−49.217, 60.721)
Medium altitude	−1.934	(−135.626, 124.012)	−5.349	(−62.890, 53.146)
Year:low altitude	0.023	(−0.036, 0.084)	−0.001	(−0.030, 0.025)
Year:medium altitude	0.001	(−0.062, 0.069)	0.003	(−0.02, 0.032)

best model in that it did not include the interaction of altitude and snow depth with ungulates. This model was 2.04 AIC points away from the best model. This tells us that the effect of these interactions might not be very strong, but it is important to take them into account, especially in areas with contrasting numbers of different ungulate species. In conclusion, the access to moose and reindeer carcasses may have sustained the population of red foxes in northern Sweden during harsh winters and years of low density of rodents (Killengreen et al. 2011; Needham et al. 2014). Nowadays, the recovery of large carnivores in Scandinavia (Chapron et al. 2014) may increase the availability of ungulate carcasses for red foxes. We believe that a higher availability of carcasses for the red fox could stabilize the temporal dynamics of the red fox populations in Scandinavia.

Tetraonids species such as black grouse and ptarmigan represent an important alternative prey for red foxes (Lindström et al. 1987, 1994; Smedshaug et al. 1999). Indeed, the presence of these species had a pronounced effect on the red fox distribution in our study. However, the confidence intervals of the interactions of tetraonids with altitude and snow depth contained zero. Although the interactions per se were important for the distribution of red fox, the direction of the effects was inconclusive. This uncertainty may be attributed to the fact that we did not differentiate different tetraonid species and pooled species with different ecologies like capercallies and rock ptarmigans. Future studies differentiating bird prey into species may reveal more detailed patterns.

The presence of hares was also an important factor explaining the distribution of the red fox in northern Sweden. Many studies have previously shown the role of this species as an alternative prey of the red fox (Danell and Hornfeldt 1987; Jedrzejewski and Jedrzejewska 1992; Lindström et al. 1994; Kauhala and Helle 2000). However, here, we show that the importance of this species decreased with snow depth. On the other hand, the interaction between hares and altitude was positive. In contrast to tetraonids, hares may be more exposed in the open landscape and thus easier to detect and catch by the red fox at higher altitudes.

According some authors (e.g. Hersteinsson and Macdonald 1992; Fuglei and Ims 2008), warmer temperatures during recent years may have facilitated an expansion of the red fox populations to higher altitudes. Even though a warming trend has been reported in our study area during the period of our study (Jonsell et al. 2013), neither the distribution nor the relative abundance of the red fox showed an increase in northern Sweden. Instead, our data showed a stable population that, despite annual fluctuations, did not manifest any positive or negative temporal linear trend during the study period (i.e. 1974–1985). The red fox was present in an average of 70 % (±2.27 S.E.) of the sampling blocks in the highest altitudes (>1016.1 masl) which were areas consisting almost solely of open tundra and glaciers. Hence, it seems that the red fox was well-established in high altitudes in northern Sweden during the study period. According to Lönnberg (1926), the red fox was breeding in the open tundra already in the early twentieth century.

The sarcoptic mange had a pronounced negative impact on the red fox population in Scandinavia on a large scale (Mörner 1992; Lindström et al. 1994). However, our data show no decrease in the distribution and relative abundance of the red fox despite sarcoptic mange appearing in our study area around 1977–1978 (Lindström and Mörner 1985). We therefore suggest that the sarcoptic mange had a low impact on the red fox population in this part of northern Sweden due to the low population densities and harsh winter conditions.

In our study, we have depicted factors explaining the distribution of the red fox in northern Sweden and their interactions with snow depth and altitude. Moreover, we show that there is a relationship between the distributions of red foxes and ungulates. Management of the Scandinavian red fox populations in high altitudes should take into account the increasing availability of carcasses given the increase in the abundance of several ungulate species (e.g. moose and semi-domestic reindeer; Ims et al. 2007). Furthermore, the relationship between small game, altitude and snow depth has not previously been described. Our study thus demonstrates that several interacting factors may be important for predicting the distribution and dynamics of the red fox in mountain ecosystems.

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References

Anderson DR, Burnham KP, White GC (1998) Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. J Appl Stat 25:263–282

Angelstam P, Lindström E, Widen P (1984) Role of predation in short-term population fluctuations of some birds and mammals in fennoscandia. Oecologia 62(2):199–208. doi:10.1007/bf00379014

Angerbjörn A et al (2013) Carnivore conservation in practice: replicated management actions on a large spatial scale. J Appl Ecol 50:59–67. doi:10.1111/1365-2664.12033

Barton KA, Zalewski A (2007) Winter severity limits red fox populations in Eurasia. Glob Ecol Biogeogr 16:281–289. doi:10.1111/j.1466-8238.2007.00299.x

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, http://CRAN.R-project.org/package=lme4

Begon M, Sait SM, Thompson DJ (1996) Predator–prey cycles with period shifts between two- and three-species systems. Nature 381:311–315. doi:10.1038/381311a0

Cagnacci F, Lovari S, Meriggi A (2003) Carrion dependence and food habits of the red fox in an Alpine area. Ital J Zool 70:31–38

Cederlund G, Bergstrom R (1996) Trends in the moose-forest system in Fennoscandia, with special reference to Sweden. In: DeGraaf RM, Miller RI (eds) Conservation of faunal diversity in forested landscapes. Chapman & Hall, London, pp 265–281

Chapron G et al (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346(6216):1517–1519. doi:10.1126/science.1257553

Courchamp F, Langlais M, Sugihara G (1999) Cats protecting birds: modelling the mesopredator release effect. J Anim Ecol 68(2):282–292. doi:10.1046/j.1365-2656.1999.00285.x

Danell K, Hornfeldt B (1987) Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. Oecologia 73(4):533–536. doi:10.1007/bf00379412

Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimäki E (2007) Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecol-Int J Ecol 31:276–281. doi:10.1016/j.actao.2006.12.007

Elmhagen B, Rushton SP (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol Lett 10:197–206. doi:10.1111/j.1461-0248.2006.01010.x

Englund J (1970) Some aspects of reproduction and mortality rates in Swedish foxes (Vulpes vulpes) 1961–63 and 1966–69. Viltrevy 8:1–82

ESRI (2009) ARCGIS desktop. Environmental Systems Research Institute, Redland

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fuglei E, Ims RA (2008) Global warming and effects on the Arctic fox. Sci Prog 91(Pt 2):175–191. doi:10.3184/003685008x327468

Gallant D, Slough BG, Reid DG, Berteaux D (2012) Arctic fox versus red fox in the warming Arctic: four decades of den surveys in north Yukon. Polar Biol 35:1421–1431. doi:10.1007/s00300-012-1181-8

Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Analytical methods for social research. Cambridge University Press, Cambridge

Halpin MA, Bissonette JA (1988) Influence of snow depth on prey availability and habitat use by red fox. Can J Zool 66:587–592. doi:10.1139/z88-086

Hartova-Nentvichova M, Salek M, Cerveny J, Koubek P (2010) Variation in the diet of the red fox (Vulpes vulpes) in mountain habitats: effects of altitude and season. Mamm Biol 75:334–340. doi:10.1016/j.mambio.2009.09.003

Henden JA, Ims RA, Yoccoz NG (2009) Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. J Anim Ecol 78:636–645. doi:10.1111/j.1365-2656.2008.01510.x

Henden JA, Ims RA, Yoccoz NG, Hellström P, Angerbjörn A (2010) Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. Oikos 119:27–34. doi:10.1111/j.1600-0706.2009.17604.x

Henden JA, Stien A, Bårdsen BJ, Yoccoz NG, Ims RA (2014) Community-wide mesocarnivore response to partial ungulate migration. J Appl Ecol 51(6):1525–1533. doi:10.1111/1365-2664.12328

Hersteinsson P, Macdonald DW (1992) Interspecific competition and the geographical distribution of red and arctic foxes vulpes-vulpes and alopex-lagopus. Oikos 64:505–515. doi:10.2307/3545168

Hersteinsson P, Angerbjörn A, Frafjord K, Kaikusalo A (1989) The arctic fox in fennoscandia and iceland: management problems. Biol Conserv 49:67–81. doi:10.1016/0006-3207(89)90113-4

Ims RA, Yoccoz NG, Bråthen KA, Fauchald P, Tveraa T, Hausner V (2007) Can reindeer overabundance cause a trophic cascade? Ecosystems 10:607–622. doi:10.1007/s10021-007-9060-9

Jedrzejewski W, Jedrzejewska B (1992) Foraging and diet of the red fox vulpes vulpes in relation to variable food resources in bialowieza-national-park, poland. Ecography 15:212–220. doi:10.1111/j.1600-0587.1992.tb00027.x

Jonsell U, Hock R, Duguay M (2013) Recent air and ground temperature increases at Tarfala Research Station, Sweden. Polar Res 32. doi:10.3402/polar.v32i0.19807

Kauhala K, Helle P (2000) The interactions of predator and hare populations in Finland - a study based on wildlife monitoring counts. Ann Zool Fenn 37(3):151–160

Killengreen ST, Ims RA, Yoccoz NG, Brathen KA, Henden J-A, Schott T (2007) Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic fox. Biol Conserv 135:459–472. doi:10.1016/j.biocon.2006.10.039

Killengreen ST, Lecomte N, Ehrich D, Schott T, Yoccoz NG, Ims RA (2011) The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. J Anim Ecol 80:1049–1060. doi:10.1111/j.1365-2656.2011.01840.x

Kjellander P, Nordström J (2003) Cyclic voles, prey switching in red fox, and roe deer dynamics—a test of the alternative prey hypothesis. Oikos 101:338–344. doi:10.1034/j.1600-0706.2003.11986.x

Krebs CJ, Boutin S, Boonstra R, Sinclair A, Smith J, Dale M, Martin K, Turkington R (1995) Impact of food and predation on the snowshoe hare cycle. Science 269:1112–1115. doi:10.1126/science.269.5227.1112

Kurki S, Nikula A, Helle P, Lindén H (1998) Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. J Anim Ecol 67:874–886. doi:10.1046/j.1365-2656.1998.6760874.x

Lariviere S, Pasitschniak-Arts M (1996) Vulpes vulpes. Mamm Species 537:1–11

Lavsund S, Nygren T, Solberg EJ (2003) Status of moose populations and challenges to moose management in Fennoscandia. Alces 39:109–130

Lindström E (1983) Condition and growth of red foxes (vulpes-vulpes) in relation to food-supply. J Zool 199:117–122

Lindström E (1989) Food limitation and social regulation in a red fox population. Holarct Ecol 12:70–79

Lindström E, Mörner T (1985) The spreading of sarcoptic mange among swedish red foxes (vulpes-vulpes l) in relation to fox population-dynamics. Rev Ecol Terre La Vie 40:211–216

Lindström E, Angelstam P, Widen P, Andren H (1987) Do predators synchronize vole and grouse fluctuations?: an experiment. Oikos 48(2):121–124

Lindström E, Andrén H, Angelstam P, Cederlund G, Hörnfeldt B, Jäderberg L, Lemnell PA, Martinsson B, Sköld K, Swenson JE (1994) Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology 75:1042–1049. doi:10.2307/1939428

Lönnberg E (1926) Fjällrävstammen i Sverige 1926. Kungl. Svenska Vetenskapsakademiens skrifter i naturskyddsärenden, 0374–8820; 7. Almqvist & Wiksell

Marcström V, Kenward RE, Engren E (1988) The impact of predation on boreal tetraonids during vole cycles: an experimental study. J Anim Ecol 57:859–872. doi:10.2307/5097

Michal B, Rafal Z (2014) Responses of small mammals to clear-cutting in temperate and boreal forests of Europe: a meta-analysis and review. Eur J For Res 133:1–11. doi:10.1007/s10342-013-0726-x

Moen J, Danell O (2003) Reindeer in the Swedish mountains: an assessment of grazing impacts. Ambio 32:397–402. doi:10.1639/0044-7447(2003)032[0397:ritsma]2.0.co;2

Mörner T (1992) Sarcoptic mange in Swedish wildlife. Rev Sci Tech 11:1115–1121

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. doi:10.1111/j.2041-210x.2012.00261.x

Needham R, Odden M, Lundstadsveen SK, Wegge P (2014) Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. Acta Theriol 59:391–398. doi:10.1007/s13364-014-0188-7

Osenberg CW, Mittelbach GG (1996) The relative importance of resource limitation and predator limitation in food chains. In: Polis A, Winemiller KO (eds) Food webs: integration of patterns and dynamics. Chapman and Hall, pp 134–148

Persson L, Bengtsson J, Menge BA, Power ME (1996) Productivity and consumer regulation—concepts, patterns, and mechanisms. In: Polis A and Winemiller KO (ed) Food webs: integration of patterns and dynamics. Chapman and Hall, pp 396–434

Post DM, Conners ME, Goldberg DS (2000) Prey preference by a top predator and the stability of linked food chains. Ecology 81:8–14. doi:10.1890/0012-9658(2000)081[0008:ppbatp]2.0.co;2

Post E et al (2009) Ecological dynamics across the arctic associated with recent climate change. Science 325:1355–1358. doi:10.1126/science.1173113

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. Bioscience 59:779–791. doi:10.1525/bio.2009.59.9.9

R Development Core Team (2012) R: a language and environment for statistical computing, 2151st edn. R Foundation for Statistical Computing, Vienna

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998. doi:10.1111/j.1461-0248.2009.01347.x

Rosalino LM, Sousa M, Pedroso NM, Basto M, Rosario J, Santos MJ, Loureiro F (2010) The influence of food resources on red fox local distribution in a mountain area of the western mediterranean. Vie Et Milieu Life Environ 60:39–45

Saether BE, Andersen R, Hjeljord O, Heim M (1996) Ecological correlates of regional variation in life history of the moose Alces alces. Ecology 77(5):1493–1500. doi:10.2307/2265546

Selås V, Vik JO (2006) Possible impact of snow depth and ungulate carcasses on red fox (Vulpes vulpes) populations in Norway, 1897–1976. J Zool 269:299–308. doi:10.1111/j.1469-7998.2006.00048.x

Selås V, Vik JO (2007) The arctic fox Alopex lagopus in Fennoscandia: a victim of human-induced changes in interspecific competition and predation? Biodivers Conserv 16:3575–3583. doi:10.1007/s10531-006-9118-6

Smedshaug CA, Selås V, Lund SE, Sonerud GA (1999) The effect of a natural reduction of red fox Vulpes vulpes on small game hunting bags in Norway. Wildl Biol 5:157–166

Statistics Sweden (SCB) (2015). http://www.scb.se/en_/Finding-statistics/Statistics-by-subject-area/Population/Population-composition/Population-statistics/. Accessed 7 Dec 2015

Tveraa T, Fauchald P, Henaug C, Yoccoz NG (2003) An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. Oecologia 137(3):370–376. doi:10.1007/s00442-003-1373-6

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395. doi:10.1038/416389a

Zimen E (1980) The red fox (Biogeographica; v.18). Springer, Netherlands. doi:10.1007/978-94-017-5592-4

Paper II

Seasonal variation in detection probability of red foxes along an environmental gradient in southern Norway.

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Abstract

Several carnivore species are experiencing rapid changes in their range and abundance mainly due to human expansion. The Scandinavian red fox is a good example of this, as its population is increasing, partially as a result of human influence. However, the influence of humans can vary over seasons in highly seasonal areas like Scandinavia. An improved understanding of how and why red fox abundance and activity vary in space and time is needed to predict potential negative outcomes of further population increase. We used 305 camera traps distributed across an area of 18000 km^2 to monitor the probability of detection (a function of abundance and activity) of red foxes during three years in southeastern Norway. We depict how the detectability of red foxes varies seasonally, and how the influence of humans varies among seasons in a north-south gradient of habitat productivity. We studied these variations by fitting zero inflated beta regressions within a Bayesian framework. The daily detection probabilities of foxes averaged at 1.0 ± 1.8 % and the best ranked model included the interactions between season and latitude (proxy for productivity gradient), and between season and availability of hunting disposals. Winter detectability was highest in the southern region whereas seasonal differences were reduced toward the north. The availability of hunting remains increased the detectability of foxes during the autumn, when hunting of big ungulates peaks in this area. This study presents evidence of the seasonal variations of the influences affecting the detection of foxes. Whereas winter detectability was determined by a productivity gradient, autumn fox detectability was influenced by hunting activities. We did not detect any effect of the studied variables on summer detection probabilities. Further human development in marginal habitats will probably affect the detection probability of foxes by altering both the abundance during the winter and the activity patterns of this species.

Introduction

Monitoring the distribution and abundance of carnivores is increasingly important as several species and populations are experiencing rapid changes in their range and abundance (Laliberte & Ripple, 2004; Wolf & Ripple, 2017). Much attention focus on range contractions of large charismatic species such as the tiger (*Panthera tigris*) or the cheetah (*Acinonyx jubatus*) (Dinerstein et al., 2007; Durant et al., 2017). However, in Europe, protective legislation and public support has led to an increase in the numbers of large carnivores (Chapron et al., 2014). Other examples of carnivore community changes in Europe include the expansion of Golden jackals across the continent (*Canis latrans*) (Trouwborst, Krofel, & Linnell, 2015), the colonization of the north west of Italy by the pine marten (*Martes martes*) (Balestrieri et al., 2010), and the increasing abundance and range expansion of the red fox in Scandinavia (Elmhagen et al., 2017). Shifts in distributions and changes in abundance of carnivores may have pronounced impacts on community structures and interactions. An example of this is the increase in the abundance of mesocarnivores when the apex predators are reduced (i.e. mesopredator release hypothesis) (Prugh et al., 2009; Ritchie & Johnson, 2009). In this regard, documenting changes in the mesocarnivore community is particularly important given their central positions in food webs and their wide reaching impact both as potential competitors and predators (Jedrzejewski, Zalewski, & Jedrzejewska, 1993; Lindström et al., 1994).

The red fox (*Vulpes vulpes*) is one of the most widespread mammal worldwide (Sillero-Zubiri, Hoffmann, & Macdonald, 2004). In Scandinavia, foxes have an important role in the boreal ecosystem through their impact on the dynamics of their prey, including small game species such as the capercaillie (Tetrao urogallus), the black grouse (Tetrao tetrix), the mountain hare (Lepus timidus), or the willow grouse (Lagopus lagopus) (Lindström et al., 1994; Smedshaug, Selas, Lund, & Sonerud, 1999). Furthermore, Scandinavian red foxes have received attention because they compete with and prey on the endangered Arctic fox (Alopex lagopus) (Hersteinsson & Macdonald, 1992). Therefore, changes in the red fox abundance and distribution might affect the boreal ecosystem structure and function.

The abundance of Red fox has increased in Scandinavia since the first half of the twentieth century (Elmhagen & Rushton, 2007; Selås & Vik, 2006). It has been suggested that an increase in temperatures due to climate change resulted in an expansion to higher latitudes and altitudes (Elmhagen et al., 2017; Killengreen et al., 2011). Moreover, the subsidization of red foxes by humans through increased availability of hunting remains, access to carcasses originated from reindeer herding activities, or access to waste, might facilitate the colonization of new areas or affect the abundance or activity in occupied locations (Carricondo-Sanchez, Samelius, Odden, & Willebrand, 2016; Killengreen et al., 2011). However, regardless of the ultimate cause of the red fox population increase, it is important to gain an improved knowledge of the proximate factors affecting their distribution and dynamics, and to develop effective methods to monitor their populations. An improved understanding of how and why the red fox activity and distribution patterns vary in space and time is needed to predict the potential outcomes of further population increase.

During the last decades, camera traps have been used to monitor different aspects of animal populations such as distribution (McShea, Forrester, Costello, He, & Kays, 2016), density (Chandler & Royle, 2013) or daily activity patterns (Ridout & Linkie, 2009). In particular, the use of camera traps to obtain occupancy estimates have received much attention (Burton, Sam, Balangtaa, & Brashares, 2012; Linkie, Guillera-Arroita, Smith, & Rayan, 2010). Occupancy models estimate the probability that a species is present in a location as a function of a real latent state and the probability of detection (MacKenzie et al., 2002). However, the study of the detection probability per se can offer interesting insights in activity patterns. Detection probability can be defined as a function of both the abundance and the activity rate (i.e., movement patterns, daily active time) of the studied population (Royle & Nichols, 2003). Therefore, a change in any of these components will be reflected in the detection probability of the species. Regarding red foxes, activity and abundance (and thus, detection probability) are likely to vary substantially both spatially and over time, especially in low productivity and seasonally fluctuating environments like the boreal forests of Scandinavia.

In this study, we depict how the detectability of red foxes varies seasonally, and how the influence of humans varies among seasons in a north-south gradient of habitat productivity. We used camera traps to record the detectability of foxes, expressed as the daily probabilities of detection, for three years in the southeast of Norway.

According to hunting bags counts (Stubbe, 1980), we expected high red fox detectability in winter. Although low temperatures and low availability of food resources during this season might increase the mortality rate of red foxes (Barton & Zalewski, 2007), the mating season in late winter might also increase their activity (Sillero-Zubiri et al., 2004; Stubbe, 1980). Therefore, whereas red fox numbers might decrease during winter, fox activity probably increases. Additionally, we predicted that the influence of humans would be higher in winter, because preys are less available and foxes might depend more anthropogenic food resources (Killengreen et al., 2011; Needham, Odden, Lundstadsveen, & Wegge, 2014). The period from April to June correspond to the denning of foxes (Stubbe, 1980), and therefore, we expected a decrease in red fox detectability and a low influence of humans. We expected this detectability to increase again in the autumn, when the pups venture out of the dens and young adults start dispersing (Lloyd, 1980 as cited in ; Trewhella, Harris, & McAllister, 1988). In addition, hunting for big ungulates peak in the autumn in Norway, which makes more hunting remains availalbe for the red fox. We expected the detectability of red fox to associate positively with hunting activities. Likewise, the proximity of the harsh winter conditions might increase the dependence of foxes on alternative food sources, and therefore, we expected the detectability of foxes to be higher in locations close to human settlements.

Material and methods

Study area

The study area is situated in the southeastern part of Norway and covers approximately 18000 km^2 (Fig. 1). It extends from 58.918N to 61.167N latitude (approximately 250 km) with an altitude ranging from three m.a.s.l. on the coast in the south, to 833 m.a.s.l. in the inland alpine areas in the north. The main climate types are temperate humid with cold summers in the south and temperate humid with very cold winters in the northern alpine areas (Peel, Finlayson, & McMahon, 2007). The human population density ranges from 1.2 inhabitants per square kilometer in the northern marginal areas to 6535.5 in the most populated areas close to Oslo (http://ssb.no).

The study area comprises an environmental gradient extending from periurban and suburban areas in a matrix of forest and agriculture land in the south (counties of Oslo, Ostfold, Akershus and Vestfold), to a low productivity landscape of alpine tundra and forest in the north (counties of Oppland, Telemark and Buskerud). The topography consist on flat and hilly areas in the south to higher altitudes of alpine tundra in the north. The main tree species are Norwegian spruce (*Picea abies*) and Scots pine (*Pinus silvestris*), with other deciduous species like birch (*Betula pubescens*) or hoary alder (*Alnus incana*) (Bouyer et al., 2015).

Camera trapping

The data used in this study is part of a camera trapping design initiated to complement the monitoring program of the Scandinavian lynx population (Linnell, Broseth, Odden, & Nilsen, 2010; Linnell et al., 2007). We used data from 305 cameras obtained from 01/12/2011 to 31/11/2014.

The camera traps were distributed across the study area to ensure total coverage (Fig. 1). Each site was selected to maximize detection by using forest roads, human and animal trails, or natural movement routes. At each site, the camera traps (Reconix models HC500, HC600, PC800, and PC900) were placed 30-60cm above the ground, pointing towards a natural path. They were functional 24 hours a day, all year round. They were set up to be triggered by movement and to take three pictures per activation. A few drops of lure (catnip oil, valerian oil or beaver castorium) were placed in front of each camera, to attract passerby. The sites were visited once a month for maintenance and to collect the photographs that were later uploaded to http://viltkamera.nina.no. See Carricondo-Sanchez, Odden, Linnell, and Odden (2017) for a detailed description of the study design and camera setup.

Data extraction

We extracted (i) the agricultural land, (ii) altitude, and (iii) extra-urban houses from the NT50 map of Norway (http://kartkatalog.geonorge.no) and retrieved (iv) the average population density from a 5 by 5 km^2 map from Statistics Norway (http://kart.ssb.no). We converted agricultural land and population density polygons to rasters of 100m cell size and subsequently to points. We then calculated the planar kernel density of agriculture land, human density, and extra-urban houses with a bandwidth equal to the diameter of an average home range of red fox (26 ± 6.7 km^2) (Walton, Samelius, Odden, & Willebrand, 2017). Additionally, we calculated (v) the distance from each camera to the closest urban area, and obtained (vi) the latitude from each site. We used ArcGis 10.3 (ESRI, 2009) to extract these values. Finally, we calculated the (vii) cumulative numbers of moose and red deer culled (www.ssb.no) per square kilometer at a municipality level each year as a measure of hunting remains available to red fox ('hunting remains' hereafter). All variables were standardized by two standard deviations (Gelman & Hill, 2007). To ensure spatial independence of the camera sites, we grouped cameras too close to each other by creating a grid of square cells of 10.

In order to investigate the seasonal variation in detectability, we defined three 121-days seasons as winter, summer and autumn, based on the biology of the red fox. The winter season (December 1st -- March 31st) represents the months with snow cover and harsh climate conditions. It includes the mating period (Sillero-Zubiri et al., 2004; Stubbe, 1980). The Summer season (May 1st --August 31st) coincides with the denning period (Stubbe, 1980). During the autumn season (September 1st – November 30th), the pups will venture out of the dens and most juvenile dispersal will take place (Lloyd, 1980 as cited in; Trewhella et al., 1988) (Fig. 2).

The daily probability of detection was calculated as the proportion of days per season with at least one red fox detection for each camera. We weighted these values with the number of days that the cameras were active per season. We only considered the cameras that were operational for at least half a season (60 days or more).

Analyses

We checked for collinearity between the variables with Pearson’s correlation tests. We found a high collinearity between latitude and altitude (r= 0.709), so we removed altitude and kept latitude, because it explained a higher proportion of the variation. Exploratory models using year and season as covariates revealed these variables collinear (Fig. 3). As we were mostly interested in seasonal variations, we retained season and discarded year in subsequent models. Nevertheless, we used the exploratory model to show the annual variation in detectability.

We used zero-inflated beta regressions within a Bayesian framework to model the relationship between the probability of detection and the explanatory variables. These models allow for an “excess” of zeros by separating a process generating zeros from a process generating zero and non-zero observations (Martin et al., 2005). With our data, for example, a zero-detection could be due to the absence of fox or to the failure of the camera to detect a fox.

We built 26 candidate models by considering ecologically meaningful combinations of variables and interactions between season and other predictors (Appendix I). The 10km^2 grids were used as a random intercept for both the beta regression and the zero-inflated part of the models. We used season to correct for the seasonal variation in the zero-inflated part in all the models. The models were fitted with the brm function in package brms (Buerkner, 2016) in R (R Core Team, 2017). We used a normal (μ=0, σ=10) and a t-student distribution (df=3) as weakly-informative priors for the fixed coefficient and the random intercept, respectively. We ran three chains with 3000 iterations, discarding the 1000 iterations as as burn-in. Convergence was assessed by visually investigating the convergence plots and with the Gelman and Rubin's convergence diagnostics ($\hat{R}$) (Gelman & Hill, 2007). The leave-one-out cross-validation values (hereafter LOO) were used as a model selection method (Vehtari, Gelman, & Gabry, 2016).

Results

The average daily detection probability was 0.01 ± 0.018 with 58.3% of the observations being zeros. All the models converged visually (Apendix II) and presented a $\hat{R}$ of one. The best ranked model according to the LOO value (Table 1) included the variables season, latitude, hunting remains, and the interactions between season and latitude, and between season and hunting remains.

The highest red fox detectability occurred during the winter season (Fig. 4), consistently over the three years (Fig. 3). Nevertheless, winter detectability decreased from 2013 to 2014, which in turn affected the overall probability of detection between 2013 and 2014 (Fig. 3). Red fox detection probabilities decreased as latitude increased following the productivity gradient (Table 2). Interestingly, this effect was stronger during the winter season. Indeed, at the highest latitudes of low productivity there was no marked differences in detectability among the three seasons (Fig. 5). Whereas there was almost no effect of the availability of hunting remains during summer and winter seasons, this factor had a positive effect on the detection probability of red foxes during the autumn, when the hunting of big ungulates was more intense (Fig. 6). Surprisingly, the variables related to human impact (i.e., density of agriculture, density of extra-urban houses, distance to urban area, and population density) did not show any effect on the probability of detecting a red fox (Table 2).

Discussion

This study presents evidence of the seasonal variations of the influences affecting the detection probabilities of red foxes. Whereas detectability was determined by a habitat productivity gradient in winter, it was influenced by human hunting activities in the autumn. We did not detect any effect of the studied variables on summer probabilities of detection.

We found that the detectability of foxes during winter was markedly higher than during summer and autumn. Winter, as we defined it here, comprises both the mating season and the late dispersion of young individuals (Lloyd, 1980; Stubbe, 1980). During the mating season, the males increase their activity when searching for receptive females, whereas the activity of the females increases when searching for a suitable denning place (Macdonald, 1980). Red foxes may also forage more actively in winter when food is less available. Furthermore, given the nocturnal character of the red fox (Macdonald & Reynolds, 2004), the long winter nights probably favor longer active periods. A higher activity of red foxes during this season may have a greater influence in the detection probabilitiy than the mortality due to harsh conditions (Barton & Zalewski, 2007). A peak in the winter has been also reported in hunting bag counts (Stubbe, 1980).

However, the differences in fox detectability between seasons decreased toward the north of our study area, where detectability in winter was lower. This reflects, at a lower scale, the negative latitudinal gradient in fox densities shown in Barton and Zalewski (2007) which has also been observed in microtine rodents, the main prey of red fox (Jedrzejewski & Jedrzejewska, 1996). Here we show that this gradient also affects the detectability of the fox. The latitudinal gradient comprises a productivity gradient in our study area. It encompassed the transition from more productive areas in the south, corresponding to the boreonemoral vegetation zone, to the higher and less productive boreal vegetation zone in the north, mainly composed of alpine areas (Hagen et al., 2013). The harsh winter conditions found in the latter, especially during periods of low availability of prey, can be physiologically challenging for red foxes and may affect survival, reducing their numbers (Barton & Zalewski, 2007), and thus causing the lower detectability and the low seasonal differences in northern areas.

As expected, the summer months showed the lowest detectability of red foxes. This season mostly comprises the gestation, suckling and weaning periods, most of which taking place in or nearby the den (Macdonald, 1980). These activities are carried out by females while males are still actively foraging. Moreover, sex ratio is male-biased in red foxes (approximately 1.5:1) (Stubbe, 1980). Nonetheless, the proportion of females in the population which activity goes undetected may be sufficient to lower the overall red fox activity. In consequence, the probability of detecting red foxes decreased during this period.

The detectability of foxes during the autumn slightly increased after the summer months, and was positively associated with the availability of hunting remains. The moose hunting season in Norway is open from September 25th to December 23th with small variations between municipalities, and it overlaps with red deer hunting which is only closed from mid-April to mid-July (http://www.miljodirektoratet.no). Moose hunting represented 92.78% of all hunting in our analyses, and therefore it had the highest influence in the detectability of foxes. It has been shown that the availability of carcasses improves the survival of red foxes low prey availability periods like winter (Cagnacci, Lovari, & Meriggi, 2003; Carricondo-Sanchez et al., 2016). During the peak of the hunting season, the availability of hunting disposals is probably at its highest. Therefore, the detection probability of foxes may increase by an increased movement rate when foxes search for carcasses or cache remaining parts in preparation for the harsh winter period (Sklepkovych & Montevecchi, 1996; Vander Wall, 1990).

However, the detectability of foxes was lower than expected during autumn. Detection probabilities of red fox could potentially increase due to the recruitment and the dispersal of young adults mostly happening during the autumn months (Lloyd, 1980 as cited in ; Trewhella et al., 1988). Nevertheless, the movement of pups when they venture out of the dens is restricted (Devenish-Nelson, Richards, Harris, Soulsbury, & Stephens, 2014), and therefore, the increase in activity due to this early recruitments may not influence the probability of detecting red foxes in our camera traps.

Interestingly, we did not detect any association of the detection probability of red foxes with the density of agriculture, exurban houses or distance to urban areas. It has been previously reported that the proportion of agriculture land has a negative impact on the size of red fox home ranges (Walton et al., 2017), and that the availability of anthropogenic food increases the presence of red foxes and other canid species close to human settlements (Fedriani, Fuller, & Sauvajot, 2001; Killengreen et al., 2011; Novak, Wolf, Coblentz, & Shepard, 2017). Furthermore, Carricondo-Sanchez et al. (2017) showed that red foxes affected by sarcoptic mange were more often encountered in the vicinity of human settlements than healthy foxes. The density of agriculture land and human settlements could affect some aspects of the red fox population dynamics like abundance or territory size, but these effects might not be mirrored in fox detectability. Dissociations between abundance and probability of detection (i.e. lower detectability at higher densities) have been already reported between two similar species, the Andean cat (*Leopardus jacobita*) and the Pampas cat (*Leopardus colocolo*) (Reppucci, Gardner, & Lucherini, 2011). Moreover, Parsons et al. (2017) found similar dissociations for white tail deer that were close to urban areas and in natural areas were the deer was hunted. They argued that different movement patterns in these areas might be the cause of this dissociation; deer might be less active during daytime in the forest and might forage more actively closer to humans during the night. This was also the case with pumas and bobcats in urbanized areas (Lewis et al., 2015). It can be similar for foxes in developed areas. They might be less active in natural patches, where our cameras were located, and forage more widely for alternative food sources close to human settlements or agricultural fields. Further analyses on these data should focus on the temporal activity patterns of the red fox in relation to human development (Frey, Fisher, Burton, & Volpe, 2017).

In conclusion, our results suggest that human activity might influence the changes in detectability of foxes in southeastern Norway. High human disturbance and food subsidization may reduce winter mortality and alter activity patterns respectively, which in turn, affect the detectability in the winter. On the other hand, autumn detection probabilities are mainly influenced by subsidization through hunting disposals. Further human development in marginal habitats and a lack of management of hunting disposal and human waste will probably affect the detection probability of foxes by altering both the abundance during winter and the activity patterns.

The use of camera traps for the study of animal activity is a topic that is increasingly gaining interest in the scientific community, especially for the study of daily temporal patterns (Carricondo-Sanchez, Vanak, Kulkarni, & Odden, 2018; Frey et al., 2017). Here, we demonstrate the validity of camera traps to study the variation in the detectability of foxes across seasons and show how habitat characteristics and human activities can affect this detectability. The dissociation between probability of detection and density might mislead management decisions. Parsons et al. (2017) recommended not using detection rates for making management decisions in heterogeneous landscapes since variations in a particular landscape feature (e.g. variation in house density or agriculture land) might influence the detection of the animal. However, good density estimates are difficult to obtain, especially for species where individual recognition is not possible. In these cases, indexes are commonly used. Population density will influence detection probabilities to some extent, and thus, the study of this aspect will be useful to inspect and monitor changes over time, which would be otherwise difficult to observe.

References

Balestrieri, A., Remonti, L., Ruiz-Gonzalez, A., Gomez-Moliner, B. J., Vergara, M., & Prigioni, C. (2010). Range expansion of the pine marten (Martes martes) in an agricultural landscape matrix (NW Italy). *Mammalian Biology, 75*(5), 412-419. doi:10.1016/j.mambio.2009.05.003

Barton, K. A., & Zalewski, A. (2007). Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography, 16*(3), 281-289. doi:10.1111/j.1466-8238.2007.00299.x

Bouyer, Y., Martin, G. S., Poncin, P., Beudels-Jamar, R. C., Odden, J., & Linnell, J. D. C. (2015). Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. *Biological Conservation, 191*, 291-299. doi:10.1016/j.biocon.2015.07.007

Buerkner, P. (2016). brms: Bayesian regression models using stan. . *R package version 0.8.0. https://CRAN.R-project.org/package=brms*.

Burton, A. C., Sam, M. K., Balangtaa, C., & Brashares, J. S. (2012). Hierarchical Multi-Species Modeling of Carnivore Responses to Hunting, Habitat and Prey in a West African Protected Area. *PLoS One, 7*(5). doi:10.1371/journal.pone.0038007

Cagnacci, F., Lovari, S., & Meriggi, A. (2003). Carrion dependence and food habits of the red fox in an Alpine area. *Italian Journal of Zoology, 70*(1), 31-38.

Carricondo-Sanchez, D., Odden, M., Linnell, J. D. C., & Odden, J. (2017). The range of the mange: Spatiotemporal patterns of sarcoptic mange in red foxes (Vulpes vulpes) as revealed by camera trapping. *PLoS One, 12*(4). doi:10.1371/journal.pone.0176200

Carricondo-Sanchez, D., Samelius, G., Odden, M., & Willebrand, T. (2016). Spatial and temporal variation in the distribution and abundance of red foxes in the tundra and taiga of northern Sweden. *European Journal of Wildlife Research, 62*(2), 211-218. doi:10.1007/s10344-016-0995-z

Carricondo-Sanchez, D., Vanak, A. T., Kulkarni, A., & Odden, M. (2018). Co-occurrence of meso-carnivores in a human dominated landscape in Maharashtra, Inda.*, In preparation.*

Chandler, R. B., & Royle, J. A. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *Annals of Applied Statistics, 7*(2), 936-954. doi:10.1214/12-aoas610

Chapron, G., Kaczensky, P., Linnell, J. D. C., von Arx, M., Huber, D., Andren, H., . . . Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science, 346*(6216), 1517-1519. doi:10.1126/science.1257553

Devenish-Nelson, E. S., Richards, S. A., Harris, S., Soulsbury, C., & Stephens, P. A. (2014). Demonstrating frequency-dependent transmission of sarcoptic mange in red foxes. *Biology Letters, 10*(10). doi:10.1098/rsbl.2014.0524

Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., . . . Songer, M. (2007). The fate of wild tigers. *Bioscience, 57*(6), 508-514. doi:10.1641/b570608

Durant, S. M., Mitchell, N., Groom, R., Pettorelli, N., Ipavec, A., Jacobson, A. P., . . . Young-Overton, K. (2017). The global decline of cheetah Acinonyx jubatus and what it means for conservation. *Proceedings of the National Academy of Sciences of the United States of America, 114*(3), 528-533. doi:10.1073/pnas.1611122114

Elmhagen, B., Berteaux, D., Burgess, R. M., Ehrich, D., Gallant, D., Henttonen, H., . . . Angerbjorn, A. (2017). Homage to Hersteinsson and Macdonald: climate warming and resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Research, 36*. doi:10.1080/17518369.2017.1319109

Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters, 10*(3), 197-206. doi:10.1111/j.1461-0248.2006.01010.x

ESRI. (2009). ARCGIS desktop. Environmental Systems Research Institute, Redland.

Fedriani, J. M., Fuller, T. K., & Sauvajot, R. M. (2001). Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography, 24*(3), 325-331. doi:10.1034/j.1600-0587.2001.240310.x

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 Sensing in Ecology and Conservation, 3*(3), 123-132. doi:10.1002/rse2.60

Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models.* . Cambridge: Cambridge University Press.

Hagen, D., Svavarsdottir, K., Nilsson, C., Tolvanen, A. K., Raulund-Rasmussen, K., Aradottir, A. L., . . . Halldorsson, G. (2013). Ecological and Social Dimensions of Ecosystem Restoration in the Nordic Countries. *Ecology and Society, 18*(4), 14. doi:10.5751/es-05891-180434

Hersteinsson, P., & Macdonald, D. W. (1992). Interspecific competition and the geographical-distribution of red and arctic foxes Vulpes-vulpes and Alopex-lagopus. *Oikos, 64*(3), 505-515. doi:10.2307/3545168

Jedrzejewski, W., & Jedrzejewska, B. (1996). Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta Theriologica, 41*(1), 1-34.

Jedrzejewski, W., Zalewski, A., & Jedrzejewska, B. (1993). Foraging by pine marten martes martes in relation to food resources in Bialowieza national-park, Poland.

. *Acta Theriologica, 38*(4), 405-426.

Killengreen, S. T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N. G., & Ims, R. A. (2011). The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. *Journal of Animal Ecology, 80*(5), 1049-1060. doi:10.1111/j.1365-2656.2011.01840.x

Laliberte, A. S., & Ripple, W. J. (2004). Range contractions of North American carnivores and ungulates. *Bioscience, 54*(2), 123-138. doi:10.1641/0006-3568(2004)054[0123:rconac]2.0.co;2

Lewis, J. S., Logan, K. A., Alldredge, M. W., Bailey, L. L., VandeWoude, S., & Crooks, K. R. (2015). The effects of urbanization on population density, occupancy, and detection probability of wild felids. *Ecological Applications, 25*(7), 1880-1895. doi:10.1890/14-1664.1

Lindström, E. R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., . . . Swenson, J. E. (1994). Disease reveals the predator - sarcoptic mange, red fox predation, and prey populations. *Ecology, 75*(4), 1042-1049. doi:10.2307/1939428

Linkie, M., Guillera-Arroita, G., Smith, J., & Rayan, D. M. (2010). Monitoring tigers with confidence. *Integrative Zoology, 5*(4), 342-350. doi:10.1111/j.1749-4877.2010.00215.x

Linnell, J. D. C., Broseth, H., Odden, J., & Nilsen, E. B. (2010). Sustainably Harvesting a Large Carnivore? Development of Eurasian Lynx Populations in Norway During 160 Years of Shifting Policy. *Environmental Management, 45*(5), 1142-1154. doi:10.1007/s00267-010-9455-9

Linnell, J. D. C., Odden, J., Andren, H., Liberg, O., Andersen, R., Moa, P., . . . Okarma, H. (2007). Distance rules for minimum counts of Eurasian lynx Lynx lynx family groups under different ecological conditions. *Wildlife Biology, 13*(4), 447-455. doi:10.2981/0909-6396(2007)13[447:drfmco]2.0.co;2

Lloyd, H. G. (1980). *The Red Fox*: Batsford.

Macdonald, D. W. (1980). Social factors affecting reproduction amongst red foxes. In E. Zimen (Ed.), *The red fox. Symposium on behaviour and ecology.* (pp. 123-175): The Hague-Boston-London.

Macdonald, D. W., & Reynolds, J. C. (2004). Red fox Vulpes vulpes. In C. Sillero-Zubiri, M. hoffmann, & D. W. Macdonald (Eds.), *Canids: Foxes, Wolves, Jackals and Dogs* (pp. 129:135). Gland, Switzerland and Cambridge, UK.: IUCN/SSC Canid Specialist Group.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology, 83*(8), 2248-2255. doi:10.2307/3072056

Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., . . . Possingham, H. P. (2005). Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters, 8*(11), 1235-1246. doi:10.1111/j.1461-0248.2005.00826.x

McShea, W. J., Forrester, T., Costello, R., He, Z. H., & Kays, R. (2016). Volunteer-run cameras as distributed sensors for macrosystem mammal research. *Landscape Ecology, 31*(1), 55-66. doi:10.1007/s10980-015-0262-9

Needham, R., Odden, M., Lundstadsveen, S. K., & Wegge, P. (2014). Seasonal diets of red foxes in a boreal forest with a dense population of moose: the importance of winter scavenging. *Acta Theriologica, 59*(3), 391-398. doi:10.1007/s13364-014-0188-7

Novak, M., Wolf, C., Coblentz, K. E., & Shepard, I. D. (2017). Quantifying predator dependence in the functional response of generalist predators. *Ecology Letters, 20*(6), 761-769. doi:10.1111/ele.12777

Parsons, A. W., Forrester, T., McShea, W. J., Baker-Whatton, M. C., Millspaugh, J. J., & Kays, R. (2017). Do occupancy or detection rates from camera traps reflect deer density? *Journal of Mammalogy, Advance online publication*. doi:10.1093/jmammal/gyx128

Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Koppen-Geiger climate classification. *Hydrology and Earth System Sciences, 11*(5), 1633-1644.

Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The Rise of the Mesopredator. *Bioscience, 59*(9), 779-791. doi:10.1525/bio.2009.59.9.9

Reppucci, J., Gardner, B., & Lucherini, M. (2011). Estimating detection and density of the Andean cat in the high Andes. *Journal of Mammalogy, 92*(1), 140-147. doi:10.1644/10-mamm-a-053.1

Ridout, M. S., & Linkie, M. (2009). Estimating Overlap of Daily Activity Patterns From Camera Trap Data. *Journal of Agricultural Biological and Environmental Statistics, 14*(3), 322-337. doi:10.1198/jabes.2009.08038

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters, 12*(9), 982-998. doi:10.1111/j.1461-0248.2009.01347.x

Royle, J. A., & Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology, 84*(3), 777-790. doi:10.1890/0012-9658(2003)084[0777:eafrpa]2.0.co;2

Selås, V., & Vik, J. O. (2006). Possible impact of snow depth and ungulate carcasses on red fox (Vulpes vulpes) populations in Norway, 1897-1976. *Journal of Zoology, 269*(3), 299-308. doi:10.1111/j.1469-7998.2006.00048.x

Sillero-Zubiri, C., Hoffmann, M., & Macdonald, D. W. (2004). *Canids: Foxes, Wolves, Jackals and Dogs*: IUCN/SSC Canid Specialist Group.

Sklepkovych, B. O., & Montevecchi, W. A. (1996). Food availability and food hoarding behaviour by red and arctic foxes. *Arctic, 49*(3), 228-234.

Smedshaug, C. A., Selas, V., Lund, S. E., & Sonerud, G. A. (1999). The effect of a natural reduction of red fox Vulpes vulpes on small game hunting bags in Norway. *Wildlife Biology, 5*(3), 157-166.

Stubbe, M. (1980). Population ecology of the Red Fox *Vulpes vulpes* (L., 1758) in the G.D.R. In E. Zimen (Ed.), *The red fox. Symposium on behaviour and ecology.* (pp. 71-96): The Hague-Boston-London.

Trewhella, W. J., Harris, S., & McAllister, F. E. (1988). Dispersal distance, home-range size and population-density in the red fox (vulpes-vulpes) - a quantitative-analysis. *Journal of Applied Ecology, 25*(2), 423-434. doi:10.2307/2403834

Trouwborst, A., Krofel, M., & Linnell, J. D. C. (2015). Legal implications of range expansions in a terrestrial carnivore: the case of the golden jackal (Canis aureus) in Europe. *Biodiversity and Conservation, 24*(10), 2593-2610. doi:10.1007/s10531-015-0948-y

Vander Wall, S. B. (1990). *Food hoarding in animals.* . Chicago: University of Chicago Press.

Vehtari, A., Gelman, A., & Gabry, J. (2016). Practical bayesian model evaluation using leave-one-out cross-validation and WAIC. *arXiv:1507.04544v5 [stat.CO]*.

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

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science, 4*(7). doi:10.1098/rsos.170052

Tables

Table 1. Leave-One Out cross validation values and standard error for the highest ranked candidate models in ascendant order.

Model ID	Model structure*	LOO	SE
Model19	latitude + season + hunt + hunt : season + latitude : season	-902.78	78.13
Model18	latitude + season + hunt + hunt : season	-901.68	78.13
Model14	latitude + season + latitude : season	-899.62	78.03
Model16	latitude + season + hunt	-899.08	78.07

*All models included grid ID as a random intercept in the zero inflated and the beta regressions.
All models included season in the zero inflated regression.

Table 2. Parameter estimates from the best ranked model when studying the variation in the detection probability of red foxes.

	Estimate	Est.Error	l-95% CRI	u-95% CRI	$\hat{R}$
Beta distribution effects					
Intercept	-3.39	0.05	-3.49	-3.28	1
Latitude	-0.12	0.06	-0.24	-0.01	1
Summer	-0.42	0.08	-0.58	-0.26	1
Autumn	-0.27	0.08	-0.43	-0.11	1
Hunting/km^2	-0.05	0.05	-0.15	0.05	1
Hunting/km^2 : Summer	0.04	0.09	-0.14	0.2	1
Hunting/km^2 : Autumn	0.23	0.09	0.06	0.39	1
Latitude : Summer	0.14	0.08	-0.02	0.31	1
Latitude : Autumng	0.03	0.08	-0.13	0.18	1
Random intercept	0.17	0.08	0.01	0.3	1.01
Zero-inflated effects					
zi_Intercept	-0.5	0.19	-0.87	-0.14	1
zi_Summer	0.63	0.21	0.22	1.03	1
zi_Autumn	0.79	0.21	0.4	1.22	1
Random intercept	1.13	0.17	0.82	1.46	1

Figures

Figure 1. Location of the study area in southeastern Norway where we studied the seasonal variation in the detection probabilities of red foxes. Gray squares are the 10 km^2 sampled cells grouping close cameras.

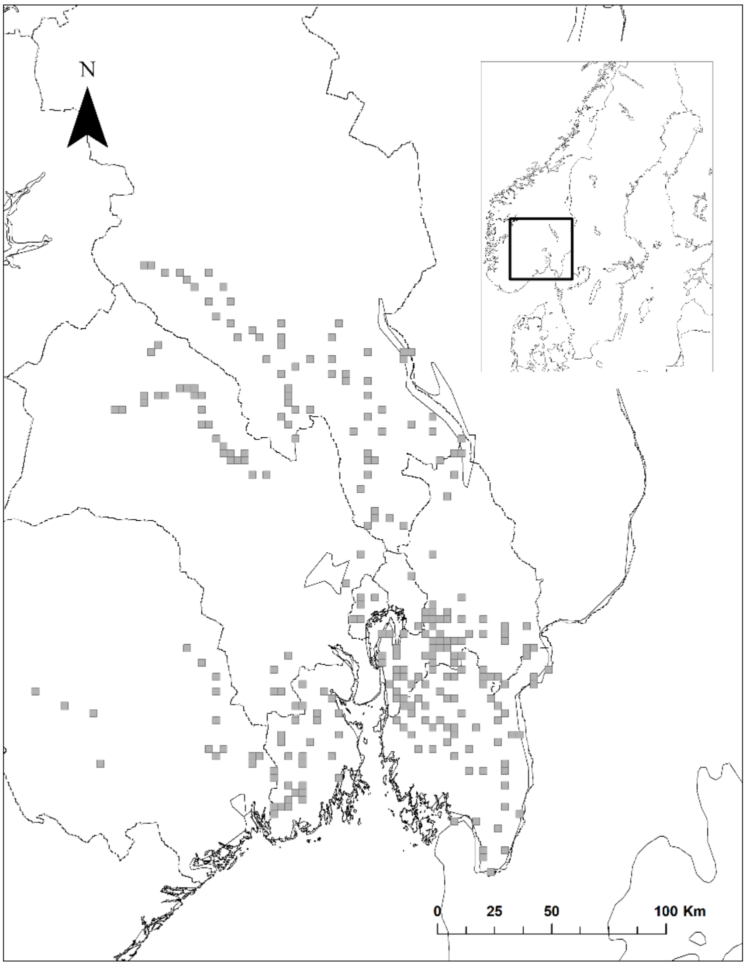


Figure 2. Justification of the three studied seasons defined according the biology of the red fox to investigate the variations in detectability of red fox.

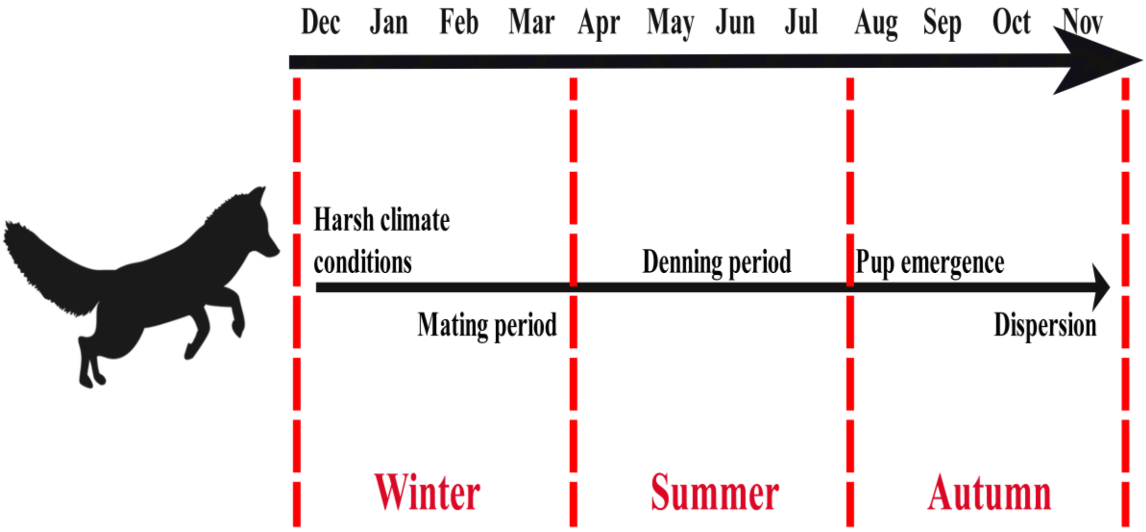


Figure 3. Detection probabilities of red foxes for each season and year of the study period. Dots represent the posterior means and bars are the 95% credible intervals.

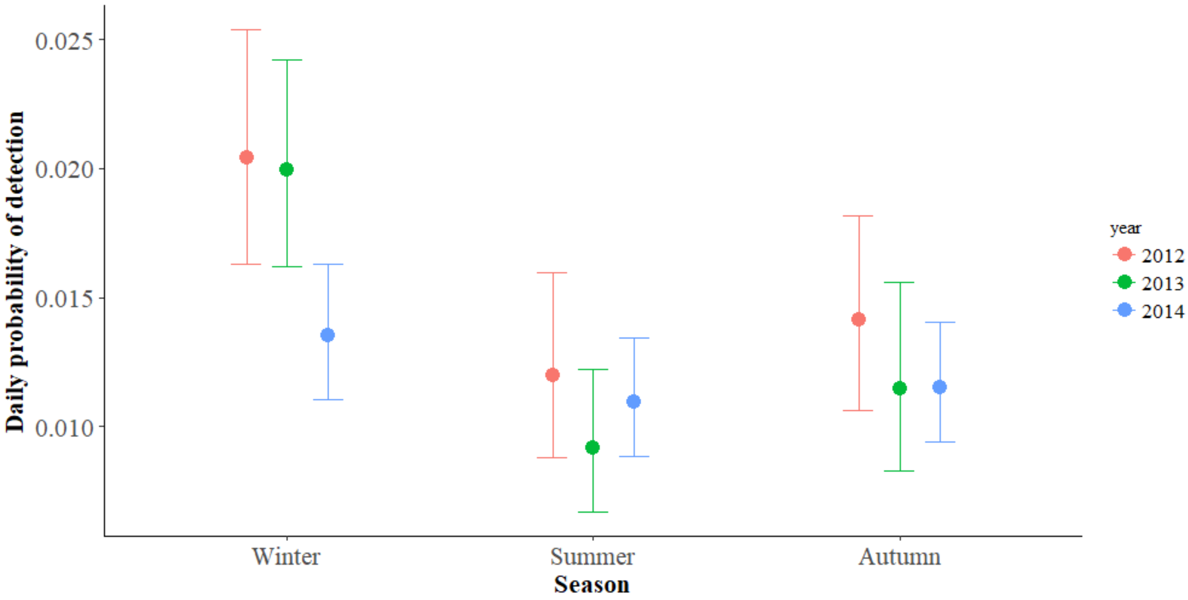


Figure 4. Variation in the detection probability of red fox per season. Dots represent the posterior means and bars are the 95% credible intervals.

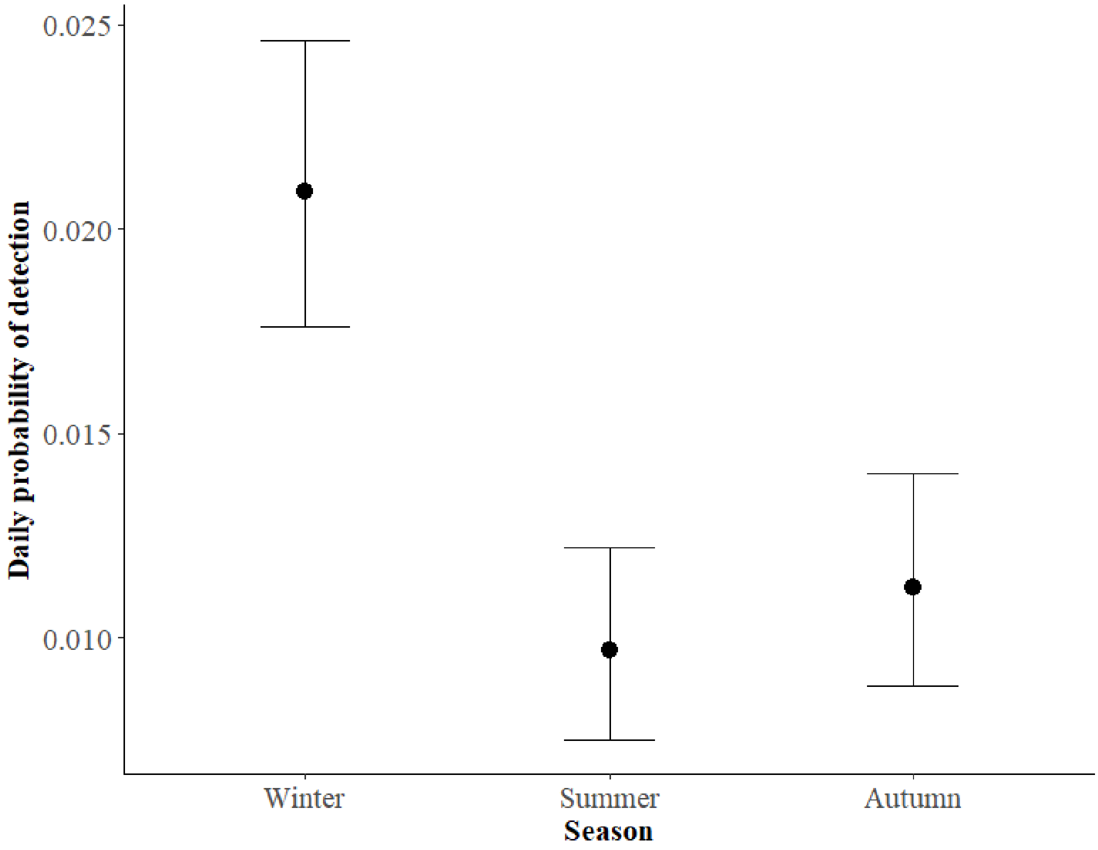


Figure 5. Marginal daily detection probabilities of red foxes as a function of the latitude for each season. Solid lines represent the posterior mean s and ribbons are the 95% credible intervals.

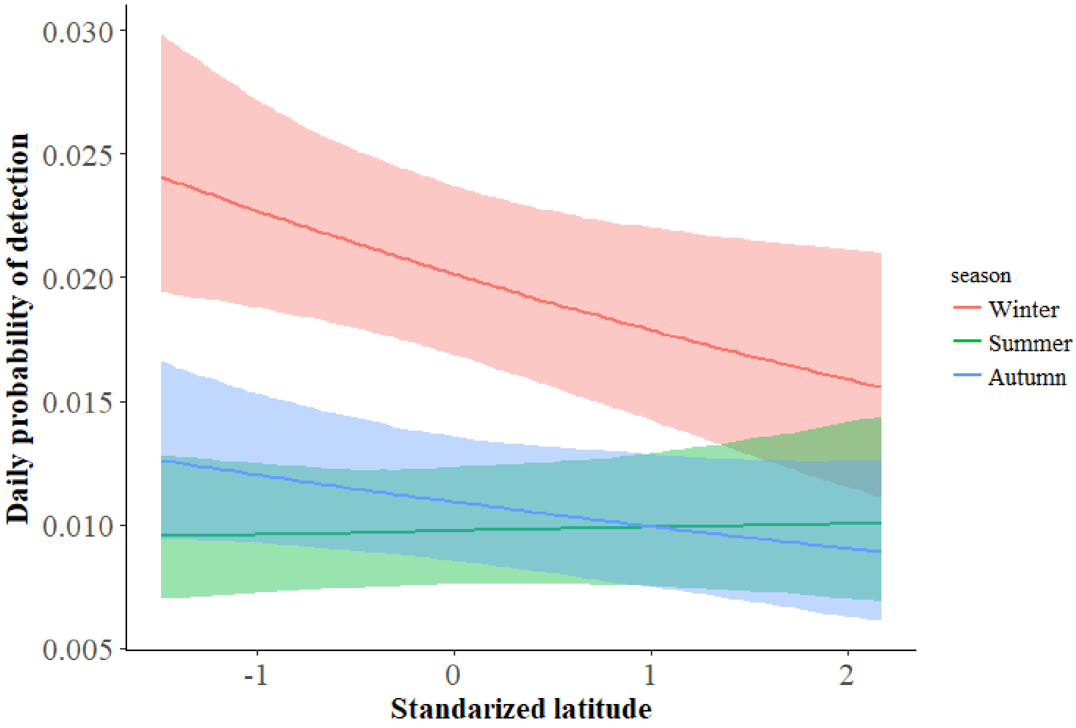
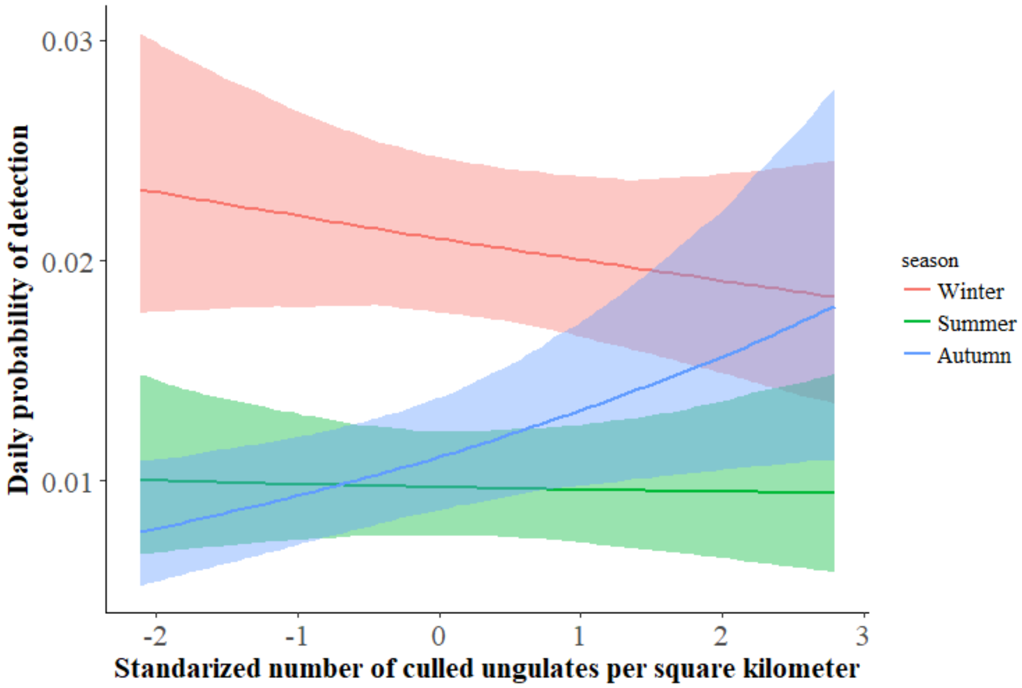


Figure 6. Marginal daily detection probabilities of red foxes as a function of the standardized number of culled ungulates per square kilometer (i.e. availability of hunting disposals) for each season. Solid lines represent the posterior mean s and ribbons are the 95% credible intervals.



Appendices

Appendix I. List of candidate models for the spatial and temporal variation of the detection probability of red fox in the boreal forest.

Model1

prob.eff ~ (1|grid),
zi~ (1|grid)

Model2

prob.eff ~ agriculture_st+humsett_st+dist_set_st+pop_den_st+latitude_st+season+ (1|grid),
zi~ (1|grid)

Model3

prob.eff ~ agriculture_st+humsett_st+dist_set_st+pop_den_st+latitude_st+season+
agriculture_st:season +humsett_st:season +dist_set_st:season +pop_den_st:season +
latitude_st:season+ (1|grid),
zi~ (1|grid)

Model4

prob.eff ~ agriculture_st+humsett_st+dist_set_st+pop_den_st+latitude_st+season+
agriculture_st:season +humsett_st:season +dist_set_st:season +pop_den_st:season +
latitude_st:season+ (1|grid)
zi~ season+(1|grid)

Model5

prob.eff ~ agriculture_st+latitude_st+season+
agriculture_st:season +latitude_st:season+ (1|grid)
zi~ season+(1|grid)),

Model6

prob.eff ~ agriculture_st+humsett_st+latitude_st+season+
agriculture_st:season +humsett_st:season +latitude_st:season+ (1|grid)
zi~ season+(1|grid)

Model7

prob.eff ~ agriculture_st+humsett_st+dist_set_st+latitude_st+season+
agriculture_st:season +humsett_st:season +pop_den_st:season +
latitude_st:season+ (1|grid)
zi~ season+(1|grid)),

Model8

prob.eff ~ humsett_st+latitude_st+season+
humsett_st:season +latitude_st:season+ (1|grid)
zi~ season+(1|grid)

Model9

prob.eff ~ humsett_st+dist_set_st+season+
humsett_st:season +dist_set_st:season +latitude_st:season+1|grid)
zi~ season+(1|grid)

Model10

prob.eff ~ humsett_st+dist_set_st+pop_den_st+latitude_st+season+
humsett_st:season +dist_set_st:season +pop_den_st:season +latitude_st:season+
(1|grid)
zi~ season+(1|grid)

Model11

prob.eff ~ dist_set_st+latitude_st+season+
dist_set_st:season +latitude_st:season+ (1|grid)
zi~ season+(1|grid)

Model12

prob.eff ~ dist_set_st+pop_den_st+latitude_st+season+
dist_set_st:season +pop_den_st:season +latitude_st:season+ (1|grid)
zi~ season+(1|grid)

Model13

prob.eff ~ pop_den_st+latitude_st+season+pop_den_st:season +latitude_st:season+(1|grid)
zi~ season+(1|grid)

Model14

prob.eff ~ latitude_st+season+latitude_st:season+ (1|grid)
zi~ season+(1|grid)

Model15

prob.eff ~ season+hunt+(1|grid)

zi~ season+(1|grid)

Model16

prob.eff ~ latitude_st+season+hunt+ (1|grid)

zi~ season+(1|grid)

Model17

prob.eff ~ latitude_st+season+hunt+ latitude_st:season+(1|grid)

zi~ season+(1|grid)

Model18

prob.eff ~ latitude_st+season+ hunt+hunt:season+ (1|grid)

zi~ season+(1|grid)

Model19

prob.eff ~ latitude_st+season+hunt+hunt:season+latitude_st:season+ (1|grid)

zi~ season+(1|grid)

Model20

prob.eff ~ agriculture_st+humsett_st+dist_set_st+pop_den_st+latitude_st+hunt+season+ (1|grid)

zi~ season+(1|grid)

Model21

prob.eff ~ agriculture_st+humsett_st+dist_set_st+pop_den_st+latitude_st+hunt +season+ agriculture_st:season +humsett_st:season +dist_set_st:season +pop_den_st:season + latitude_st:season+hunt:season+(1|grid)

zi~ (1|grid)

Model22

prob.eff ~dist_set_st+latitude_st+hunt+season+dist_set_st:season+ latitude_st:season+hunt:season + (1|grid)

zi~ (1|grid)

Model23

prob.eff ~dist_set_st+hunt+season+dist_set_st:season+hunt:season+ (1|grid)

zi~ (1|grid)

Model24

prob.eff ~ agriculture_st+latitude_st+hunt+season+ agriculture_st:season+dist_set_st:season+latitude_st:season+hunt:season+(1|grid)

zi~ (1|grid)

Model25

prob.eff ~humsett_st+latitude_st+hunt+season+ humsett_st:season+latitude_st:season+hunt:season+(1|grid)

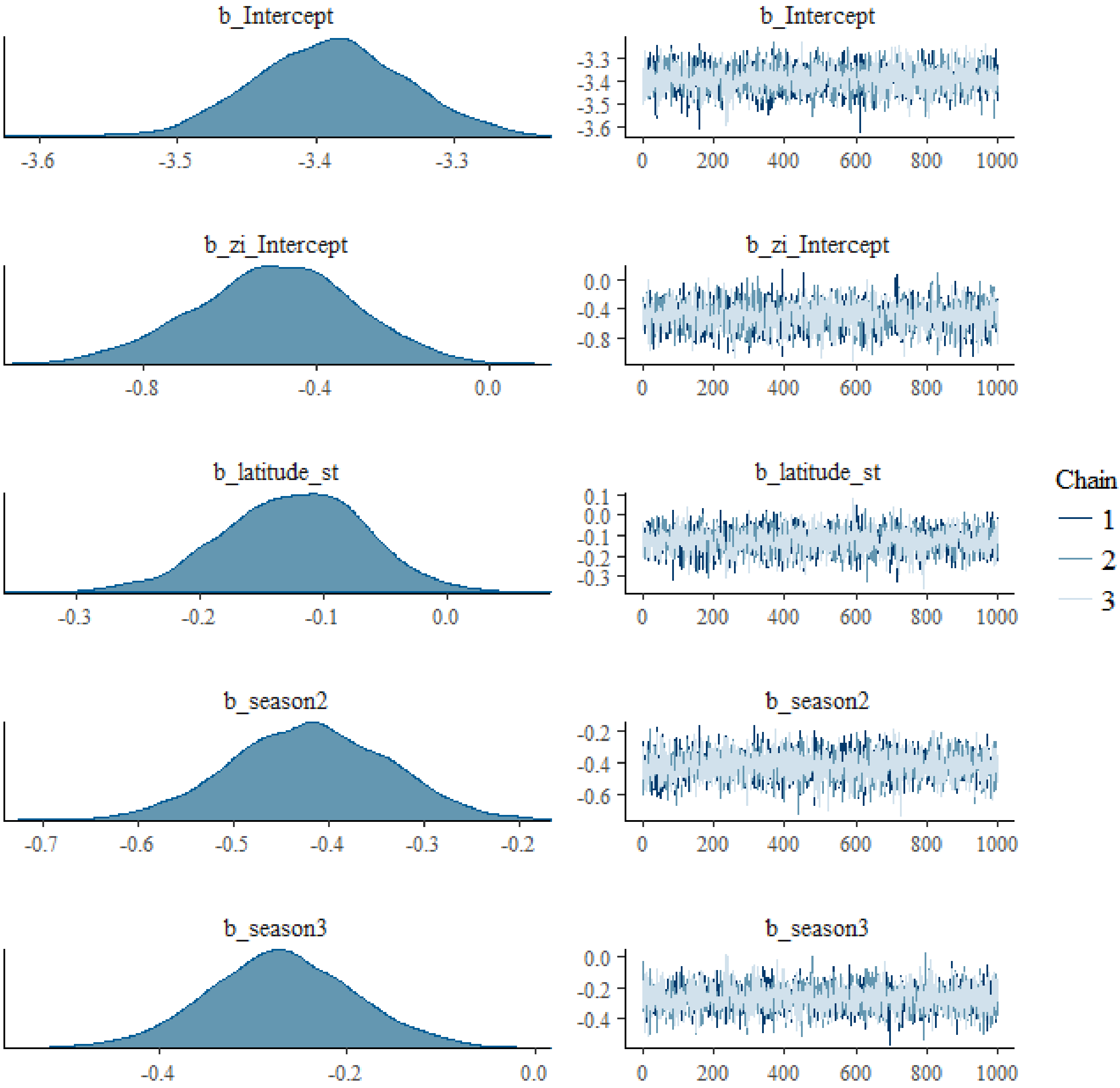
zi~ (1|grid)

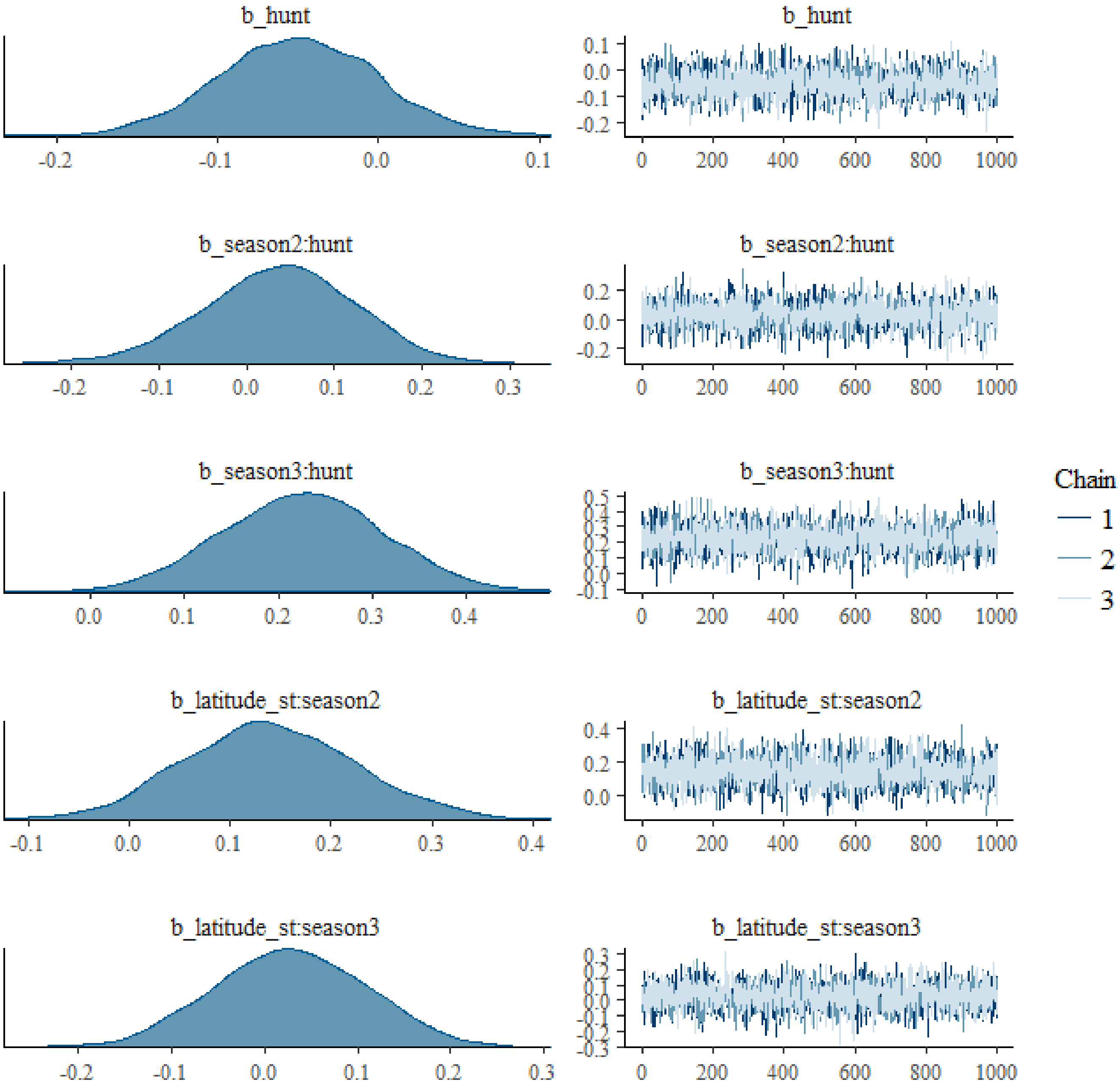
Model26

prob.eff ~pop_den_st+latitude_st+hunt+season+ pop_den_st:season+latitude_st:season+hunt:season+ (1|grid)

zi~ (1|grid)

Appendix II. Density plots and traceplots of the beta coefficients of the best ranked model according to its LOO value.




b_hunt
-0.2
-0.1
0.0
0.1
b_hunt
0.1
0.0
-0.1
-0.2
0
200
400
600
800
1000
b_season2:hunt
-0.2
-0.1
0.0
0.1
0.2
0.3
b_season2:hunt
0.2
0.0
-0.2
0
200
400
600
800
1000
b_season3:hunt
0.0
0.1
0.2
0.3
0.4
b_season3:hunt
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
0
200
400
600
800
1000
Chain
1
2
3
b_latitude_st:season2
-0.1
0.0
0.1
0.2
0.3
0.4
b_latitude_st:season2
0.4
0.2
0.0
0
200
400
600
800
1000
b_latitude_st:season3
-0.2
-0.1
0.0
0.1
0.2
0.3
b_latitude_st:season3
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0
200
400
600
800
1000

Paper III

RESEARCH ARTICLE

The range of the mange: Spatiotemporal patterns of sarcoptic mange in red foxes (*Vulpes vulpes*) as revealed by camera trapping

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Abstract

Sarcoptic mange is a widely distributed disease that affects numerous mammalian species. We used camera traps to investigate the apparent prevalence and spatiotemporal dynamics of sarcoptic mange in a red fox population in southeastern Norway. We monitored red foxes for five years using 305 camera traps distributed across an 18000 km^2 area. A total of 6581 fox events were examined to visually identify mange compatible lesions. We investigated factors associated with the occurrence of mange by using logistic models within a Bayesian framework, whereas the spatiotemporal dynamics of the disease were analysed with space-time scan statistics. The apparent prevalence of the disease fluctuated over the study period with a mean of 3.15% and credible interval [1.25, 6.37], and our best logistic model explaining the presence of red foxes with mange-compatible lesions included time since the beginning of the study and the interaction between distance to settlement and season as explanatory variables. The scan analyses detected several potential clusters of the disease that varied in persistence and size, and the locations in the cluster with the highest probability were closer to human settlements than the other survey locations. Our results indicate that red foxes in an advanced stage of the disease are most likely found closer to human settlements during periods of low wild prey availability (winter). We discuss different potential causes. Furthermore, the disease appears to follow a pattern of small localized outbreaks rather than sporadic isolated events.

Introduction

Sarcoptic mange is a parasitic disease caused by the burrowing mite *Sarcoptes scabiei* (L., 1758, Latrielle, 1802). This disease is widely distributed around the world and it affects a wide range of mammalian species. Sarcoptic mange has been reported in Eurasian lynx (*Lynx lynx*) [1], European rabbits [2], Iberian ibex (*Capra pyrenaica*) [3] and different wolf populations (*Canis lupus*) [4–6] in Europe. It has also been reported in coyotes (*Canis latrans*) in North America [7], wombats (*Vombatus ursinus*) in Australia [8, 9] or recently in Kenyan giraffes (*Giraffa*

15S8929D, 15SFD167, 15S16550, 15SE02F8, 14S45EDF, 14SC0029, 14SB22EC, 14SD5FF3, 14SCB72C, 13S80C87, 1377EF0, 13FD9B6, 1311C1E, 2012/397, 2012/395, 2011/404, 2011/506, 14SBF770).

Competing interests: The authors have declared that no competing interests exist.

camelopardalis reticulata) [10]. Overall, it affects over 100 mammalian species and the red fox (*Vulpes vulpes*) is one of the most important hosts [11].

Due to the burrowing activity of the mite, the host can develop thickening of the skin (hyperkeratosis), irritation of the skin (erythema), dermatitis (seborrhea) and patchy hair loss (alopecia) as the most common symptoms [12–15]. In species like the red fox, death usually occurs within 2–4 months [16, 17].

Epizootics of sarcoptic mange can affect the dynamics and behaviour of the affected population, for example by increasing natural mortality rates [18] or altering the territoriality of the animals [19]. These epizootics can be especially dramatic in endangered and fragmented populations [20, 21], and can even lead to extinction [22]. Host populations can eventually recover from epizootics of mange, although times are relatively long, ranging from 15 to 20 years [7, 23, 24]. After recover, the disease can enter an enzootic phase in which the parasite is still, locally or globally, present in the population [14, 25]. At this stage, the disease can re-emerge in short-term fluctuations or even causing new outbreaks [24, 26].

Sarcoptic mange has received much attention in studies of red foxes [13, 14, 23, 27], mainly due to dramatic outbreaks like the one that occurred in Scandinavia in the late 1970´s, or the later and more localized outbreak in Bristol (UK) in 1994 [28]. The social behaviour of this species [29] and their natal-dispersal and exploratory movements facilitate these outbreaks [30–32]. These behaviours promote the spread of the disease either by direct physical contact or indirectly (e.g. from sharing dens) [33].

In Fennoscandia, the disease spread from southeastern Finland in 1967 to Sweden where the first mangy foxes were reported in 1972, and in Norway in 1975 [16, 25]. The outbreak reduced red fox numbers drastically [23, 34]. The reduction in the red fox population revealed a pronounced impact on grouse populations [35], and on other alternative prey species such as the mountain hare (*Lepus timidus*) and roe deer (*Capreolus capreolus*) fawns [23, 36].

Monitoring enzootic diseases within a population is especially important in social species like the red fox [29] that utilize resources of anthropogenic origin as a supplement to their diet [37, 38]. An advanced state of sarcoptic mange undermines the body condition of red foxes [17, 26, 27], which in turn, can lead to a decrease in their hunting success or a poor ability to compete for carcasses [27, 39]. These individuals may be forced to look for “easier” food resources such as garbage. Mangy foxes close to human settlements might represent a threat to the health of wild and companion animals or livestock, and even to humans [40–43]. It is therefore important to understand the spatiotemporal dynamics of the disease in order to assess this threat and to take the necessary measures.

We used the non-invasive technique of camera trapping in order to investigate the spatiotemporal dynamics of sarcoptic mange in red foxes. Traditionally, researchers have inspected hunting bags or used physical capture-recapture techniques to study this disease on wildlife. This may lead to biases since red foxes with poor body condition might show a different trapability as well as being easier targets for hunters. To date, very few studies have used camera traps to detect or monitor sarcoptic mange outbreaks. Nevertheless, some studies have applied this tool along with laboratory techniques to assess sarcoptic mange in wolves [4, 5]. Borchard et al. [9] also used motion-sensing cameras to study the activity of mangy wombats. However, in our study we carried out the most extensive camera trap assessment of sarcoptic mange in wildlife that have been conducted so far.

In our study, we used five years of camera trap data to investigate large-scale patterns of sarcoptic mange apparent prevalence in red foxes. We hypothesize that patterns of spatial distribution differ between healthy and infected red foxes, as the latter may be more dependent on easily accessible food resources due to the negative impact of sarcoptic mange on body condition [17, 26, 27]. Therefore, we predicted that red foxes showing evident symptoms of sarcoptic mange would occur in areas closer to human settlements more frequently than healthy red foxes. Our second hypothesis states that if the disease is in an enzootic state in Norway, and given the social character of the red fox there are frequent intraspecific interactions that facilitate transmission, then the dynamic of the disease should follow patterns of local outbreaks rather than random isolated events. This is the case in other fox populations where sarcoptic mange is in an enzootic state [24, 26].

Material and methods

Study area

We used data from a long-term camera trapping study of Eurasian lynx (Scandlynx, http://scandlynx.nina.no). The study was conducted in the southeastern part of Norway (Fig 1), in three study areas covering a total of ca. 18000 km^2. Area A covered ca. 6573 km^2 to the east of Oslo fjord, and included parts of the counties of Oslo, Akershus and Østfold. Area B was situated west of Oslo fjord and covered ca. 7145 km^2. It included parts of the counties of Vestfold, Buskerud and Telemark. Area C covered ca. 4474 km^2, and was situated north of the other two areas and included parts of the counties of Oppland and Buskerud (Fig 1). For cameras placed in national park land, permissions were obtained from the Country administrations in Oslo and Akershus and Østfold. Most cameras were placed on private land, and here permissions were obtained from the landowner. No other specific permission are required for these locations according to Norwegian law.

The study areas cover a gradient from periurban or suburban areas to a fragmented forest —farmland mosaic in the areas closest to Oslo and Oslo fjord, to forest dominated landscapes towards the north, west, and east [44]. The forests are mainly composed of Norwegian spruce (*Picea abies*), Scots pine (*Pinus silvestris*), interspersed with deciduous species such as hoary alder (*Alnus incana*) and birch (*Betula pubescens*) [44].

Camera trapping

The camera trapping was initiated to complement the lynx population monitoring program in areas where the commonly used method of snowtracking was inefficient due the unpredictable snow conditions [45, 46]. The project started as a pilot study in Area A during the winter of 2010/2011, and in Area B during the summer of 2011. Later, the project was fully implemented in Area A in the winter of 2011/2012, in the summer of 2012 in Area B, and in the winter of 2013/2014 in area C. Areas A and B were expanded in the summer of 2014 and Area A expanded again in the winter of 2015. We used data from the winter of 2010/2011 to the summer of 2015.

Cameras were dispersed across a grid overlaid over the study areas to ensure that all parts of the areas were covered. However, within each grid cell the specific locations were selected to maximise the probability of detecting lynx; typically forest roads, human and game trails, or natural movement routes at the base of steep cliffs. At each location, a camera trap was placed 30–60 cm above the ground pointing 90 degrees towards the path. All sites had one Reconyx camera with infrared flash (Models HC500, HC600, PC800, and PC900). In Area A and B most locations had an additional camera with white flash (Cuddeback Capture or Reconyx PC850) on the other side of the path so that pictures of both sides of the lynx could be photographed for individual recognition. Previous studies have shown that the use of lures do not affect population or individual parameters like immigration rates, maximum movement distance or temporal activity [47, 48]. On the other hand, not using attractants may underestimate the number of individuals [49]. Therefore, we added some drops of lure (catnip oil, valerian oil or beaver castorium) in front of the camera. The cameras ran for 24 hours a day, all year

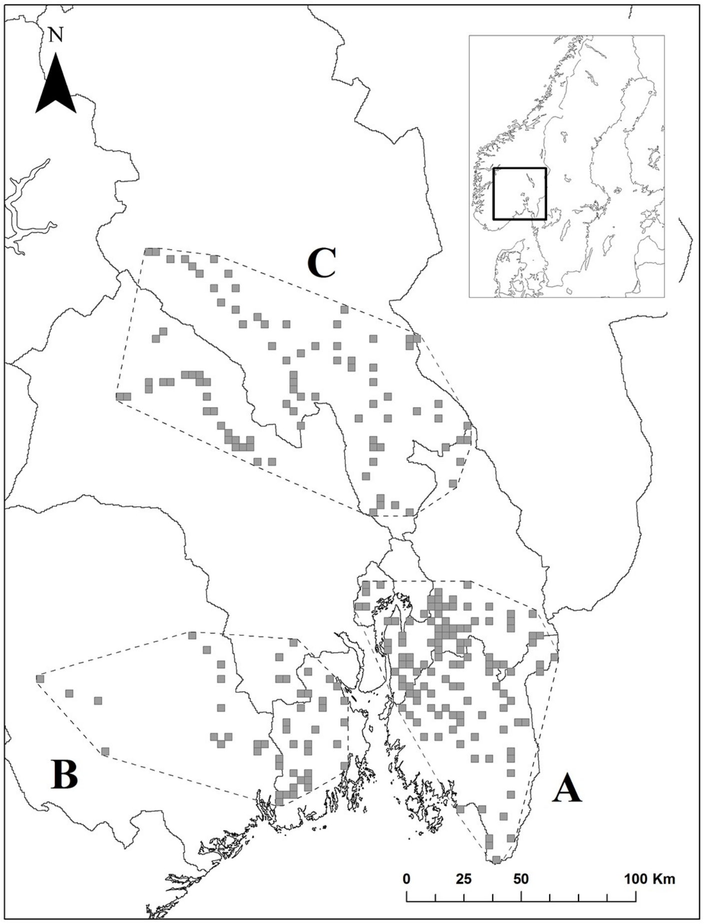

Fig 1. Study area. Location and extent of three areas (A, B, and C) in southeastern Norway where we studied spatiotemporal patterns of sarcoptic mange in red foxes with camera traps. Gray squares are sampled 10 km^2 cells. Dashed lines are minimum convex polygons around camera locations in each of the study areas.

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round, and were set up to be triggered by movement and take three pictures per event. The camera traps were checked once a month, to download pictures, change batteries and add lure. All the pictures from these camera traps were uploaded online at http://viltkamera.nina.no.

All the pictures obtained from the cameras were visually checked online and from the raw data obtained from Scandlynx. Each group of three pictures taken consecutively by a camera was considered a single event. Red fox events were selected and visually checked for mange-compatible lesions like alopecia in the lower back and tail of the animal as previously described by Oleaga et al. [5] (e.g. Fig 2). A single researcher conducted a first round of identification, and subsequently, two other researchers rechecked events that had been difficult to classify. Red foxes with low or moderate infections can be more difficult to identify in locations with only infrared cameras than in locations with both infrared and white flash cameras. We classified as infected only red foxes with distinct patterns of mange-compatible lesions. For example, we were careful not to classify as infected individuals that only had poor body condition, but no alopecic patches. Likewise, we did not consider individuals showing only small alopecic patches as infected, as this could be other external wounds. Furthermore, we disregarded pictures that were out of focus or burned, and hence, we avoided potential bias caused by the use of cameras with different types of flash.

Fig 2. An example of two camera trapped red foxes with mange-compatible lesions.

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Analyses

We used data from 305 camera trap locations working for 146607 effective trapping nights from winter 2010/2011 to summer 2015. We used all the cameras with red fox detection events for the analyses.

Pseudoreplication is a common problem when working with photographic material from naturally unmarked species. For this study, we created a fishnet grid of square cells of 10 km^2 in order to group cameras too close together. This cell size exceeded the average area of red fox home ranges (7.06 km^2; [50]). Following this method, we ensured spatial independence of observations from each grid cell. Red foxes usually die, from two to four months after infection; although this time can vary [16, 17, 27]. Accordingly, in order to investigate how the disease developed over time and to ensure temporal independence among observations, we divided the total study period into six-months time periods. Winter periods spanned from October until March (roughly the months with snow cover) and summer periods from April to September (snow free months).

Apparent prevalence. We defined prevalence as the proportion of camera trapping events of red foxes with mange-compatible lesions over the total number of red fox events. However, since we did not conduct serological tests to confirm that the infected cases corresponded to actual sarcoptic mange cases, we considered the prevalence calculated in this study as apparent prevalence. We calculated the apparent prevalence of the disease for each of the three areas in each of the time periods and calculated the Bayesian credible intervals (CRI hereafter) by using Beta (0.5, 0.5) prior distributions of the probability of success (i.e. a mangy fox event). For this we used the function binom.bayes in the R package binom [51].

Model selection. In each 10 km^2 cell, we calculated (i) the proportion of agricultural land, (ii) the proportion of the area covered by human settlements, and (iii) human population density (Table 1). For the two former variables, we extracted data from the Vegetation Map of Norway [52], and for the latter, we retrieved data from a 5x5 km resolution map of population density from Statistics Norway (http://kart.ssb.no). For each camera location, we calculated (iv) the distances to the nearest settlement. We used the software ArcGis 10.3 [53] for all GIS analyses. In addition to the covariates listed above, we included (v) the time each event occurred expressed as the number of months that had passed since the initiation of the study, (vi) the frequency of red fox photographic events, i.e. the average number of fox events per day in each six months time period and area (A, B or C), (vii) season (winter or summer) and (viii) area (A, B or C; Table 1).

Table 1. Variables used in logistic models of the occurrence of red foxes showing mange-compatible lesions in southeastern Norway.

Name of variable	Definition of variable	Type of variable
Dist_Settle	Distance to closest settlement from camera location in kilometres.	Numeric
Agriculture	Percentage of the grid cell covered by agriculture land.	Numeric
HumSettle	Percentage of the grid cell covered by human settlements.	Numeric
Hum_pop	Human population density with 5km resolution.	Numeric
Time	Continuous variable indicating the number of months since the beginning of the study (from 1 to 60).	Numeric
Avg_pic_day	Average number of events per area and per day in each time period.	Numeric
Season	Winter (October to March) or Summer (April-September).	Factor
Area	Factor designating the three study areas.	Factor
Grid_id	Individual id for the 10 km^2 sampling grid cells.	Factor
Time period	Number of the six-months time period in which the study was divided	Numeric

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We ran Pearson correlation tests for all combinations of covariates. The correlation coefficients (r) ranged from -0.26 to 0.31, and we considered these values too small to indicate dependency among the covariates. Therefore, we included all the variables in the models. We also produced spline correlograms in order to check for spatial autocorrelation. The spline correlogram indicated some spatial autocorrelation that we corrected by including individual cell id as random effect in the models. All the numeric variables were standardized by $(x_i - \bar{X})/(2 \times SD)$ [54].

We created a list of nine candidate models based on our predictions. We included models with different combinations of covariates related to activity and distribution of humans, red fox distribution, time and area (Table 2). We also constructed models that included interactions between season and the most relevant human related variables, and interactions between time and area. We included a *null model* of variation around the grand mean (Table 2). We used a grid cell id and time period as random factors to avoid spatial and temporal autocorrelation of the response respectively.

We used each event as an observation of a binomial process (presence of mange-compatible lesion on the fox or not) and modelled them in a Bayesian framework using the brm function in the brm package [55] in R (www.r-project.com), version 3.3.1. We used normal distributions with mean = zero and standard deviation = 10 as non-informative priors for the explanatory variables and a t-student distribution with three degrees of freedom as a non-informative prior for the random effects. Models were fitted using four chains with 3000 iterations each, of which 1000 were discarded as a burn-in process. Following this procedure, we obtained a total of 8000 posterior samples per model. We used leave-one-out-cross correlation values (LOO) as indicators of model fit and used it for model selection [56]. We visually checked for the convergence of the models by looking at the density distribution plots and by using the Gelman and Rubin´s converge diagnosis [57] represented by $\hat{R}$ in our analyses.

Spatiotemporal scan analysis

For the detection of potential clusters of disease occurrence, we used the Kulldorff algorithm [58] based on a Bernouilli probability model. This algorithm is implemented in the scan analysis software SATSCAN (www.satscan.org), version 9.4.2, and analyses three dimension cylindrical windows centered at the discrete locations of the study. It takes into account the positive and negatives events in the scanned cylindrical window where the height of the cylinder

Table 2. Set of candidate logistic models for the occurrence of red foxes showing mange-compatible lesions in southeastern Norway.

	NULL	Model1	Model2	Model3	Model4	Model5	Model6	Model7	Model8
Agriculture			*	*			*		
Hum_Settle			*	*			*		
Hum_pop			*	*					
Season			*	*		*	*	*	*
Dist_Settle			*	*	*	*	*	*	*
Avg_Pict_day			*	*					
Time			*	*				*	*
Area			*	*				*	
Time:Area				*				*	
Dist_Settle:Season				*		*	*	*	*
Agriculture:Season				*			*		
Random:Grid_id		*	*	*	*	*	*	*	*
Random: Time period		*	*	*	*	*	*	*	*
LOO	1510.05	1185.26	1184.29	1184.29	1185.29	1181.20	1185.30	1179.95	1179.42

See Table 1 for the definitions of the variables. LOO are leave-one-out values from the regressions.

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represents the time and the base is the space. Both dimensions are flexible, meaning that the algorithm will analyse any area up to a specified maximum and every time block within the study period [59]. The scan window moves across the study area and the maximum likelihood ratio of the potential clusters are compared to the maximum likelihood of random simulations of the data under the null hypothesis obtained by Monte Carlo simulations [59]. We specified a maximum temporal and spatial cluster size of a 50% of the population, and a maximum cluster radius of 50 km. We used 999 Monte Carlo simulations to compute p-values at the 0.05 level.

Additionally, we investigated if resulted clustered locations were closer to human settlements than other locations. In order to do this, we fitted a linear regression within a Bayesian framework with distance to settlement as a response variable and the explanatory variable indicating whether a location belonged to the most likely cluster or not. We used the same model settings as in the previous model selection analyses.

Results

We obtained red fox photographs from 224 of the 305 camera locations. In total, 6579 red fox events were identified, among which 173 showed mange-compatible lesions (S1 Appendix). The camera locations were located within 201 cells of 10 km^2. We detected foxes with mange-compatible lesions at least once in 19.40% of these cells over the study period.

Apparent prevalence

The apparent prevalence of sarcoptic mange in the study areas fluctuated over the time of the study. The mean overall prevalence was 3.15% CRI [1.25, 6.37]. It reached a maximum of 10.70% CRI [7.9, 13.83] during the summer of 2013 in Area A that corresponded with a maximum occurrence in Area B at 6.28% CRI [4.01, 9.01]. The maximum in area C was 3.12% CRI [2.30, 9.51]. The minimum was 0.01% CRI [0, 0.06] in Area B in the winter of 2015 (Fig 3).

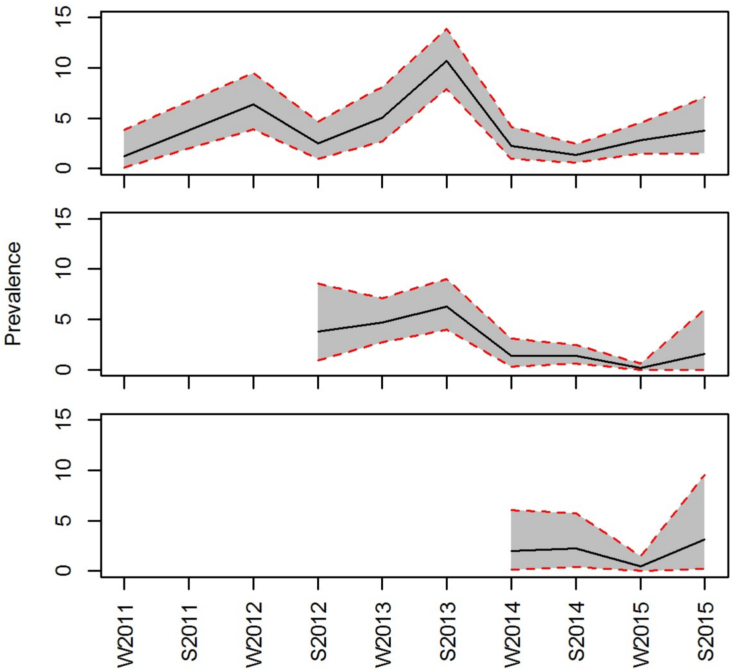

Fig 3. Apparent prevalence of sarcoptic mange in red foxes in southeastern Norway during the five years of study. Red dashed lines and grey area represent the 95% credible intervals.

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Model selection

All models visually converged and presented a $\hat{R}$ of one. Models seven and eight had the lowest LOO value (Table 2), and the two models differed only in that the former included the covariate area and the interaction between time and area. Therefore, we selected model eight as the best fit as it was the most parsimonious model.

The linear covariate for time had a weak negative effect on the probability of obtaining photographs of mangy foxes, meaning that the apparent prevalence of sarcoptic mange slightly decreased over the study period. The interaction between season and distance to settlement had a negative effect in the winter season; and thus, mangy fox events occurred more frequently closer to human settlements during this season (Table 3). The credible intervals of the

Table 3. Parameter estimates form the best model (see Table 2) explaining the presence of red foxes with mange-compatible lesions in southeastern Norway.

	Estimate	l-95% CRI	u-95% CRI	$\hat{R}$
Intercept	-3.90	-5.74	-1.86	1
Time	-0.04	-0.11	-0.01	1
Dist_Settle	-0.14	-0.88	0.54	1
SeasonW	0.14	-0.78	1.69	1
Dist_Settle:SeasonW	-0.62	-1.24	-0.03	1
Grid_id(sd(Intercept))	2.14	1.60	2.86	1
Time period(sd(Intercept))	0.77	0.13	2.36	1

l-CRI and u-CRI refer to 95% lower- and upper credible intervals, and $\hat{R}$ refer to Gelman and Rubin´s converge diagnosis.

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main effects of distance to settlement and season included zero, and therefore, we were uncertain of the signs of these effects.

Given the results, we investigated whether the number of red fox events close to human settlements varied during the winter period. We created a binary variable indicating whether a fox event occurred closer than the mean distance to settlement or further from it. We used this variable as a response in a linear regression in a Bayesian framework. We used season as an explanatory variable and grid IK as a random effect. However, we did not find an effect of season on the distribution of red fox events in relation to human settlements (Linear regression estimate: -0.10, CRI [-0.83, -0.63]).

Spatiotemporal scan analysis

The spatiotemporal scan analysis produced nine significant clusters of potentially infected animals (Table 4, Fig 4). The cluster with the highest likelihood ratio persisted for five time periods (i.e. 30 months) and nine cells with a total radius of 22.71 km. The locations included in this cluster were closer to human settlements than the rest of the locations (Linear regression estimate: -2.84, CRI [-4.9, -0.82]). This cluster presented a difference of likelihood ratio of 177.516 compared with the second most likely cluster. The likelihood ratio decreased again dramatically from cluster four to cluster five. There is a possibility that repeated photographs of the same individual could cause four of the clusters that included only one camera location and only one period of six months. Nevertheless, these four clusters are still important areas to be consider in the future as potential areas of risk, since they could be precursors of bigger outbreaks. However, given the spatial independence of our data and the independence of the time periods, the remaining clusters that had more than one camera location and several periods most probably included several different individuals.

Discussion

Our study showed that red foxes with mange-compatible lesions were more frequently located closer to human settlements during winter when compare to healthy red foxes. Human settlements are a source of easily available food for several wildlife species, including the red fox [37, 60, 61]. In some cases, this source of food can fulfil the daily requirements of one pair of foxes [28]. Anthropogenic food is most important during the winter period, when prey availability is low [62–65], and it may be particularly important for foxes affected by sarcoptic mange. Several studies have shown that sarcoptic mange deteriorates the body condition of the host [5, 66, 67]. Accordingly, a poor body condition may affect the ability of the red fox to hunt live prey or locate and fight for carrion, and therefore induce foraging close to humans (see [68] for an example with coyotes). Balestrieri et al. [67] suggested that a source of bias in their study was the tendency of mangy foxes often found close to villages looking for easy food. The results of our logistic models are in accordance with our spatiotemporal scan analysis results; the cluster with the highest likelihood encompassed cells closer to human settlements than the rest of the cells within the study areas (-2.84 kilometers, CRI [-4.9, -0.82]). However, it is also important to consider alternative, but not mutually exclusive, mechanisms, such as the possibility that heavy use of anthropogenic food sources that tend to occur in concentrated points in areas close to settlements may facilitate scabies transfer between foxes. We did not detect a variation in the number of red fox events closer to human settlements during the winter; therefore, we discarded a density dependent transmission of the disease. This dissociation between the population density and the transmission of sarcoptic mange have been demonstrated in other places [26, 69]. In the other hand, concentrated anthropogenic food can facilitate an increase in the contact rate independent of density, for example by increasing overlapping

Table 4. Spatiotemporal clusters of red foxes potentially infected with sarcoptic mange detected by the scan analyses.

Cluster	Radius (km)	Duration (Months)	Start date	End date	Number Cells	LLR	P_value	Observed Cases	Expected Cases
1	**22.71**	**30**	**October_2013**	**March_2015**	**9**	**317.556**	**<0.001**	**391**	**94.41**
2	0	6	October_2014	March_2015	1	177.516	<0.001	71	3.31
3	11.36	12	October_2012	September_2013	8	160.737	<0.001	124	16.20
4	8.90	24	October_2012	September_2014	3	145.155	<0.001	182	41.37
5	40.94	6	October_2011	March_2012	40	58.246	<0.001	65	12.70
6	16.05	6	April_2012	September_2012	3	28.692	<0.001	8	0.22
7	9.44	12	October_2012	September_2013	3	28.595	<0.001	11	0.47
8	0	3	April_2015	June_2015	1	25.102	<0.001	7	0.19
9	0	6	October_2013	March_2014	1	24.675	<0.001	14	1.14
10	0	6	April_2014	September_2014	1	6.849	0.437	5	0.58

Radius of the circular cluster, duration, starting and ending date, number of cells included in the cluster, likelihood ratio values and p-values. "Observed cases" are the actual numbers of photographed events of foxes with mange-compatible lesions in that cluster, while the "Expected cases" are numbers expected conditioning on the total number of cases (see Kulldorff et al. 2005 for a detailed description)

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among home ranges especially during winter. This pattern is a frequency dependant transmission of the disease (see Begon et al. [70] for a thorough definition of the terms). This transmission mechanism has previously been shown in other urban fox population [69]. The large scale data used in this study does not permit a finer scale analysis of the actual mechanisms, but it clearly identifies important areas for future investigations.

The spatiotemporal scan analyses detected nine significant clusters of mange-compatible lesion observations, among which six included three or more grid cells. The clustered patterns suggest that the dynamics of sarcoptic mange in this red fox population is characterised by small-localized outbreaks that emerge and disappear rather than sporadic events in the population. This pattern of local outbreaks has been observed in other populations where mange is enzootic, like in Britain [24] or Spain [26]. Furthermore, the apparent prevalence of the disease in our study fluctuated over time below ca 11% (Fig 3) with peaks that corresponded in time to some of the potential clusters, including the one with the highest likelihood. Other studies have found similar patterns of mange prevalence in other species like chamois or Iberian ibex [3, 71]. Currently, 30 years after the epizootic outbreak of sarcoptic mange in Fennoscandia, the multiple clusters and fluctuations in the disease apparent prevalence suggest that the disease is in an enzootic state with low prevalence (average 3.16 ± 0.56%). However, this prevalence might be somewhat underestimated in our study, as camera traps only allow for the detection of visually evident symptoms (e.g. alopecia). Hence, we failed to identify infected foxes in early stages of the disease with non-symptomatic infections. The degree of infection can reveal important insight on the dynamic of the disease [7]. However, photographic material is not always reliable when assessing the stage of the infection of an individual. We did not include a degree of infection in our analyses but since we only used clear cases of mange-compatible lesions, we can assume that these individuals were in advanced stages of the disease. We believe that our data accurately reflect spatiotemporal patterns of clinically advanced cases of sarcoptic mange. Regarding the relationship with human settlements, the detriment in body condition occurs in the last stages of the disease [17]; that is the moment when the animal may be more dependent on easily available food. Furthermore, analysing the spatiotemporal variation only in severe cases still allows for detecting potential outbreaks given that the relative proportions of individuals in early and later stages of the disease is relatively constant.

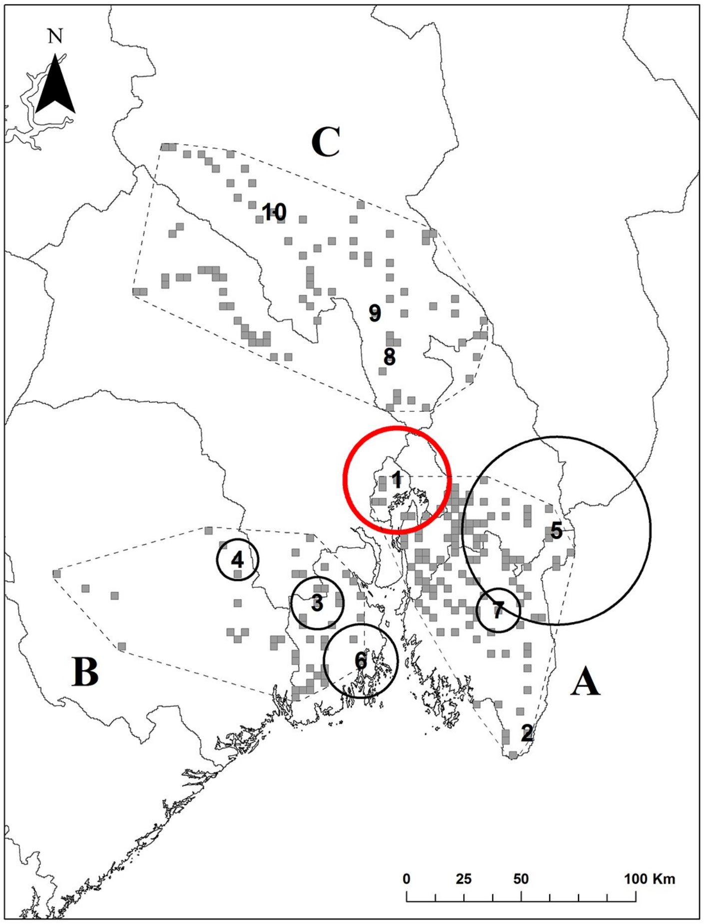

Fig 4. Geographic distribution of significant clusters of red foxes potentially infected with sarcoptic mange identified by scan analysis. The circles define the size of the clusters and the numbers refer to the ID of each cluster (see Table 4 for further details). The red circle represents the cluster with the highest likelihood ratio.

https://doi.org/10.1371/journal.pone.0176200.g004

It is important to highlight the potential weaknesses of the use of camera traps for disease epidemiology assessment. Given the nature of the data, we were not able to include variables like sex or age of the photographed individuals. Previous studies showed age specific prevalence of sarcoptic mange in red foxes [69] and sex specific infection rates in coyotes [7]. We did not identify any pup with mange-compatible lesions, but the restricted movement of young individuals [69] might decrease their detectability by camera traps.

The actual origin of the lesions in the animal represent another limitation in the use of camera traps as other causes of hair loss might be confused with sarcoptic mange. Fungal infections known as dermatophytosis can cause alopecia in red foxes [72, 73] but this is not common and has never been reported in Norway. Notoedric mange caused by the mite *Notoedres cati* has symptoms similar to sarcoptic mange, and it affects mainly felines [1]. Other mites like *Demodex canis* affect dogs and has not been reported in foxes [74]. Hence, even though the mange-compatible lesions reported in our study (e.g. Fig 2) are probably caused by the mite *Sarcoptes scabiei*, we recommend that camera trap surveys are accompanied by serological tests of samples like ELISA test [75].

Field surveillance of wildlife diseases is imperative for the management of potential threats both to wildlife and human well-being [76, 77]. The occurrence of mangy foxes in the vicinity of human settlements and the apparent clustered pattern of the disease raise important implications for the management of the Scandinavian red fox population. Clusters appearing close to human settlements might represent a source of contagiousness for domestic animals, livestock or other wildlife [43]. Tools like the StatScan software allow for prospective analyses of surveillance data in order to detect potentially emerging clusters.

Here we show that camera traps are an effective tool to use in surveillance of wildlife diseases with visually apparent symptoms like sarcoptic mange. Oleaga et al. [5] also illustrated the usefulness of camera traps for detecting mange in wolves and red foxes, and other methods such as thermal imaging cameras are on the rise [66, 78]. Nonetheless, surveillance in the field is only a first step towards a holistic monitoring of a wildlife disease, and serological and genetic analyses of the pathogen should accompany them [77, 79]. These analyses can reveal the directionality of the disease transfer (e.g. prey to predator, intraguild contagion) [79], and can increase the accuracy of prevalence estimations.

Supporting information

S1 Appendix. Dataset. Red fox events detected by camera traps from 2010 until 2015 in the southeast of Norway and covariates used in the study.
(XLSX)

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References

1. Ryser-Degiorgis MP, Ryser A, Bacciarini LN, Angst C, Gottstein B, Janovsky M, et al. Notoedric and Sarcoptic mange in free-ranging lynx from Switzerland. Journal of Wildlife Diseases. 2002; 38(1):228–32. https://doi.org/10.7589/0090-3558-38.1.228 PMID: 11838224
2. Millan J. First description of sarcoptic mange in wild European rabbit (Oryctolagus cuniculus). European Journal of Wildlife Research. 2010; 56(3):455–7.
3. Pérez JC I; Granados JE; Cano-Manuel FJ; Fandos P; Espinosa J; Soriguer RC. Does Sarcoptes scabiei synchronize its breeding cycle with that of the Iberian Ibex, Capra pyrenaica? International Journal of Acarology. 2016;Published online.
4. Galaverni M, Palumbo D, Fabbri E, Caniglia R, Greco C, Randi E. Monitoring wolves (Canis lupus) by non-invasive genetics and camera trapping: a small-scale pilot study. European Journal of Wildlife Research. 2012; 58(1):47–58.
5. Oleaga A, Casais R, Balseiro A, Espi A, Llaneza L, Hartasanchez A, et al. New techniques for an old disease: Sarcoptic mange in the Iberian wolf. Veterinary Parasitology. 2011; 181(2–4):255–66. https://doi.org/10.1016/j.vetpar.2011.04.036 PMID: 21600696
6. Fuchs B, Zimmermann B, Wabakken P, Bornstein S, Mansson J, Evans AL, et al. Sarcoptic mange in the Scandinavian wolf Canis lupus population. Bmc Veterinary Research. 2016; 12.
7. Pence DB, Windberg LA. Impact of a sarcoptic mange epizootic on a coyote population. Journal of Wildlife Management. 1994; 58(4):624–33.
8. Skerratt LF, Middleton D, Beveridge L. Distribution of life cycle stages of Sarcoptes scabiei var wombati and effects of severe mange on common wombats in Victoria. Journal of Wildlife Diseases. 1999; 35 (4):633–46. https://doi.org/10.7589/0090-3558-35.4.633 PMID: 10574522
9. Borchard P, Eldridge DJ, Wright IA. Sarcoptes mange (Sarcoptes scabiei) increases diurnal activity of bare-nosed wombats (Vombatus ursinus) in an agricultural riparian environment. Mammalian Biology. 2012; 77(4):244–8.
10. Alasaad S, Ndeereh D, Rossi L, Bornstein S, Permunian R, Soriguer RC, et al. The opportunistic Sarcoptes scabiei: A new episode from giraffe in the drought-suffering Kenya. Veterinary Parasitology. 2012; 185(2–4):359–63. https://doi.org/10.1016/j.vetpar.2011.10.039 PMID: 22137348
11. Bornstein S, Mörner T., Samuel W.M. Sarcoptes scabiei and sarcoptic mange. In: Samuel WM, Pybus M.J., Kocan A.A., editor. Parasitic Diseases of Wild Mammals 2nd ed ed. Ames: Iowa State University Press; 2001. p. 107–19.

12. Newman TJ, Baker PJ, Simcock E, Saunders G, White PCL, Harris S. Changes in red fox habitat preference and rest site fidelity following a disease-induced population decline. Acta Theriologica. 2003; 48 (1):79–91.
13. Little SE, Davidson WR, Howerth EW, Rakich PM, Nettles VF. Diseases diagnosed in red foxes from the southeastern United States. Journal of Wildlife Diseases. 1998; 34(3):620–4. https://doi.org/10.7589/0090-3558-34.3.620 PMID: 9706573
14. Davidson RK, Bornstein S, Handeland K. Long-term study of Sarcoptes scabiei infection in Norwegian red foxes (Vulpes vulpes) indicating host/parasite adaptation. Veterinary Parasitology. 2008; 156(3–4):277–83. https://doi.org/10.1016/j.vetpar.2008.05.019 PMID: 18586406
15. Bornstein S, Zakrisson G, Thebo P. Clinical picture and antibody response to experimental Sarcoptes scabiei var vulpes infection in red foxes (Vulpes vulpes). Acta Veterinaria Scandinavica. 1995; 36 (4):509–19. PMID: 8669378
16. Borg K. A review of wildlife diseases from scandinavia. Journal of Wildlife Diseases. 1987; 23(4):527–33. PMID: 3316719
17. Newman TJ, Baker PJ, Harris S. Nutritional condition and survival of red foxes with sarcoptic mange. Canadian Journal of Zoology-Revue Canadienne De Zoologie. 2002; 80(1):154–61.
18. Uraguchi K, Ueno M, Iijima H, Saitoh T. Demographic Analyses of a Fox Population Suffering From Sarcoptic Mange. Journal of Wildlife Management. 2014; 78(8):1356–71.
19. Potts JR, Harris S, Giuggioli L. Quantifying Behavioral Changes in Territorial Animals Caused by Sudden Population Declines. American Naturalist. 2013; 182(3):E73–E82. https://doi.org/10.1086/671260 PMID: 23933730
20. Kalema-Zikusoka G, Kock RA, Macfie EJ. Scabies in free-ranging mountain gorillas (Gorilla beringei beringei) in Bwindi Impenetrable National Park, Uganda. Veterinary Record. 2002; 150(1):12–5. PMID: 11817857
21. Fernandez-Moran J, Gomez S, Ballesteros F, Quiros P, Benito JL, Feliu C, et al. Epizootiology of sarcoptic mange in a population of cantabrian chamois (Rupicapra pyrenaica parva) in Northwestern Spain. Veterinary Parasitology. 1997; 73(1–2):163–71. PMID: 9477502
22. Serrano E, Colom-Cadena A, Gilot-Fromont E, Garel M, Cabezon O, Velarde R, et al. Border Disease Virus: An Exceptional Driver of Chamois Populations Among Other Threats. Frontiers in Microbiology. 2015; 6.
23. Lindström ER, Andren H, Angelstam P, Cederlund G, Hornfeldt B, Jaderberg L, et al. Disease reveals the predator—sarcoptic mange, red fox predation, and prey populations. Ecology. 1994; 75(4):1042–9.
24. Soulsbury CD, Iossa G, Baker PJ, Cole NC, Funk SM, Harris S. The impact of sarcoptic mange Sarcoptes scabiei on the British fox Vulpes vulpes population. Mammal Review. 2007; 37(4):278–96.
25. Mörner T. Sarcoptic mange in Swedish wildlife. Rev sci tech Off int Epiz. 1992; 11(4):1115–21.
26. Gortazar C, Villafuerte R, Blanco JC, Fernandez-De-Luco D. Enzootic sarcoptic mange in red foxes in Spain. Zeitschrift Fur Jagdwissenschaft. 1998; 44(4):251–6.
27. Mörner T, Christensson D. Experimental-infection of red foxes (vulpes-vulpes) with sarcoptes-scabiei var vulpes. Veterinary Parasitology. 1984; 15(2):159–64. PMID: 6541832
28. Baker PJ, Funk SM, Harris S, White PCL. Flexible spatial organization of urban foxes, Vulpes vulpes, before and during an outbreak of sarcoptic mange. Animal Behaviour. 2000; 59:127–46. https://doi.org/10.1006/anbe.1999.1285 PMID: 10640375
29. Lindström E. Food limitation and social regulation in a red fox population. Holarctic Ecology. 1989; 12 (1):70–9.
30. Cavallini P. Variation in the social system of the red fox. Ethology Ecology & Evolution. 1996; 8:323–42.
31. Soulsbury CD, Iossa G, Baker PJ, White PCL, Harris S. Behavioral and spatial analysis of extraterritorial movements in red foxes (Vulpes vulpes). Journal of Mammalogy. 2011; 92(1):190–9.
32. Woollard T, Harris S. A behavioral-comparison of dispersing and non-dispersing foxes (vulpes-vulpes) and an evaluation of some dispersal hypotheses. Journal of Animal Ecology. 1990; 59(2):709–22.
33. Pence DB, Ueckermann E. Sarcoptic mange in wildlife. Revue Scientifique Et Technique De L Office International Des Epizooties. 2002; 21(2):385–98.
34. Lindström E. Pattern of spread and effects of sarcoptic mange among red fox populations of Sweden1991. 591–5 p.
35. Smedshaug CA, Selås V, Lund SE, Sonerud GA. The effect of a natural reduction of red fox Vulpes vulpes on small game hunting bags in Norway. Wildlife Biology. 1999; 5(3):157–66.
36. Danell K, Hornfeldt B. Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. Oecologia. 1987; 73(4):533–6. https://doi.org/10.1007/BF00379412 PMID: 28311970

37. Killengreen ST, Lecomte N, Ehrich D, Schott T, Yoccoz NG, Ims RA. The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. Journal of Animal Ecology. 2011; 80(5):1049–60. https://doi.org/10.1111/j.1365-2656.2011.01840.x PMID: 21477201

38. Plumer L, Davison J, Saarma U. Rapid Urbanization of Red Foxes in Estonia: Distribution, Behaviour, Attacks on Domestic Animals, and Health-Risks Related to Zoonotic Diseases. PLoS One. 2014; 9(12).

39. Overskaug K. Behavioral-changes in free-ranging red foxes (vulpes-vulpes) due to sarcoptic mange. Acta Veterinaria Scandinavica. 1994; 35(4):457–9. PMID: 7676933

40. McCarthy P. The transmission of sarcoptic mange from the wild fox (Vulpes vulpes) to man and other species in Central Queensland. Australian Veterinary Journal. 1960; 34:600–11.

41. Bornstein S. Experimental infection of dogs with Sarcoptes scabiei derived from naturally infected wild red foxes (Vulpes vulpes): clinical observations. Veterinary Dermatology. 1991; 2:151–9.

42. Alasaad S, Rossi L, Heukelbach J, Perez JM, Hamarsheh O, Otiende M, et al. The neglected navigating web of the incomprehensibly emerging and re-emerging Sarcoptes mite. Infection Genetics and Evolution. 2013; 17:253–9.

43. Kolodziej-Sobocinska M, Zalewski A, Kowalczyk R. Sarcoptic mange vulnerability in carnivores of the BiaowieA1/4a Primeval Forest, Poland: underlying determinant factors. Ecological Research. 2014; 29 (2):237–44.

44. Bouyer Y, Martin GS, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC. Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. Biological Conservation. 2015; 191:291–9.

45. Linnell JDC, Odden J, Andren H, Liberg O, Andersen R, Moa P, et al. Distance rules for minimum counts of Eurasian lynx Lynx lynx family groups under different ecological conditions. Wildlife Biology. 2007; 13(4):447–55.

46. Linnell JDC, Broseth H, Odden J, Nilsen EB. Sustainably Harvesting a Large Carnivore? Development of Eurasian Lynx Populations in Norway During 160 Years of Shifting Policy. Environmental Management. 2010; 45(5):1142–54. https://doi.org/10.1007/s00267-010-9455-9 PMID: 20213233

47. Gerber BD, Karpanty SM, Kelly MJ. Evaluating the potential biases in carnivore capture-recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Population Ecology. 2012; 54(1):43–54.

48. Braczkowski AR, Balme GA, Dickman A, Fattebert J, Johnson P, Dickerson T, et al. Scent Lure Effect on Camera-Trap Based Leopard Density Estimates. Plos One. 2016; 11(4):14.

49. Garrote G, Gil-Sanchez JM, McCain EB, de Lillo S, Telleria JL, Simon MA. The effect of attractant lures in camera trapping: a case study of population estimates for the Iberian lynx (Lynx pardinus). European Journal of Wildlife Research. 2012; 58(5):881–4.

50. Lindström E. Population ecology of the red fox (Vulpes vulpes L.) in relation to food supply. Ph D thesis, University of Stockholm 1982.

51. Dorai-Raj S. binom: Binomial confidence intervals for several parameterizations. R package version 11–1 https://CRANRprojectorg/package=binom. 2014.

52. Johansen B. Vegetasjonskart for Norge basert på Landsat TM/ETM+ data. Norut-Tromsø Rapport 4/ 2009 86 s. 2009.

53. ESRI. ARCGIS desktop. Environmental Systems Research Institute, Redland. 2009.

54. Gelman A, Hill J. Data analysis using regression and multilevel/hierarchical models. Cambridge: Cambridge University Press; 2007.

55. Buerkner P. brms: Bayesian regression models using stan. R package version 080 https://CRANR-projectorg/package=brms. 2016.

56. Vehtari A, Gelman A, Gabry J. Practical bayesian model evaluation using leave-one-out cross-validation and WAIC. arXiv:150704544v5 [statCO]. 2016.

57. Gelman A, Rubin D. Inference from iterative simulation using multiple sequences. Statistical Science. 1992; 7(4):457–72.

58. Kulldorff M. A spatial scan statistic. Communications in Statistics-Theory and Methods. 1997; 26 (6):1481–96.

59. Kulldorff M. Prospective time periodic geographical disease surveillance using a scan statistic. Journal of the Royal Statistical Society Series a-Statistics in Society. 2001; 164:61–72.

60. Tigas LA, Van Vuren DH, Sauvajot RM. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation. 2002; 108(3):299–306.

61. Spencer RD, Beausoleil RA, Martorello DA. How agencies respond to human-black bear conflicts: a survey of wildlife agencies in North America. Ursus. 2007; 18(2):217–29.

62. Panek M, Bresinski W. Red fox Vulpes vulpes density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. Acta Theriologica. 2002; 47(4):433–42.

63. Selås V, Vik JO. Possible impact of snow depth and ungulate carcasses on red fox (Vulpes vulpes) populations in Norway, 1897–1976. Journal of Zoology. 2006; 269(3):299–308.

64. Rosalino LM, Sousa M, Pedroso NM, Basto M, Rosario J, Santos MJ, et al. The influence of food resources on red fox local distribution in a mountain area of the western mediterranean. Vie Et Milieu-Life and Environment. 2010; 60(1):39–45.

65. Selås V, Johnsen BS, Eide NE. Arctic fox Vulpes lagopus den use in relation to altitude and human infrastructure. Wildlife Biology. 2010; 16(1):107–12.

66. Simpson K, Johnson CN, Carver S. Sarcoptes scabiei: The Mange Mite with Mighty Effects on the Common Wombat (Vombatus ursinus). Plos One. 2016; 11(3).

67. Balestrieri A, Remonti L, Ferrari N, Ferrari A, Lo Valvo T, Robetto S, et al. Sarcoptic mange in wild carnivores and its co-occurrence with parasitic helminths in the Western Italian Alps. European Journal of Wildlife Research. 2006; 52(3):196–201.

68. Todd A, Gunson J, Samuel W. Sarcoptic mange: an important disease in coyotes and wolves of Albertya, Canada. Worldwide Furbearer Conference Proceedings, Frostburg, Maryland. 1981:706–29.

69. Devenish-Nelson ES, Richards SA, Harris S, Soulsbury C, Stephens PA. Demonstrating frequency-dependent transmission of sarcoptic mange in red foxes. Biology Letters. 2014; 10(10).

70. Begon M, Bennett M, Bowers RG, French NP, Hazel SM, Turner J. A clarification of transmission terms in host-microparasite models: numbers, densities and areas. Epidemiology and Infection. 2002; 129 (1):147–53. PMID: 12211582

71. Turchetto S, Obber F, Permunian R, Vendrami S, Lorenzetto M, Ferre N, et al. Spatial and temporal explorative analysis of sarcoptic mange in Alpine chamois (Rupicapra r. rupicapra). Hystrix-Italian Journal of Mammalogy. 2014; 25(1):25–30.

72. Malmasi A, Khosravi AR, Ghaffari MS, Tabrizi AS. Microsporum canis infection in a red fox (Vulpes vulpes). Iranian Journal of Veterinary Research. 2009; 10(2):189–91.

73. Knudtson WU, Gates CE, Ruth GR, Haley LD. Trichophyton-mentagrophytes dermatophytosis in wild fox. Journal of Wildlife Diseases. 1980; 16(4):465–8. PMID: 7463597

74. Chesney CJ. Short form of Demodex species mite in the dog: occurrence and measurements. Journal of Small Animal Practice. 1999; 40(2):58–61. PMID: 10088084

75. Bornstein S, Frossling J, Naslund K, Zakrisson G, Morner T. Evaluation of a serological test (indirect ELISA) for the diagnosis of sarcoptic mange in red foxes (Vulpes vulpes). Veterinary Dermatology. 2006; 17(6):411–6. https://doi.org/10.1111/j.1365-3164.2006.00548.x PMID: 17083572

76. Daszak P, Cunningham AA, Hyatt AD. Wildlife ecology—Emerging infectious diseases of wildlife—Threats to biodiversity and human health. Science. 2000; 287(5452):443–9.

77. Ryser-Degiorgis MP. Wildlife health investigations: needs, challenges and recommendations. Bmc Veterinary Research. 2013; 9.

78. Cross PC, Almberg ES, Haase CG, Hudson PJ, Maloney SK, Metz MC, et al. Energetic costs of mange in wolves estimated from infrared thermography. Ecology. 2016; 97(8):1938–48. https://doi.org/10.1890/15-1346.1 PMID: 27859195

79. Alasaad S, Sarasa M, Heukelbach J, Mijele D, Soriguer RC, Zhu XQ, et al. Advances in studies of disease-navigating webs: Sarcoptes scabiei as a case study. Parasites & Vectors. 2014; 7.

Paper IV

Co-occurrence of meso-carnivores in a human dominated landscape in Maharashtra, India

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Abstract

Identifying factors influencing the distributions and interactions within carnivore communities is particularly important in human dominated landscapes. Within the carnivore guild, species differ in their ability to adapt to human influence depending on their degree of specialization in habitat use and feeding habits. There is an increasing recognition of the conservation value of these areas in India. Nevertheless, few ecological studies of wildlife focus on the human impact on the native species in carnivore communities. We investigated determinant factors for the occurrence and coexistence of meso-carnivores in an agricultural landscape in Maharashtra, India. We used camera traps to record the presence of Indian foxes, jungle cats, jackals and domestic dogs during their most active hours (i.e. from sunset to sunrise). We recorded 395 events of the target species during 233 trapping nights from 40 camera traps located within an area of 230 km2. Using co-occurrence occupancy models in a Bayesian framework, we investigated the relative influence of forest plantations, agriculture and fallow land as well as other human infrastructure variables and habitat patch sizes. Additionally, we investigated the activity patterns of the focal species. Indian foxes revealed the most specialized habitat use, being positively associated with forest plantations and the size of the habitat patches. Indian fox showed spatial niche partitioning with jackals and temporal niche partitioning with dogs. Jackals, jungle cats and dogs overlapped in their habitat use and were positively associated with human settlements at the finest spatial scale, which may imply a dependence on human food resources. This study provides evidence of contrasting impact of humans among species in a mesocarnivore community. Future management actions aimed at conserving biodiversity in highly human dominated landscapes should take into account the intra- and interguild interactions of the local carnivore communities.

Introduction

Human dominated landscapes are expanding throughout the Earth's surface. In order to minimize the impact of this expansion in the biodiversity without compromising food production and development, two alternatives are debated: land sharing (i.e. biodiversity and human development sharing space) and land sparing (i.e. segregate spaces) (Phalan, Onial, Balmford, & Green, 2011; Tscharntke et al., 2012). However, determining which alternative is the most suitable requires a deep understanding of the different parts of the ecosystem. In this context, identifying factors influencing the distribution of and, interactions within carnivore communities is particularly important in human dominated areas. In these landscapes, the natural habitat is altered to give way to agricultural development and urban expansion (Saunders, Hobbs, & Margules, 1991). Consequently, natural habitats turn into a fragmented mosaic of natural patches and cultivated land in which humans and wildlife coexist (Saunders et al., 1991).

Changes in the natural habitat of a species and its exposure to human influence can affect its distribution and habitat use. Whether this effect is positive or negative will typically depend on the degree of specialization in habitat use and feeding habits. For example, Cougars *Felis concolor* are negatively affected by habitat fragmentation and avoid paved roads (Beier, 1995; Dickson, Jenness, & Beier, 2005). Endangered species like the Sumatran rhinoceros *Dicerorhinus sumatrensis* and the Sumatran tiger *Panthera tigris sumatrae* are threatened by habitat loss due to deforestation (Kinnaird, Sanderson, O'Brien, Wibisono, & Woolmer, 2003). In North America, a number of species have experienced a reduction on their distribution range due to a combination of human factors including population density, land use and human infrastructure (Laliberte & Ripple, 2004). On the contrary, other species may benefit from human impact, for example by an increased habitat carrying capacity through anthropogenic food subsidization. This is the case of the red fox *Vulpes vulpes* throughout its distribution range

(Bino et al., 2010; Elmhagen & Rushton, 2007), or raccoons *Procyon lotor* and coyotes *Canis latrans* in the USA (Ordenana et al., 2010; Prange, Gehrt, & Wiggers, 2003). An increased food subsidization due to urban expansion can even benefit endangered species like the San Joaquin kit fox *Vulpes macrotis mutica* (Newsome, Ralls, Job, Fogel, & Cypher, 2010).

Another important factor affecting the distribution and habitat use of a species is the intraguild interactions within the community (Linnell & Strand, 2000); both with other native species (Berger & Gese, 2007; Lindstrom, Brainerd, Helldin, & Overskaug, 1995; Palomares & Caro, 1999; Ritchie & Johnson, 2009), and species associated with humans (Vanak & Gompper, 2009b). These interactions can lead to spatial niche partitioning, segregating the distribution and habitat use of competitive species (Linnell & Strand, 2000; Schoener, 1974). Although some studies have focused on these interactions at a community level (Bu et al., 2016; Cruz, Sarmento, & White, 2015; Farris, Kelly, Karpanty, & Ratelolahy, 2016), there is limited information on the effects of human alteration of natural habitat on intraguild interactions in the mesocarnivore community (Gompper, Lesmeister, Ray, Malcolm, & Kays, 2016; Lesmeister, Nielsen, Schauber, & Hellgren, 2015; Rota et al., 2016). In particular, few studies have yet been conducted in landscapes of very high human population density.

With over 1.3 billion inhabitants, India is the second-most populous country in the world. It has a population density of 446 inhabitants per square kilometer (http://data.un.org/), and approximately 48% of the total land is dedicated to agriculture (http://www.fao.org/). In this context, native fauna have to coexist in a human altered landscape. Moreover, native fauna also have to contend with amongst the highest densities of free-ranging domestic dogs in the world. Dogs in India can reach densities of 719 dogs per km^2 in some areas (Belsare & Gompper, 2013), and they can affect native carnivores through interference competition, intraguild killing and disease transmission (Vanak & Gompper, 2009b). Despite the high human pressure on the environment, recent research has revealed a rich faunal diversity in areas of high human population density (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2013). Although coexistence of humans with large carnivores and emblematic species is well documented in India (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2016; Chartier, Zimmermann, & Ladle, 2011; Dhanwatey et al., 2013; Suryawanshi, Bhatia, Bhatnagar, Redpath, & Mishra, 2014), few ecological studies focus on the coexistence of mesopredators with humans at a community level. Specifically, how these carnivore communities adapt to altered landscapes and the presence of species associated with humans.

In this study we used multi-occupancy modelling in a Bayesian framework to investigate how habitat composition and human infrastructure affect the habitat use of Indian foxes (*Vulpes bengalensis*), jungle cats (*Felis chaus*), jackals (*Canis aureus*), and dogs in a landscape of high human population density in Maharashtra, India. Next, we explored interspecific interactions between the species in the habitat models to assess the nature of their coexistence. We evaluated whether there is evidence of spatial niche partitioning among the four species. We predicted that dogs were positively associated to humans and interacted negatively with the other three species (Vanak & Gompper, 2009b). We expected that jackals and jungle cats were partially associated with human activities (Jaeger, Haque, Sultana, & Bruggers, 2007; Nowell & Jackson, 1996), whereas Indian foxes were more closely associated with natural habitats (Vanak & Gompper, 2010). Given the larger body mass of jungle cats and jackals compared to that of the Indian fox, we predicted a negative interaction between the former and Indian fox due to interference competition (Palomares & Caro, 1999).

Materials and methods

Study area

Our study area in Maharashtra, central India (Fig. 1), covered 230 square kilometers, and included several villages that belong to the municipalities of Baramati and Daund, with population densities of 397.19/km^2 and 380/km^2, respectively (www.census2011.com). The area has a semi-arid climate with a cool-dry season from November to February, a hot-dry season from March to June, and a wet season from July to October during which 95% of the precipitation occurs.

The landscape consists of a matrix of sugarcane fields, seasonal crops, communal grazing lands and forestry plantations. Common species in the mesocarnivore community in the area are Indian fox, jackal and jungle cat. Palm civet (*Paradoxurus hermaphrodites*), Small Indian civet (*Viverra zibetha*), grey mongoose (*Herpestes edwardsii*), and herbivores like the Indian gazelle (*Gazella bennettii*) and Indian hare (*Lepus nigricollis*) are common. Free-ranging domestic dogs are found throughout the entire study area forming packs or as solitary individuals.

Camera trapping

The activity of the study species was recorded during six weeks in the months of November and December by deploying camera traps at 40 trapping locations. Potential locations were selected based on satellite imagery to ensure that the whole area was covered. For that, the locations were spaced at least two kilometers apart from each other (except for two locations that were placed 1.2 kilometers apart due to accessibility). Once in the field, the locations were adjusted to maximize the likelihood of detection of the target species (e.g. by using trails or natural paths) and minimize direct human disturbance. At each location, we attached and secured a camera trap to a tree at 30 to 50 cm high. The cameras were movement triggered and set up to take pictures every five seconds during periods of movement detection. At every trap location, some drops of lure (Red Fox Gland Lure; Carman's superior animal lures) were added between one and two meters from the camera trap. The use of lures does not affect temporal activity, maximum movement distance or immigration rates of species like leopard *Panthera pardus* or Malagasy civet *Fossa fossana* (Braczkowski et al., 2016; Gerber, Karpanty, & Kelly, 2012). GPS telemetry data from jungle cats and jackals (Vanak, A. T. unpublished) revealed that the average home ranges of these species exceed the separation between the cameras. Therefore, the study design violates the assumption of independence between camera locations. Therefore, the habitat use rather than the occupancy of the study species was investigated in this study.

The camera traps were active for six consecutive trapping nights. Preliminary studies in the area showed that, given the density of the target species in the area, four trapping nights was sufficient to ensure the detection of a species given presence in the area. In order to avoid theft, the camera traps were deployed from 16.30 to 18.30 every day and retrieved from 6:30 to 8:30 the next morning. Due to this constraint, we divided the study period in six blocks, managing six to seven cameras at a time in each block. However, the hours when the cameras were deployed accurately capture the maximum activity period of the study species (Boitani & Ciucci, 1995; Vanak & Gompper, 2007). Therefore, our data is a good representation of the habits and activity of these species.

Covariate data extraction

Satellite imagery of our study area dated the 15th of November of 2016 was retrieved from Google Earth (Google Earth, 2017) and digitized by creating polygons or lines of the features of interest for our study (i.e. forestry plantation, agriculture land, fallow land, human settlements, length of canals and length of tarmac roads). Buffers of 100 meters radius, 500 meters radius and 1000 meters radius were created around each camera trapping location. Using zonal statistics tools, we extracted habitat data from the digitized map for each of the buffers around each camera location (Table 1). Digitation of satellite imagery and data extraction was performed using ArcGis 10.3.1 (ESRI, 2009).

Spatial co-occurrence

We created detection histories for Indian foxes, jackals, jungle cats and domestic dogs. For that, at each location *i*, we used ones (y_{sij}=1) if the species *s* was detected at least once during trapping night *j*, and zeros (y_{sij}=0) if the species *s* was not detected during trapping night *j* (e.g. y_{si}=100101; species *s* was detected in location *i* at least once during the first, third and sixth trapping nights).

We used these histories to model habitat use and interactions among the studied species by fitting the multispecies occupancy model described in Rota et al. (2016). MacKenzie et al. (2002) described a single-species model to estimate the probability of a site being occupied when the detection probability of the species is less than one; the model from Rota et al. (2016) is a generalization of this single species model to include two or more interacting species. In contrast to other co-occurrence models like the one described in MacKenzie, Bailey, and Nichols (2004), the interactions between species do not have to be asymmetrical. Moreover, the model allows the use of covariates to predict the probability that two or more species occupy the same site.

First, a multispecies model per buffer size was created without including species interactions. This step is, in essence, similar to creating one single-species occupancy model for each species at each buffer size. In order to model the detection probability of the four species, 'Trail' variable was used. Additionally, the number of events of dog occurrence at each trapping night was included to model the detection probability of fox, jackal and jungle cat. We used two types of variables to model habitat use in the 500 and 1000 meters buffer sizes: (i) habitat types (i.e. proportional coverage of forest plantations, fallow land, agriculture and human settlements within the buffers) and (ii) infrastructure (i.e. the length of roads and canals within the buffers). We avoided placing the cameras close to roads to avert theft, and thus, we did not include the 'Road' variable in the 100 meter buffer size. Instead, we used the 'Distance to settlement' variable. Given that ‘Distance to settlement’ represents a value obtained from the specific location of the camera, its effect was assumed to be better revealed at the smallest buffer size.

Next, constant interactions were added (i.e. intercept modelling) between pairs of species to test whether the fit of the initial models improved by adding species interactions. Interactions were retained or removed from the model depending on their strength (i.e. it was removed if the 80% credible interval overlapped with zero).

We used non-informative normal distributions with mean = zero, and standard deviation = 10 as priors. Models were fitted by running three Monte Carlo Markov chains of 6000 iterations each, discarding the first 2000 as burn-in process. We diagnosed the convergence of the models by visually checking trace-plots and by using the Gelman and Rubin´s converge diagnosis (Gelman & Rubin, 1992). We used WAIC values to evaluate the models fit.

Activity patterns

We investigated the temporal interactions between the study species following two approaches: (1) by examining night activity density plots and the coefficients of overlap of the native species and dogs (Ridout & Linkie, 2009), and (2) by investigating the Avoidance-Attraction Ratios (AARs) described in Parsons et al. (2016).

To investigate the night activity of the species, we used the time of the events expressed as radians. We created density curves of activity by calculating the kernel densities of the radian times, and estimated the coefficients of overlap (Δ) (Ridout & Linkie, 2009) by using the R package Overlap (Meredith & Ridout, 2017). The coefficient of overlap is an estimate of the overlapping area in two density curves. Of five possible estimators of the coefficient of overlap, we chose the estimator Δ_1 since it performs better for small sample sizes ($n < 50$) (Ridout & Linkie, 2009). We then used the Bayesian bootstrapping to calculate the credible intervals of the overlapping coefficients by using the bayesboot R package (Bååth, 2016). We used the coefficients of overlap and the visual inspection of the activity density plots to estimate the temporal interactions of the species.

To obtain the AARs, we calculated two types of time interval; (1) the time interval between the detection of the target species and the posterior detection of a dog (T1) and, (2) the time interval between the detection of a dog and the posterior detection of the target species (T2). AARs were calculated as the proportion of T2s over T1s for each camera trap separately to avoid differences in detection probability (Parsons et al., 2016). The averages of the log AARs for each species were calculated and the bayesboot package (Bååth, 2016) in R was used to calculate the credible intervals of these averages. Positive values of log AARs might reflect that the target species avoid dogs or that dogs are attracted to the target species and the opposite for negative values.

Results

Spatial co-occurrence

During 233 trapping nights, we obtained 395 photographic events of the target species. Among the 40 locations, we recorded foxes at least once in 14 locations, whereas jackals, jungle cats and domestic dogs were recorded in eight, 15 and 29 locations, respectively.

Dogs showed the highest occupancy in our study area, while jackals showed the lowest (Fig. 2).

The probability of detection of the three wild species increased when the camera was placed on a trail. On the contrary, it decreased for dogs when the camera was placed on a trail (Fig. 3a). The number of dog events in a trapping night had a negative effect on the detectability of foxes, but not on the other species (Fig. 3b).

Regarding the model coefficients, we considered of interest those effects where the 80 percent credible interval did not overlap zero (i.e. we were 90 percent certain about the direction of the effect). Foxes were affected positively by the mean size of the habitat patches on the 1000m and the 500m buffer size (Fig. 4 and 5). Likewise, the percentage of forest plantations and the length of canals had a positive effect on the habitat use of foxes at the two largest buffer sizes, but not at the 100m buffer size. In contrast, the proportion of human settlements had a negative effect on the probability of Indian fox occurrence at the 500m buffer size. The proportion of forest and distance of roads affected the habitat use of jackals negatively at 1000m and 500m buffer sizes. Fewer variables had a clear directional effect on the habitat use of jungle cats and dogs. However, roads had a slightly negative effect at 500m buffer size for jungle cats. Interestingly, jackals, dogs and jungle cats showed a positive association with the proportion of human settlements at 100m buffer size. Dogs and jungle cats appeared to be less specialized in their habitat use than jackals and Indian foxes (Fig. 4).

Interestingly, we did not detect a strong interaction effect between the species except for a negative interaction between fox and jackals at the 1000m buffer size (Fig. 6). Moreover, the WAIC values of the models including the species interaction terms were larger than the corresponding model without interactions (Table 2). Nonetheless, the fit of the 1000m buffer size improved when including the fox and jackal interaction term without the rest of the species interactions (Table 2).

Activity patterns

The coefficients of overlap revealed a high coincidence in the activity patterns of the native species and dogs. It was highest for jackal ($\Delta = 0.801$, CRI (0.799, 0.803)) and jungle cat ($\Delta = 0.800$, CRI (0.798, 0.802)), followed by Indian fox ($\Delta = 0.792$, CRI (0.790, 0.794)). Although the overlap was high, the density curves of activity for Indian fox and dogs suggested some avoidance of dogs by the former (Fig. 7). The plot showed bimodal distributions for both species in which the peaks of dog activity coincided with the valleys of Indian fox activities. The density curves of activity for jungle cat and jackal showed bimodal and unimodal distribution respectively, and less clear patterns in relation to dog activity (Fig. 7).

The averaged log AARs for Indian fox, jungle cat and jackal with dogs were 1.201, CRI (0.409, 2.002), 0.312, CRI (-0.222, 0.914), and -0.233, CRI (-0.776, 0.313) respectively. Indian fox showed temporal avoidance of dogs whereas log AAR values for jungle cats and jackals did not reveal a temporal avoidance behavior by these species. Nonetheless, these results should be treated as preliminary given the small sample size of cameras in which the sequence of events allowed for the calculations of the time intervals (n=3 for Indian fox, n=4 for jungle cat and n=6 for jackal). All the analyses were conducted in R 3.4.1 (Team, 2017).

Discussion

According to the competitive exclusion principle, two coexisting and ecologically similar species will show some form of niche differentiation (Gause, 1934). Our study provides evidence of spatial niche partitioning between Indian fox and Jackal in a highly human dominated landscape of Maharashtra, India. In contrast, the other study species in this mesocarnivore community utilized similar habitats. Lesmeister et al. (2015) found a similar carnivore assemblage with little evidence of spatial niche partitioning except for the interaction between the gray fox and the coyote. The spatial differentiation between Indian fox and jackal is probably caused by differences in the habitat use of the two species. As revealed by our results, Indian fox was more associated with natural habitats and avoided human settlements, whereas jackal was more likely found close to humans. On the contrary, jungle cats appeared to be the most opportunistic of the three wild study species, and therefore, utilized a variety of habitats that overlapped with the other species. Spatial overlap in the habitat used by species on the same trophic level also occurs in more natural habitats (Bianchi, Olifiers, Gompper, &

Mourao, 2016; Gompper et al., 2016), especially among generalist species. Nonetheless, some degree of habitat specialization will favor spatial niche partitioning (Soto & Palomares, 2015) which seem to be the case between fox and jackals in this area.

Competitive species can avoid interference by other means apart from spatial niche partitioning. An example is temporal segregation, which occurs between coyotes and wolves (Atwood & Gese, 2010), or foxes and dingoes (Mitchell & Banks, 2005). Our results suggest a comparable interaction between Indian foxes and dogs. Although we detected no spatial niche separation between the two species, the detectability of foxes decreased as the number of dog events per trapping night increased. Moreover, the Avoidance-Attraction Ratios showed longer time intervals to the detection of Indian foxes after the camera trap detected a dog. Likewise, the activity patterns showed that Indian fox activity peaked when dog activity was lowest. These results strongly suggest a temporal avoidance of dogs among the Indian foxes. Vanak and Gompper (2009a) suggested that Indian foxes had limited access to human derived food and agricultural land due to interference competition with dogs. Moreover, Vanak, Thaker, and Gompper (2009) found that Indian foxes reduced visitation rates at food trays when exposed to dog odor. Spatial avoidance of dogs may not be possible since dogs were detected in large parts of the area (72.5% of the camera locations); therefore, we believe that the Indian fox avoids domestic dogs at a smaller scale by temporal niche partitioning. Despite the fact that jackals and jungle cats commonly use areas near villages where dogs are dominant (Aiyadurai & Jhala, 2006; Nowell & Jackson, 1996), we did not find evidence of interactions among these species and dogs. The body size of jackals (approx. 8.8 kg for males and 7.3kg for females (Jhala & Moehlman, 2004)), jungle cat (approx. 6.1kg for males and 4.2 for females (Nowell & Jackson, 1996)) and dogs is more similar than that of Indian foxes (approx. 2.9 and 1.8 for males and females respectively (Belsare & Vanak, 2013; Johnsingh & Jhala, 2004)). In solitary carnivores, intraguild killing is less likely between similar body size species (Palomares & Caro, 1999).

Likewise, avoidance behavior might not be as marked in species with similar body sizes. Indeed, among the eight camera locations that detected jackals, four also detected jungle cats and six detected dogs. Moreover, of the 15 camera locations with jungle cats, 11 also detected dogs. Therefore, although we cannot exclude the possibility that interference interactions occur among these three species, they might not be as pronounced as in foxes.

Indian foxes showed the most specialized habitat use among the four study species, since they were affected by the habitat and infrastructure variables to a greater extent. The associations were stronger at the 1000m and 500m buffer sizes for Indian fox, which suggest that the habitat selection process takes place at a landscape scale rather than at a patch scale. This pattern has been also shown in the denning habits of this species (Punjabi, Chellam, & Vanak, 2013). Indian foxes were strongly associated to forestry plantations at the largest buffer sizes (1000 m and 500 m). This species is commonly associated to forest patches, but also to grassland savannah (Vanak & Gompper, 2010). In our study, only two locations had some grassland habitat cover within the buffer areas, and therefore, we included grassland in the fallow land category that consisted mainly of open areas between agricultural fields. Length of canals also had a strong positive effect on the habitat use of Indian foxes at the 1000 and 500m buffer sizes. Indian foxes might use canals as borders between their territories or as a water source during the wet season. Interestingly, the mean area of the habitat patch was an important predictor of the habitat use of the Indian fox. Further expansion of urban and agricultural areas might increase fragmentation and habitat loss by reducing the size of the natural patches required for their habitat use.

The negative effect of tarmac roads on jackal habitat use may reflect a strategy to avoid human interference with a consequent reduction of road kills. Although we did not detect any effect of agriculture on its habitat use, previous studies have found that jackals use agriculture land, especially sugar cane plantations, as cover during daytime (Jaeger et al., 2007; Poche et al., 1987). The lack of association in our study is probably due to the fact that this habitat category included both irrigated (e.g. sugarcane) and non-irrigated cultivation (e.g. maze and grain). A more detailed classification of agricultural land may have revealed a stronger association of these two canid species with different agriculture types.

Jungle cats and domestic dogs were detected in a variety of habitat types. They appear to be the most opportunistic of the four studied species and less affected by human activity in this area. This is not surprising, since dogs are closely associated to humans and jungle cats are not considered habitat specialists (Mukherjee et al., 2010), although they show some preferences for open habitats (Mukherjee et al., 2010; Nowell & Jackson, 1996). Jungle cats are also well adapted to cultivated land, and like the jackal, they use irrigated cultivation like sugarcane as cover (Nowell & Jackson, 1996). Interestingly, dogs, jackals and jungle cats showed a positive association with human settlements at the smallest buffer size. A dependency on human food resources probably explains this pattern. Jungle cats are often found in the proximities of human settlements (Nowell & Jackson, 1996) and jackals are commonly associated with human settlements where they feed on garbage and other anthropogenic food (Jaeger et al., 2007; Jhala & Moehlman, 2004).

In conclusion, habitat specialization and differences in body size seem to shape the structure of this mesocarnivore community. More opportunistic species with similar body size overlap spatially whereas specialized and smaller sized mesocarnivores are displaced. In addition, human impact on habitat use differs among species depending on the degree of habitat specialization. Whereas human influence can benefit jungle cats and jackals through food resource subsidization, it may affect Indian foxes negatively through loss and fragmentation of habitats and by interactions with domestic dogs. It is important to take into account both the potentially positive and negative effects of human influence in future land management actions aimed at conserving biodiversity in highly human dominated landscapes.

References

Aiyadurai, A., & Jhala, Y. V. (2006). Foraging and habitat use by golden jackals (Canis aureus) in the Bhal Region, Gujarat, India. . *Journal of the Bombay Natural History Society*(103), 5–12.

Athreya, V., Odden, M., Linnell, J. D. C., Krishnaswamy, J., & Karanth, K. U. (2016). A cat among the dogs: leopard Panthera pardus diet in a human-dominated landscape in western Maharashtra, India. *Oryx, 50*(1), 156-162. doi:10.1017/s0030605314000106

Athreya, V., Odden, M., Linnell, J. D. C., Krishnaswamy, J., & Karanth, U. (2013). Big Cats in Our Backyards: Persistence of Large Carnivores in a Human Dominated Landscape in India. *PLoS One, 8*(3), 8. doi:10.1371/journal.pone.0057872

Atwood, T. C., & Gese, E. M. (2010). Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids. *Journal of Mammalogy, 91*(2), 490-499. doi:10.1644/09-mamm-a-078.1

Bååth, R. (2016). An implementation of Rubin's (1981) Bayesian Bootstrap. *R Package version 0.2.1 https://cran.r-project.org/web/packages/bayesboot/bayesboot.pdf*.

Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management, 59*(2), 228-237. doi:10.2307/3808935

Belsare, A. V., & Gompper, M. E. (2013). Assessing demographic and epidemiologic parameters of rural dog populations in India during mass vaccination campaigns. *Preventive Veterinary Medicine, 111*(1-2), 139-146. doi:10.1016/j.prevetmed.2013.04.003

Belsare, A. V., & Vanak, A. T. (2013). Use of xylazine hydrochloride-ketamine hydrochloride for immobilization of indian fox (vulpes bengalensis) in field situations. *Journal of Zoo and Wildlife Medicine, 44*(3), 753-755.

Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology, 76*(6), 1075-1085. doi:10.1111/j.1365-2656.2007.01287.x

Bianchi, R. D., Olifiers, N., Gompper, M. E., & Mourao, G. (2016). Niche Partitioning among Mesocarnivores in a Brazilian Wetland. *PLoS One, 11*(9). doi:10.1371/journal.pone.0162893

Bino, G., Dolev, A., Yosha, D., Guter, A., King, R., Saltz, D., & Kark, S. (2010). Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology, 47*(6), 1262-1271. doi:10.1111/j.1365-2664.2010.01882.x

Boitani, L., & Ciucci, P. (1995). Comparative social ecology of feral dogs and wolves. *Ethology Ecology & Evolution, 7*(1), 49-72.

Braczkowski, A. R., Balme, G. A., Dickman, A., Fattebert, J., Johnson, P., Dickerson, T., . . . Hunter, L. (2016). Scent Lure Effect on Camera-Trap Based Leopard Density Estimates. *PLoS One, 11*(4), 14. doi:10.1371/journal.pone.0151033

Bu, H. L., Wang, F., McShea, W. J., Lu, Z., Wang, D. J., & Li, S. (2016). Spatial Co-Occurrence and Activity Patterns of Mesocarnivores in the Temperate Forests of Southwest China. *PLoS One, 11*(10). doi:10.1371/journal.pone.0164271

Chartier, L., Zimmermann, A., & Ladle, R. J. (2011). Habitat loss and human-elephant conflict in Assam, India: does a critical threshold exist? *Oryx, 45*(4), 528-533. doi:10.1017/s0030605311000044

Cruz, J., Sarmento, P., & White, P. C. L. (2015). Influence of exotic forest plantations on occupancy and co-occurrence patterns in a Mediterranean carnivore guild. *Journal of Mammalogy, 96*(4), 854-865. doi:10.1093/jmammal/gyv109

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*(2), 221-227. doi:10.1017/s0030605311001803

Dickson, B. G., Jenness, J. S., & Beier, P. (2005). Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management, 69*(1), 264-276. doi:10.2193/0022-541x(2005)069<0264:iovtar>2.0.co;2

Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters, 10*(3), 197-206. doi:10.1111/j.1461-0248.2006.01010.x

ESRI. (2009). ARCGIS desktop. Environmental Systems Research Institute, Redland.

Farris, Z. J., Kelly, M. J., Karpanty, S., & Ratelolahy, F. (2016). Patterns of spatial co-occurrence among native and exotic carnivores in north-eastern Madagascar. *Animal Conservation, 19*(2), 189-198. doi:10.1111/acv.12233

Gause, G. F. (1934). *The struggle for existence.*: Williams & Wilkins, Baltimore.

Gelman, A., & Rubin, D. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science, 7*(4), 457-472.

Gerber, B. D., Karpanty, S. M., & Kelly, M. J. (2012). Evaluating the potential biases in carnivore capture-recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population Ecology, 54*(1), 43-54. doi:10.1007/s10144-011-0276-3

Gompper, M. E., Lesmeister, D. B., Ray, J. C., Malcolm, J. R., & Kays, R. (2016). Differential Habitat Use or Intraguild Interactions: What Structures a Carnivore Community? *PLoS One, 11*(1). doi:10.1371/journal.pone.0146055

Google Earth Pro 7.1.8.3036 (November 15, 2016). Sirsuphal, Baramati municipality, India. 43Q 455623 E 20025001 N , eye alt 3km. DigitalGlove 2012. http://www.google.com/earth/index.html [January 25, 2017]

Jaeger, M. M., Haque, E., Sultana, P., & Bruggers, R. L. (2007). Daytime cover, diet and space-use of golden jackals (Canis aureus) in agro-ecosystems of Bangladesh. *Mammalia, 71*(1-2), 1-10. doi:10.1515/mamm.2007.016

Jhala, Y. V., & Moehlman, P. D. (2004). Golden jackal *Canis aureus*. In C. Sillero-Zubiri, M. Hoffmann, & D. W. Macdonald (Eds.), *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan* (pp. 156-161). Gland, Switzerland and Cambridge, Uk.: IUCN/SCC Canid Specialist Group.

Johnsingh, A. J. T., & Jhala, Y. V. (2004). Indian fox *Vulpes bengalensis*. In C. Sillero-Zubiri, M. Hoffmann, & D. W. Macdonald (Eds.), *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan* (pp. 219-222). Gland, Switzerland and Cambridge, Uk.: IUCN/SCC Canid Specialist Group.

Kinnaird, M. F., Sanderson, E. W., O'Brien, T. G., Wibisono, H. T., & Woolmer, G. (2003). Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology, 17*(1), 245-257. doi:10.1046/j.1523-1739.2003.02040.x

Laliberte, A. S., & Ripple, W. J. (2004). Range contractions of North American carnivores and ungulates. *Bioscience, 54*(2), 123-138. doi:10.1641/0006-3568(2004)054[0123:rconac]2.0.co;2

Lesmeister, D. B., Nielsen, C. K., Schauber, E. M., & Hellgren, E. C. (2015). Spatial and Temporal Structure of a Mesocarnivore Guild in Midwestern North America. *Wildlife Monographs, 191*(1), 1-61. doi:10.1002/wmon.1015

Lindstrom, E. R., Brainerd, S. M., Helldin, J. O., & Overskaug, K. (1995). Pine marten red fox interactions - a case of intraguild predation. *Annales Zoologici Fennici, 32*(1), 123-130.

Linnell, J. D. C., & Strand, O. (2000). Interference interactions, co-existence and conservation of

mammalian carnivores. *Diversity and Distributions, 6* 169–176. doi:10.1046/j.1472-4642.2000.00069.x

MacKenzie, D. I., Bailey, L. L., & Nichols, J. D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology, 73*(3), 546-555. doi:10.1111/j.0021-8790.2004.00828.x

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology, 83*(8), 2248-2255. doi:10.2307/3072056

Meredith, M., & Ridout, M. S. (2017). overlap: estimates of coefficient of overlapping for animal activity patterns. *r PACKAGE VERSION 0.3.0 https://cran.r-project.org/web/packages/overlap/index.html*.

Mitchell, B. D., & Banks, P. B. (2005). Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. *Austral Ecology, 30*(5), 581-591. doi:10.1111/j.1442-9993.2005.01473.x

Mukherjee, S., Krishnan, A., Tamma, K., Home, C., Navya, R., Joseph, S., . . . Ramakrishnan, U. (2010). Ecology Driving Genetic Variation: A Comparative Phylogeography of Jungle Cat (Felis chaus) and Leopard Cat (Prionailurus bengalensis) in India. *PLoS One, 5*(10). doi:10.1371/journal.pone.0013724

Newsome, S. D., Ralls, K., Job, C. V., Fogel, M. L., & Cypher, B. L. (2010). Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (Vulpes macrotis mutica). *Journal of Mammalogy, 91*(6), 1313-1321. doi:10.1644/09-mamm-a-362.1

Nowell, K., & Jackson, P. (1996). Jungle Cat, *Felis chaus* Schreber, 1777. In K. Nowell & P. Jackson (Eds.), *Wild Cats. Status survey and conservation action plan.*

(pp. 83-85): IUCN Publications Services Unit.

Ordenana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., . . . Van Vuren, D. H. (2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy, 91*(6), 1322-1331. doi:10.1644/09-mamm-a-312.1

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *American Naturalist, 153*(5), 492-508. doi:10.1086/303189

Parsons, A. W., Bland, C., Forrester, T., Baker-Whatton, M. C., Schuttler, S. G., McShea, W. J., . . . Kays, R. (2016). The ecological impact of humans and dogs on wildlife in protected areas in eastern North America. *Biological Conservation, 203*, 75-88. doi:10.1016/j.biocon.2016.09.001

Phalan, B., Onial, M., Balmford, A., & Green, R. E. (2011). Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. *Science, 333*(6047), 1289-1291. doi:10.1126/science.1208742

Poche, R. M., Evans, S. J., Sultana, P., Hague, M. E., Sterner, R., & Siddique, M. A. (1987). Notes on the golden jackal (canis-aureus) in bangladesh. *Mammalia, 51*(2), 259-270. doi:10.1515/mamm.1987.51.2.259

Prange, S., Gehrt, S. D., & Wiggers, E. P. (2003). Demographic factors contributing to high raccoon densities in urban landscapes. *Journal of Wildlife Management, 67*(2), 324-333. doi:10.2307/3802774

Punjabi, G. A., Chellam, R., & Vanak, A. T. (2013). Importance of Native Grassland Habitat for Den-Site Selection of Indian Foxes in a Fragmented Landscape. *PLoS One, 8*(10), 9. doi:10.1371/journal.pone.0076410

Ridout, M. S., & Linkie, M. (2009). Estimating Overlap of Daily Activity Patterns From Camera Trap Data. *Journal of Agricultural Biological and Environmental Statistics, 14*(3), 322-337. doi:10.1198/jabes.2009.08038

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters, 12*(9), 982-998. doi:10.1111/j.1461-0248.2009.01347.x

Rota, C. T., Ferreira, M. A. R., Kays, R. W., Forrester, T. D., Kalies, E. L., McShea, W. J., . . . Millspaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution, 7*(10), 1164-1173. doi:10.1111/2041-210x.12587

Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation - a review. *Conservation Biology, 5*(1), 18-32. doi:10.1111/j.1523-1739.1991.tb00384.x

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science (New York, N.Y.), 185*(4145), 27-39. doi:10.1126/science.185.4145.27

Soto, C., & Palomares, F. (2015). Coexistence of sympatric carnivores in relatively homogeneous Mediterranean landscapes: functional importance of habitat segregation at the fine-scale level. *Oecologia, 179*(1), 223-235. doi:10.1007/s00442-015-3311-9

Suryawanshi, K. R., Bhatia, S., Bhatnagar, Y. V., Redpath, S., & Mishra, C. (2014). Multiscale Factors Affecting Human Attitudes toward Snow Leopards and Wolves. *Conservation Biology, 28*(6), 1657-1666. doi:10.1111/cobi.12320

Team, R. C. (2017). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.*

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., . . . Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation, 151*(1), 53-59. doi:10.1016/j.biocon.2012.01.068

Vanak, A. T., & Gompper, M. E. (2007). Effectiveness of non-invasive techniques for surveying activity and habitat use of the Indian fox Vulpes bengalensis in southern India. *Wildlife Biology, 13*(2), 219-224. doi:10.2981/0909-6396(2007)13[219:eontfs]2.0.co;2

Vanak, A. T., & Gompper, M. E. (2009a). Dietary niche separation between sympatric free-ranging domestic dogs and indian foxes in central india. *Journal of Mammalogy, 90*(5), 1058-1065. doi:10.1644/09-mamm-a-107.1

Vanak, A. T., & Gompper, M. E. (2009b). Dogs Canis familiaris as carnivores: their role and function in intraguild competition. *Mammal Review, 39*(4), 265-283. doi:10.1111/j.1365-2907.2009.00148.x

Vanak, A. T., & Gompper, M. E. (2010). Multi-scale resource selection and spatial ecology of the Indian fox in a human-dominated dry grassland ecosystem. *Journal of Zoology, 281*(2), 140-148. doi:10.1111/j.1469-7998.2010.00690.x

Vanak, A. T., Thaker, M., & Gompper, M. E. (2009). Experimental examination of behavioural interactions between free-ranging wild and domestic canids. *Behavioral Ecology and Sociobiology, 64*(2), 279-287. doi:10.1007/s00265-009-0845-z

Tables

Table 1. Variables used for studying the occurrence and co-occurrence of Indian foxes, jackals, Jungle cats and dogs.

Variable	**Definition**	**Type**
Dist.settle	Distance to the nearest building or settlement (meters)	Continuous
Forest	Percentage of forest in the resolution buffer	Continuous
Fallow	Percentage of fallow land in the resolution buffer	Continuous
Agriculture	Percentage of agriculture land in the resolution buffer	Continuous
Settle	Percentage of human settlement in the resolution buffer	Continuous
Road	Meters of tarmac road in the resolution buffer	Continuous
Canal	Meters of canal in the resolution buffer	Continuous
Patch.area	Mean habitat patch area in the resolution buffer	Continuous
Trail	Whether the camera was placed on or off a trail or path	Factor
Dogpoisson	Number of dog events in a camera each trapping night	Continuous

Table 2. WAIC values of the models.

	W/o Interacions	With Interactions	Jackal and fox interaction
1000m buffer size	742.7711	746.8785	740.6913
500m buffer size	714.5454	715.6971	NA
100m buffer size	733.3225	741.1491	NA

Figures

Figure 1. Study area located in the vicinity of Baramati, Maharashtra, India. Dots represent camera trap locations, and circles delimit the buffer areas from which habitat data was extracted.

Figure 2. Marginal occupancy probability distributions for the four study species.

Figure 3. a) Detection probability of foxes, jackals, jungle cats and dogs when the camera locations are placed either on or outside a trail or natural path. b) Effect of the number of dogs each trapping night on the detection probability of foxes, jackals and jungle cats where the solid line represent the general trend and the shaded area the 95% credible interval.

Figure 4. Effect of the scaled coefficients on the habitat use of Indian fox, jackals, jungle cat and dogs in a human dominated land in Maharashtra, India. Thin lines represent the 95% credible interval, thick lines are the 80% credible interval. Dashed lines separate the different species. Roads/Dist.settle represents the effect of ‘distance of tarmac roads’ for the 1000 and the 500 buffer size models and ‘distance to settlement’ for the 100m buffer size model.

Figure 5. Mean patch habitat area effect on the habitat use of Indian foxes at three buffer sizes. Solid lines represent the general trend and the shaded area the 95% credible interval.

Figure 6. Posterior distributions of the marginal occupancy probability of Indan fox conditional on the presence or absence of Jackal.

Figure 7. Activity kernel density plots of the activity of Indian fox, jungle cat and jackal with domestic dog. Ticks along the y axis represent the actual observations for each of the species. Only the period between dusk and dawn was sampled and thus, the lack of activity in the middle part of the plots.

Figure 1

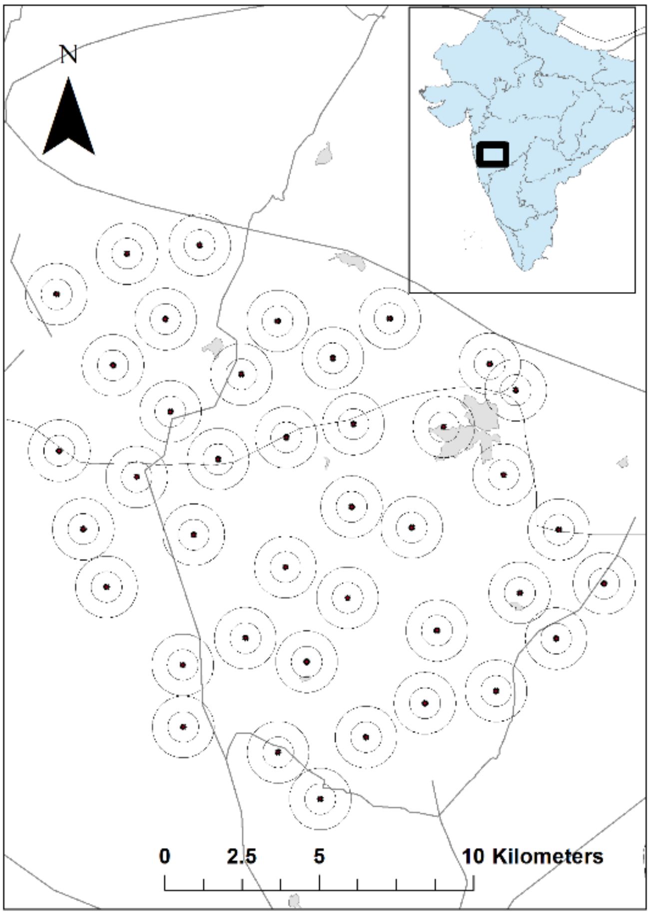
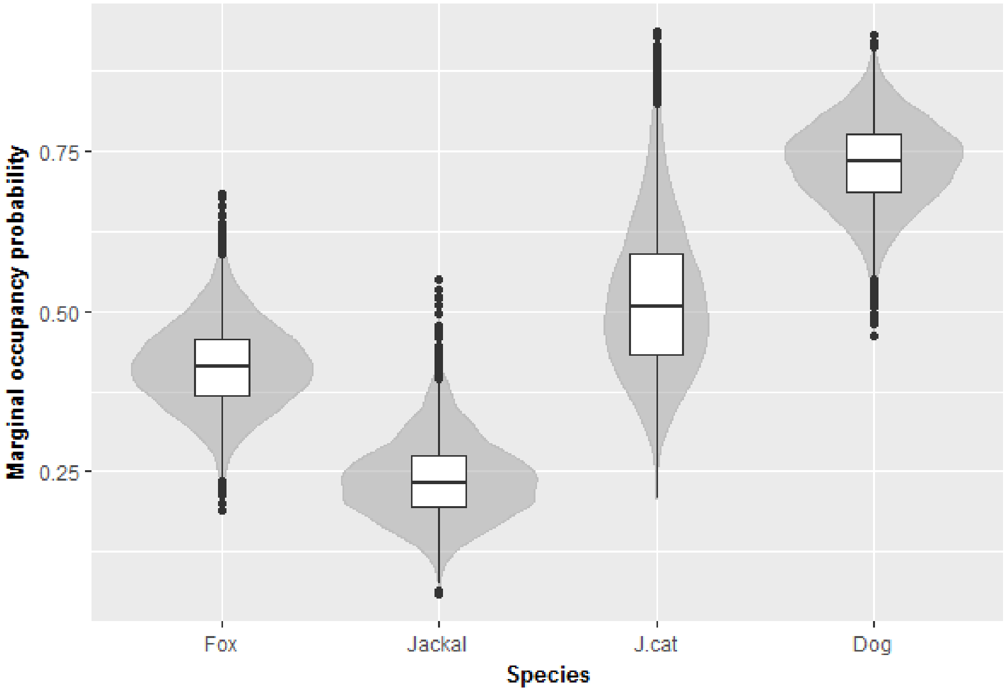


Figure 2



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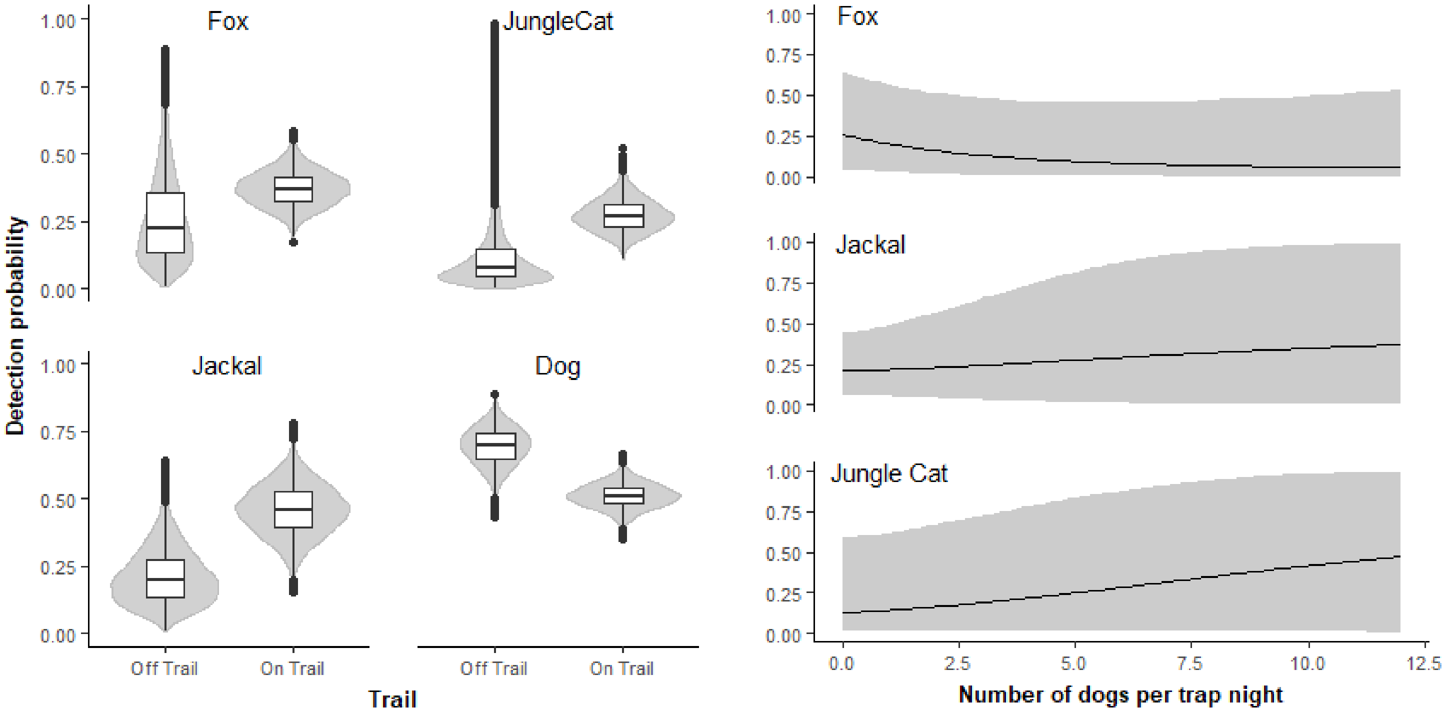


Figure 4

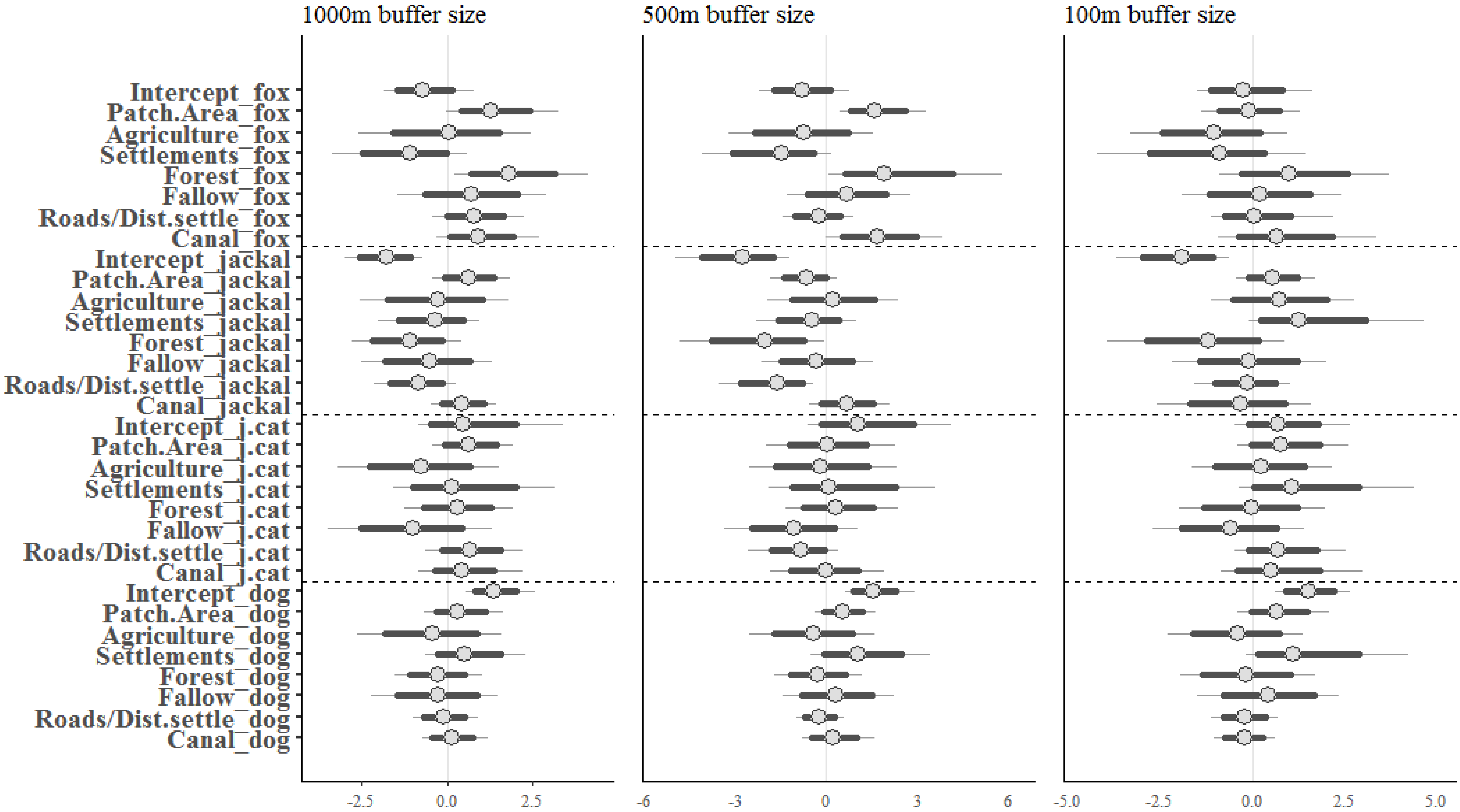

1000m buffer size
500m buffer size
100m buffer size
Intercept_fox
Patch.Area_fox
Agriculture_fox
Settlements_fox
Forest_fox
Fallow_fox
Roads/Dist.settle_fox
Canal_fox
Intercept_jackal
Patch.Area_jackal
Agriculture_jackal
Settlements_jackal
Forest_jackal
Fallow_jackal
Roads/Dist.settle_jackal
Canal_jackal
Intercept_j.cat
Patch.Area_j.cat
Agriculture_j.cat
Settlements_j.cat
Forest_j.cat
Fallow_j.cat
Roads/Dist.settle_j.cat
Canal_j.cat
Intercept_dog
Patch.Area_dog
Agriculture_dog
Settlements_dog
Forest_dog
Fallow_dog
Roads/Dist.settle_dog
Canal_dog
-2.5
0.0
2.5
-6
-3
0
3
6
-5.0
-2.5
0.0
2.5
5.0

Figure 5

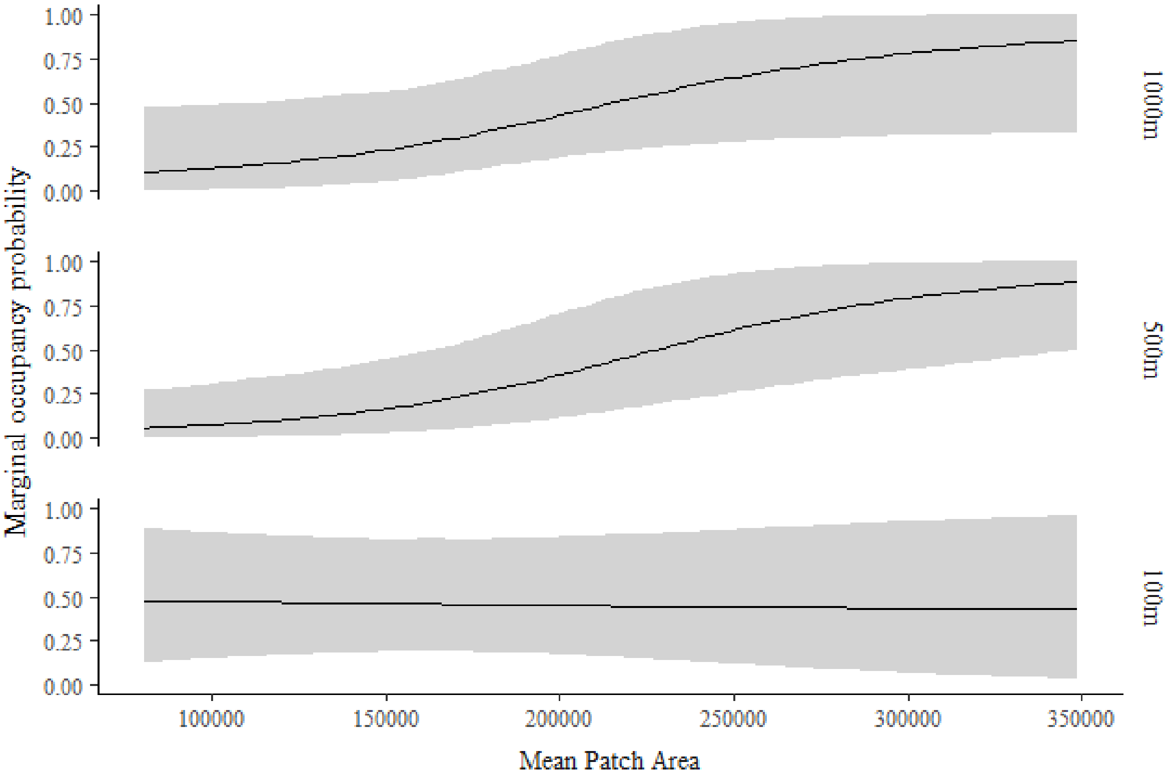


Figure 6

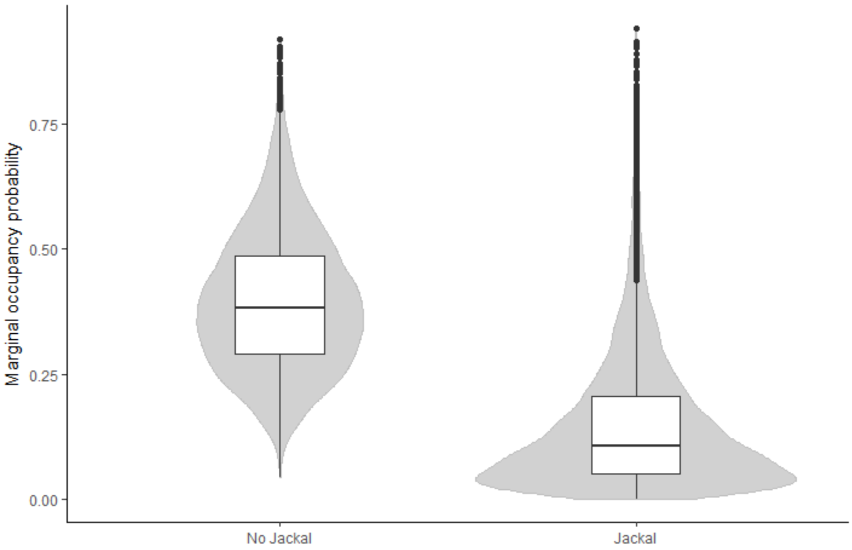
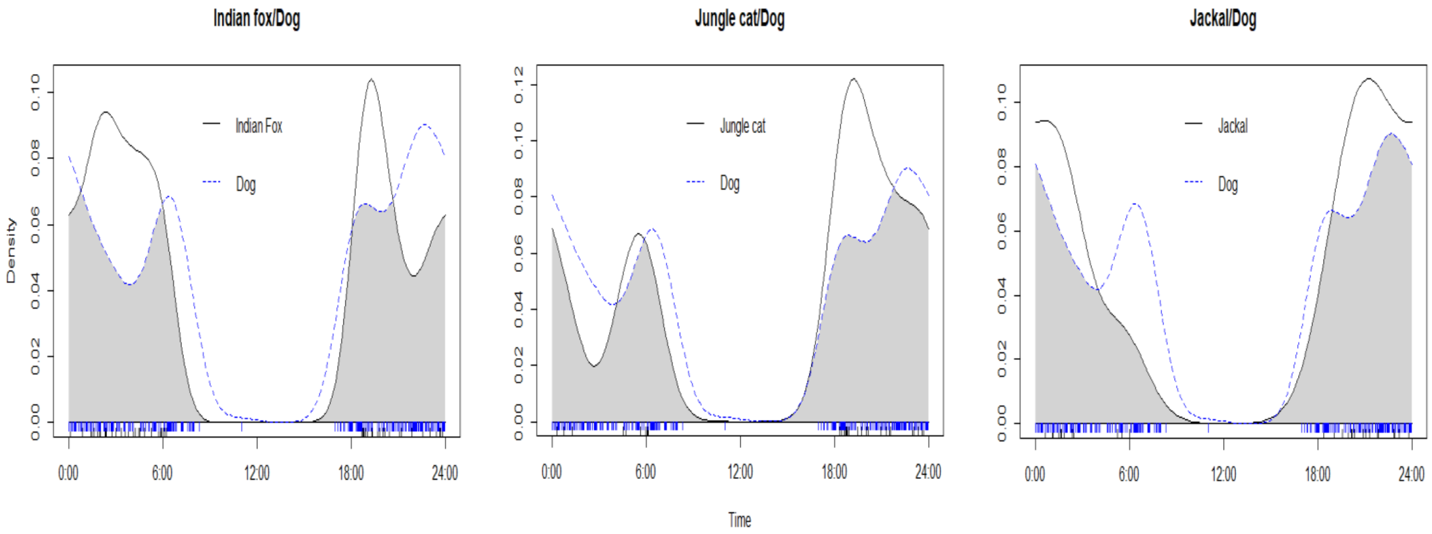


Figure 7


Indian fox/Dog
Jungle cat/Dog
Jackal/Dog
Density
0.00
0.02
0.04
0.06
0.08
0.10
0.12
Indian Fox
Jungle cat
Jackal
Dog
0:00
6:00
12:00
18:00
24:00
Time