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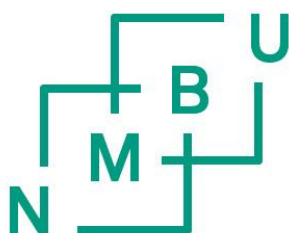
Anthropogenic effects on spatiotemporal activity patterns and interactions in a predator-prey assemblage

Neri Horntvedt Thorsen
Master of Science in Ecology

Preface

This master thesis was written at the Department of Ecology and Natural Resource management at the Norwegian University of Life Sciences. My field work has been a part of the Norwegian Institute for Nature Research's (NINA) camera trap project, which has been funded by the Norwegian Environment Agency, the Offices of Environmental Affairs in the counties of Oppland, Oslo & Akershus, Østfold, Vestfold, Telemark and Buskerud, and the Carnivore Management Boards in regions 2, 3, and 4. I would like to thank all the volunteers who have been working on this project, with data collection and sorting pictures.

I would like to especially thank my supervisors Richard Bischof (NMBU), John Odden (NINA) and Leif Egil Loe (NMBU). Thanks to Richard Bischof for all the help with the statistical analyses, writing process and valuable comments on the manuscript. Thanks to John Odden for valuable comments on the manuscript, and especially for letting me work with this project and all advices I have been given throughout these three years, it has been very educational. Thanks to Leif Egil Loe for valuable comments on the manuscript and feedbacks during the analyses and writing process.



**Norwegian University
of Life Sciences**

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Neri Horntvedt Thorsen

Abstract

Evidence is accumulating that human presence and anthropogenic features in the environment impact the spatiotemporal activity patterns of both predators and prey. This is liable to affect predator-prey interactions, one of the central themes in wildlife ecology. Predator-prey interactions are complex to begin with, and disentangling anthropogenic impacts remains a substantial challenge. Yet, understanding such effects is essential in today's increasingly human-dominated landscapes. The aim of this thesis was to test for anthropogenic effects on spatial and temporal patterns of activity in a system with two carnivores and one herbivore. I used camera trap data on Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*) and Eurasian roe deer (*Capreolus capreolus*) collected continuously in southern Norway between 2012 and 2015. I fitted Bayesian co-occupancy models and Kernel density functions to estimate co-occupancy and the degree of overlap in diel activity patterns, respectively. The results supported the notion that sympatric predators use temporal partitioning in order to avoid humans. Further, it was revealed season-specific effects of human density on the spatiotemporal activity patterns in the study species. High human density increased the activity overlap between roe deer and red fox, likely as a result of increased temporal avoidance of humans. During winter this pattern was reversed; human density decreased the activity overlap between roe deer and red fox, indicating that roe deer might use humans as a shield in time towards red fox predation. This thesis suggests that human activity and human density are able to alter the spatiotemporal activity patterns in a predator-prey assemblage and are likely to influence their interactions. Furthermore, it highlights the importance of seasonality in factors constraining single species as well as modulating predator-prey interactions, which should be considered in future studies of predator-prey interactions.

Sammendrag

Det er stadig flere indikasjoner på at menneskelige faktorer i miljøet påvirker romlige og temporære mønster hos både predatorer og byttedyr. Slike effekter kan påvirke interaksjonene mellom predatorer og byttedyr, ett av de sentrale temaene i økologien. Predator-byttedyr interaksjoner er i utgangspunktet komplekse, det å undersøke menneskelig påvirkning blir derfor utfordrende. Forståelse av disse effektene er likevel viktig, siden menneskets dominans i landskapet er økende. Hensikten med denne masteroppgaven var å teste menneskelige effekter på romlige og temporære mønster i aktivitet i et studiesystem med to rovdyr og en herbivor. Jeg brukte viltkameradata av gaupe (*Lynx lynx*), rødrev (*Vulpes vulpes*) og rådyr (*Capreolus capreolus*) fra større deler av Sør-Norge, samlet inn av Norsk Institutt for Naturforskning (NINA) i perioden mellom 2012 og 2015. Jeg tilpasset Bayesiske co-occupancy modeller og Kernel density funksjoner til å estimere henholdsvis co-occupancy og døgnaktivitet. Resultatene støttet tidligere funn av temporær unngåelse av menneske hos predatorer som sameksisterer med mennesker. Videre ble det oppdaget sesong-avhengige effekter av mennesketetthet på aktivitetsmønstrene i rom og tid hos studieartene. Høy mennesketetthet økte overlappingen i aktivitet mellom rådyr og rev, sannsynligvis som et resultat av økt unngåelse av menneske i tid. Om vinteren var dette mønsteret reversert; mennesketetthet reduserte overlappingen i aktivitet mellom rådyr og rev, noe som kan indikere at rådyr bruker mennesket som beskyttelse (i tid) mot predasjon fra rev. Resultatene fra denne oppgaven foreslår at menneskeaktivitet og mennesketetthet er i stand til å endre arters aktivitetsmønster i rom og tid, noe som trolig påvirker deres interaksjoner. I tillegg viser oppgaven viktigheten av sesongavhengighet i faktorer som kan endre interaksjoner mellom predatorer og byttedyr, noe fremtidige studier bør ta hensyn til.

Table of contents

Introduction	1
Methods	4
Study area	4
Camera trapping	5
Hunting and season definition	7
Statistical analysis	8
Occupancy analysis	8
Activity analysis	10
Results	12
Occupancy	12
Temporal patterns	15
a. Humans	15
b. Lynx	16
c. Red fox	16
d. Roe deer	18
Discussion.....	19
Association in space and avoidance in time	20
Season-specific predator avoidance.....	22
Humans modulate spatiotemporal patterns of avoidance	23
Studying predator-prey interactions using camera traps	25
Conclusion.....	26
Literature	26
Appendix	32

Introduction

Humans pose a predation risk to a wide range of vertebrates (Corlett 2007; Hirschfeld & Heyd 2005), including large carnivores (Estes et al. 2011). As such, humans are liable to influence natural predator-prey dynamics. Anthropogenic reduction of carnivore populations can lead to trophic cascades (Ripple et al. 2014) and impact a wide range of wildlife interactions (Prugh et al. 2009). Large carnivores are recovering in Europe (Chapron et al. 2014), but anthropogenic-induced predation risk still influence their behaviour (Muhly et al. 2011). Human-induced behavioural responses in large carnivores could possibly change their interactions with prey (Ordiz et al. 2013). Predator-prey interactions are also influenced by resources provided or impaired by humans (Bino et al. 2010; Newsome et al. 2015), and could potentially have far reaching effects in the ecosystem. Understanding how humans affect predator-prey interactions is important, as approximately 35 % of the terrestrial land surface has been converted to agriculture and human settlement (Ellis et al. 2010), and anthropogenic activities are seen in almost every ecosystem (Vitousek et al. 1997).

Predators have both lethal and non-consumptive effects on their prey (Lima 1998). Predation can directly affect the abundance (Andrén & Liberg 2015; Melis et al. 2010), geographic ranges (Holt & Barfield 2009) and alter the spatial distribution of prey (Creel et al. 2005; Proffitt et al. 2009). Although less conspicuous, predators also induce behavioural responses through non-consumptive effects. Predation risk is heterogeneously distributed in both time and space, as a predator's success at capturing prey is influenced by landscape variables (Kauffman et al. 2007), habitat characteristics (Lone et al. 2014) and when and where predators are active (Lima & Bednekoff 1999). This creates a "landscape of fear", which affects the prey's decision making (Laundré et al. 2001). In order to maximize their fitness, prey should find an optimal trade-off between anti-predator behaviour and the need for resources (Lima & Dill 1990). The cost of anti-predator behaviour can be foraging in less preferred habitat, reduced foraging time due to increased time spent vigilant, increased physiological stress and reduced overall energy intake (Lima 1998). Owing to these costs, non-consumptive effects of predation may have significant effects on prey demography which sometimes exceed that of lethal effects (Creel & Christianson 2008).

As predators, humans might also have extensive lethal and non-consumptive effects on predator-prey interactions, not only as a predator but also through disturbance and habitat alterations. For instance, the combined effects of release from larger, more dominant carnivores (mesopredator release, (Soule et al. 1988)) and human-provided resources might increase the abundance of mesopredators (Newsome et al. 2015), even in densely populated urban areas (Bino et al. 2010).

This can increase predation risk near human settlements and lead to avoidance of such areas by prey species (Shapira et al. 2008). On the other hand, prey species may be attracted to food sources available in human-dominated landscapes, such as foraging on cultivated land for wild herbivores. If large carnivores avoid higher human densities, herbivores could experience lower predation risk at high human density and use such areas as a spatial refuge from predation (Muhly et al. 2011), referred to as “human shield” (Barber et al. 2010; Berger 2007). The latter assumes that the predation risk posed by humans is lower than the risk posed by natural predators, or that prey is able to avoid humans through spatiotemporal segregation or other antipredator behaviour.

In this thesis, I evaluate how human activity and human density influence spatiotemporal activity patterns and species-interactions in a system with two predators and one prey along a gradient of human disturbance. I use camera trap data from Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*) and Eurasian roe deer (*Capreolus capreolus*), collected in southern Norway. Biological and anthropogenic factors change throughout the year and are liable to modulate the effects humans have on predator-prey interactions. As camera trapping has been conducted continuously since 2012, these data present a unique opportunity to assess spatiotemporal patterns and evaluate anthropogenic effects in the context of seasonality. Camera trap studies have been used to estimate population density, occupancy and to quantify behaviour (McCallum 2013). Several camera trap studies have targeted wildlife interactions, such as temporal and spatial predator-prey interactions (Bischof et al. 2014a; Linkie & Ridout 2011), and human impacts on these (Díaz-Ruiz et al. 2015; Dorresteijn et al. 2015; Rodewald et al. 2011; Wang et al. 2015)

In this study system, roe deer serve as the main prey for the lynx (Odden et al. 2006) and the main prey for red fox at high roe deer densities during the breeding season (Panzacchi et al. 2008). Furthermore, lynx also kill red fox (Linnell et al. 1998) and contributes to the red fox’s “landscape of fear”. All species are subject to legal hunting, and most mortality in lynx and a high proportion of mortality in roe deer is human-caused (Andrén et al. 2006; Melis et al. 2013; Nilsen et al. 2012). Predators that co-exist with humans have been shown to be more active at night (Carter et al. 2012; Schuette et al. 2013; Wang et al. 2015), likely due to temporal avoidance of humans, in order to reduce the probability of a human encounter. Roe deer might also show similar behaviour, as they are assumed to occur at higher density in relation to humans, due to favourable foraging habitat. Several studies have shown that the occurrence of lynx, red fox and roe deer is positively affected by anthropogenic features in the landscape, such as fields (Basille et al. 2013; Bunnefeld et al. 2006; Panzacchi et al. 2010a; Shapira et al. 2008), human disturbance (Basille et al. 2009), urban

areas (Harris 1981; Harris & Rayner 1986) and that roe deer in Norway show higher tolerance of humans (Torres et al. 2012). Thus, I hypothesize:

- H1: The study species associate with humans in space and avoid humans in time.

Predictions:

- P1.1: Occupancy of lynx, red fox and roe deer at the camera trap sites should be positively influenced by human density or human use of areas near camera trap sites.
- P1.2: Diel activity of lynx, red fox and roe deer overlap less with human diel activity at camera trap sites than would be predicted by chance.

Prey behavior should lead to a trade-off between anti-predator behavior and energy intake that optimizes fitness (Lima 1998). The result of this trade-off could be context specific and for instance vary with season. Roe deer has been shown to exhibit increased vigilance (Benhaiem et al. 2008; Sönnichsen et al. 2013), lower activity levels (Pagon et al. 2013) and spatial avoidance of humans (Lone et al. submitted manuscript) during hunting seasons. It has also been suggested that roe deer accept high predation risk during the winter and early spring (Ratikainen et al. 2007), as this period is associated with the highest rate of fat depletion and largest risk of starvation. In my study system, roe deer (fawns) experience an elevated predation risk from red fox during their breeding season, as red fox are the main predator of fawns (Aanes & Andersen 1996; Panzacchi et al. 2008). Predation risk of roe deer fawns was mainly influenced by visibility of the mother, which could give cues to the red fox (Panzacchi et al. 2007), indicating that the encounter rate between roe deer and red fox could increase predation on fawns. I hypothesize:

- H2: Spatial and temporal avoidance of predators (including humans) is season-specific.

Predictions:

- P2.1: Roe deer show the strongest temporal/spatial avoidance of red fox during the roe deer breeding season, since red fox are the main predator on fawns.
- P2.2: Roe deer show the strongest temporal/spatial avoidance of humans in the roe deer hunting season, due to elevated predation risk.

Human activity and anthropogenic features in the landscape might affect the way wildlife interacts. Stronger temporal avoidance of humans in areas with high human activity have been shown to increase the amount of activity overlap in mesopredators (Wang et al. 2015). I investigate if this also could apply for a large carnivore, a mesopredator and an herbivore in relation to high human density. I hypothesize:

- H3: Humans modulate spatiotemporal avoidance patterns in prey, exposing them to predation risk from other predators.

Prediction:

- P3.1: At high human density, reduced activity overlap with humans, will force the study species to increase their activity overlap with each other.

Methods

Study area

The 15 000 km² study area is spread across seven counties (Akershus, Buskerud, Telemark, Oppland, Oslo, Vestfold and Østfold) in the southeastern parts of Norway (Figure 1). In the northern part, the landscape is dominated by a valley system, with relatively steep hillsides. Small towns and agricultural land are found in the valleys, while forests dominate the hillsides. The elevation in the north generally ranges from approximately 200-400 m a.s.l. on the valley floor and up to between 900-1000 m a.s.l. on the hills. In the northernmost part, the valley is surrounded by mountains which extend well into the alpine zone. The landscape in the southern part is hillier and the elevation ranges from 0 to 500 m a.s.l. Agricultural land contributes to a higher proportion of the land cover and consists of a mosaic of forest, but larger areas with continuous forest exist. Four vegetation zones can be distinguished in the study area (Fremstad 1998). The southern part is mainly located in the boreonemoral zone, which has thermophilic deciduous tree species in the most favourable areas, usually the south facing slopes, elsewhere the dominating tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula sp.*) (Fremstad 1998). North of Oslo, the study area falls within the southern, intermediate and northern boreal zone, which is also dominated by Norway spruce, Scots pine and birch.

The climate ranges from coastal to continental, with quite large variations in temperature and precipitation. The mean annual precipitation varies from 1050 mm at the coastal city Larvik, to 520 mm in the continental town Fagernes, in the most northern part of the study area (<http://eklima.met.no>). Temperature is quite different between sites; in Larvik mean temperature in January and July is -2.9°C and 16.9°C, respectively, while in Fagernes mean temperature in January and July is -10.5°C and 14.5°C, respectively (<http://eklima.met.no>). Snow cover usually lasts from December to March-April, with the least snow in south-eastern parts and most in the northern parts (<http://eklima.met.no>). Measured in Oslo, the shortest day length is approximately six hours

(December 21) while the longest day is approximately 19 hours (June 21) (<http://www.timeanddate.com/sun/norway/oslo>).

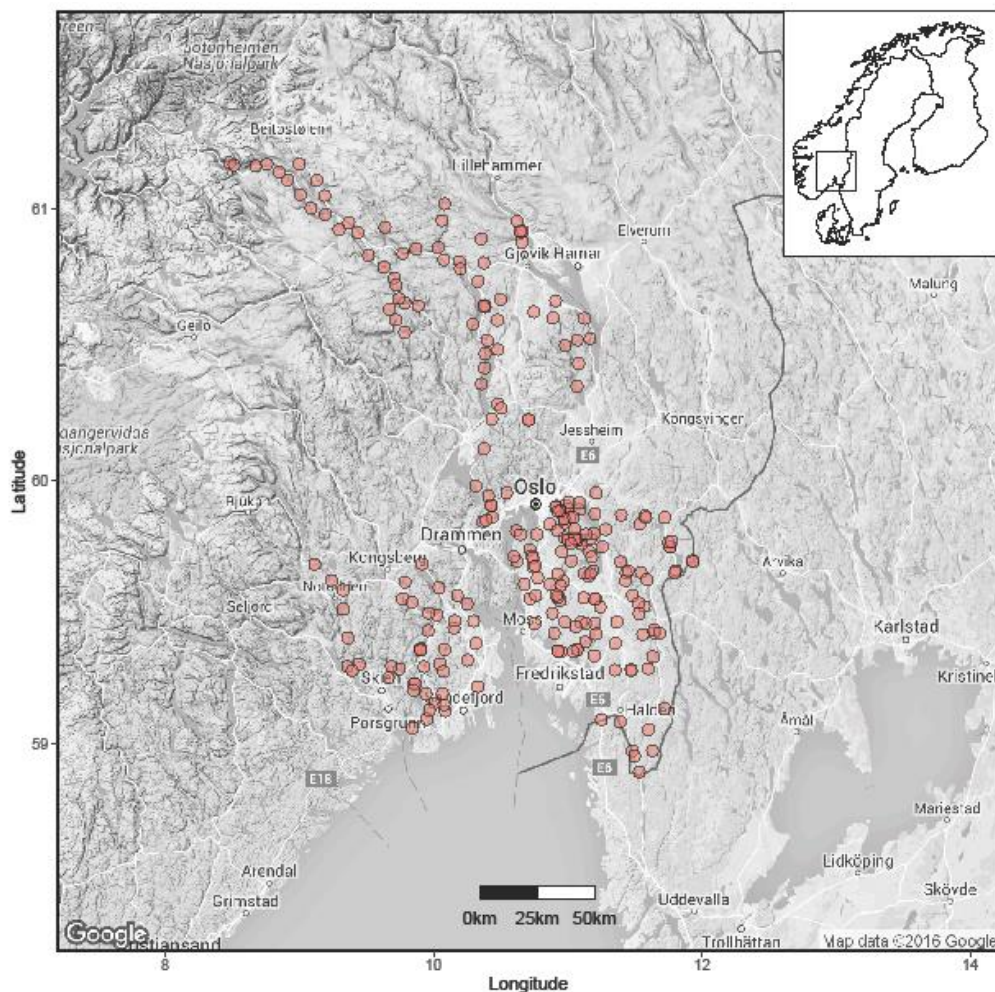


Figure 1. Map of the study area, camera trap sites are marked with red circles.

Camera trapping

The study initially began as three separate study sites within three different carnivore management regions, but has throughout the study period become almost continuous (Figure 1). Camera trap sites vary in elevation from 7 to 844 m a.s.l., with an increase in average elevation from south to north. Camera trap data were collected by the Norwegian Institute of Nature Research's (NINA) wildlife camera project (Odden 2015). The main objective of this project has been to develop methods to monitor the lynx population; hence most of the camera trap sites were selected with the intent to maximize the chance of photographically capturing lynx. The first cameras were placed in the southeastern part in 2010, later the study expanded toward the south-west (2012) and the north (2014). Due to problems with the sensitivity of the first cameras, I only included camera trap data between January 2012 and May 2015 in my analysis. By the end of that period there were 162

active camera trap sites, with a density of one camera trap site per 92.6 km². Throughout the study period camera density has varied, with higher density (but low coverage) the first two years (one camera trap site per 38 km² in 2010/11 and 44 km² in 2011/12) (Odden 2015). The project has been using the following five models of Reconyx© (address: 3828 Creekside Ln, Ste 2, Holmen, WI 54636) wildlife cameras: HC500 HyperFire Semi-Covert IR, HC600 HyperFire High Output Covert IR, PC800 Hyperfire Professional Semi-Covert IR, PC900 HyperFire Professional Covert IR and PC850 HyperFire Professional White Flash LED. All models have a trigger speed of 0.20 seconds (<http://www.reconyx.com/>). The time laps functions has been set to one picture each day, in order to make sure it was functioning properly between each check. Cameras were mounted at heights between approximately 0.2 to 1 m above ground, depending on the terrain and risk of getting covered in snow during the winter. Olfactory lures (Valerian oil, Catnip oil and Beaver *castor sp.* Castorium) were applied periodically when visiting the camera traps. Unfortunately, neither date nor camera trap site of lure application were recorded.



Figure 2. Example camera trap photos of the three wildlife species included in the study: roe deer (top left), red fox (top right), Eurasian lynx (bottom).

Hunting and season definition

Lynx, fox and roe deer are all legal game species in Norway, hunted during prescribed seasons. Male roe deer are hunted from August 10 to December 23, while the hunting season for females and fawns lasts from September 25 to December 23 (Klima- og miljødepartementet 2012). The use of dogs is allowed after September 25. There are quotas for roe deer, but they are usually set so high that they rarely constrain the hunting bags (Grøtan et al. 2005). The hunting season for red fox starts July 15 and ends April 15 (Klima- og miljødepartementet 2012). Fox are primarily hunted at baits, but hunting with dogs and predator calling are rising in popularity. Lynx are subject to strongly regulated hunting. In our study area there are three different carnivore regions, each with a politically determined population target level (Klima- og miljødepartementet 2005). The hunting season for lynx last from February 1 to March 31 (Klima- og miljødepartementet 2012). Most lynx are shot after being tracked down and chased by dogs; fewer are caught in box traps. With snow as the tracking medium, weather conditions have a large impact on hunting success. During favourable weather conditions, the hunting season last often only a few days as hunting quotas are quickly filled (Nilsen et al. 2012).

For each species, I divided the year into seasons based on the species biology and management (Figure 3). For roe deer, winter was set from the end of the hunting season and to the end of February, this being the period of largest snow depth. The spring was defined as the period between March 1 to May 15, in order to avoid any abrupt transition between the winter and breeding season. Roe deer are born in late May to June (Jarnemo et al. 2004; Panzacchi et al. 2008), so May 16 to the beginning the hunting season (August 10) was defined as breeding season. The last part of the breeding season overlaps with the mating period, as roe deer come into oestrus from mid-July to mid-August (Andersen et al. 1998). The beginning of the roe deer hunting season also overlaps with the mating period. Fox are hunted almost the entire year and the hunting period was cut in two, with the break at December 1. By doing so, the entire winter and mating period (Cavallini & Santini 1995) fall into the same season, hunting2. The entire fall and half of the summer fall into hunting1. The non-hunting season for fox contains the entire breeding period, as the pups are still independent and in the immediate surroundings of the den in June (Lindstróm 1994). Due to sample size considerations, the lynx year was only divided into two seasons; winter and summer. Summer contained the summer months and half of both fall and spring. The winter seasons contain the mating period and the hunting period, while the summer contain the breeding period.

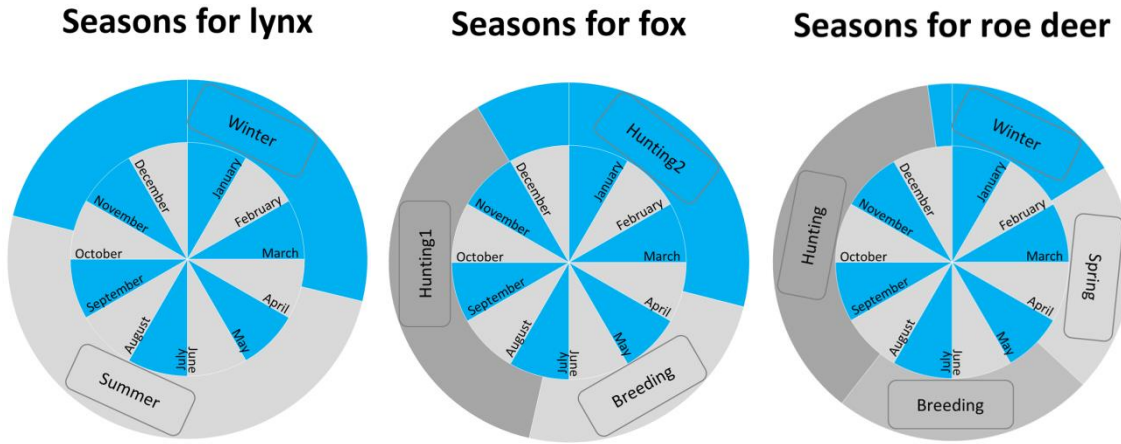


Figure 3. Graphic display of the season definitions for each species.

Statistical analysis

Occupancy analysis

I used multi-species hierarchical Bayesian co-occupancy models to evaluate how occupancy of one species affects the occupancy of another at camera trap sites. Occupancy is the fraction of sampling sites in the landscape occupied by a given species (MacKenzie & Royle 2005), alternatively it can be interpreted as the probability of a given species occupying a site. An advantage of occupancy models is that they account for imperfect detection (MacKenzie et al. 2002). I followed the approach by Waddle et al. (2010), which lets the occupancy of species A influence the detection and occupancy of species B and simultaneously estimates detection probability p and occupancy Ψ . If z^A and z^B denotes the actual state of occupancy for species A and B, then we have the following parameters in a two-species co-occupancy model:

$$\Psi^B = \text{occurrence of species B} = P(z^B = 1)$$

$$\Psi^{A|B} = P(z^A = 1 \mid z^B = 1)$$

$$\Psi^{A|\bar{B}} = P(z^A = 1 \mid z^B = 0)$$

where $\Psi^{A|B}$ denotes the probability of occurrence of species A given presence of species B and $\Psi^{A|\bar{B}}$ the probability of occurrence of species A given absence of species B.

The occupancy states of species A and B can then be written as the product of the following two Bernoulli processes:

$$z^B | \Psi^B \sim \text{Bernoulli}(\Psi^B)$$

$$z^A | z^B, \Psi^{A|B}, \Psi^{A|\bar{B}} \sim \text{Bernoulli}(z^B \Psi^{A|B} + (1 - z^B) \Psi^{A|\bar{B}})$$

This means that occupancy of species B is the result a Bernoulli process with probability Ψ^B of occurrence, whereas occupancy of species A is the result of a Bernoulli process with probability of occurrence with species B present equalling $z^B \Psi^{A|B}$, and $(1 - z^B) \Psi^{A|\bar{B}}$ with species B absent. This procedure lets species A to occur with one probability when species B is present and another probability when species B is absent. I used the following equation to estimate the effect of covariates (including the presence of another species) on the occupancy of the focal species A

$$\text{logit}(\Psi_y^A) = \alpha_y + \beta_B * z_y^B + \beta_i x_i,$$

where Ψ_y^A is occupancy of species A in year y , α_y is the intercept in year y , β_B denotes the coefficient for the co-occupancy parameter, z_y^B denotes the actual state of occupancy for species B in year y and β_i denotes the coefficient of the covariate i . Occupancy models assume static occupancy between surveys (closure assumption) (Rota et al. 2009); to reduce the likelihood of violating this assumption one intercept (α) was estimated for each year. This assumes that the occupancy does not change within a year.

I did not consider effects of co-occurring species on detection probability. If y^A represents the encounter history for species A, the detection probability in one survey can be written as $p^A = P(y^A = 1 | z^A = 1)$. Each survey in the encounter history of species A is then the result of the following Bernoulli process

$$y^A | z^A, p^A \sim \text{Bernoulli}(z^A p^A)$$

The detection probability for each species was assumed constant between year and modelled as

$$\text{logit}(p^A) = \alpha + \beta_i x_i,$$

where α is the intercept and β_i denotes the coefficient for covariate i .

The covariates considered are presented in Table 1. In order to reduce the likelihood of violating the assumption of no unexplained heterogeneity in detection probability (Royle 2006), I considered effects of all covariates on detection probability. For occupancy, I included effects of the occupancy state of predator(s) on the probability of occupancy of the subdominant predator or prey, in addition to a subset of covariates (Table 1).

Table 1. Covariates considered on occupancy and detection in the four occupancy models.

Covariates	Detection	Occupancy	Mean (range)
Human density (1 km grid) ¹	x	x	19.59 (0, 604)
Proportion of agriculture (1 km radius) ²	x	x	14.5 (0, 0.95)
Trail type(wildlife trail, foot path, road) ³	x		
Elevation ²	x	x	219.6 (7, 844)
Slope ²	x	x	12.3 (0.35, 43.71)

*Categorical variable with wildlife trail as a reference level.

¹Statistics Norway (2013)

²www.geonorge.no

³Odden (2015)

Seven days were pooled into one survey (occasion). Because camera trap stations were relatively far apart, each camera trap station was used as a separate site during occupancy modelling (i.e. one camera trap station was my observational unit at the spatial scale). I used uniform priors for all parameters ranging from -10 to 10 on a logit scale, except for the parameters involving the effect of species B occupancy on species A occupancy, the categorical covariates and the intercepts. Posterior distributions of several parameters tended the boundaries of the priors, I therefore used flat normally distributed priors with a low precision (mean=0, SD=3.16), following Bischof et al. (2014a). The model was run with three chains with a total of 45 000 iterations, including 10 000 burnins, thinned by 30. Four occupancy models were fitted, one for each roe deer season. In each model the following co-occupancy parameters were estimated: human on lynx ($\Psi^{\text{Lynx}|\text{Human}}$), human on fox ($\Psi^{\text{Fox}|\text{Human}}$), lynx on fox ($\Psi^{\text{Fox}|\text{Lynx}}$), human on roe deer ($\Psi^{\text{Roe deer}|\text{Human}}$), lynx on roe deer ($\Psi^{\text{Roe deer}|\text{Lynx}}$) and fox on roe deer ($\Psi^{\text{Roe deer}|\text{Fox}}$). I used Rhat values and trace plots of model-estimated parameters to assess mixing and convergence. The occupancy models was performed by R2JAGS (Su & Yajima 2012) in R.

Activity analysis

An event was defined as the camera detecting at least one individual of a given species. For every event captured by camera, the following were recorded: species, number of individuals, time, date and camera trap ID. Photographic captures within five minutes at the same camera trap or captures of multiple individuals in the same picture were regarded as a single event (visit). Due to Norwegian legislation, all pictures of humans have been deleted, but time and number of humans have been noted. I have pooled all human related observations as human, including bikers, vehicles (4-wheelers, motorbikes, snow scooters, cars, etc.), skiers, horses, dogs and hikers.

Species activity patterns were assessed using non-parametric Kernel density estimation, following the approach in Linkie and Ridout (2011) and Ridout and Linke (2009). Hour and minute of the day was converted to radians before producing graphical displays of season-specific activity patterns with the `overlap` package in R (Meredith & Ridout 2016).

Overlap in species activity patterns was investigated using the same Kernel density approach (Linkie & Ridout 2011; Ridout & Linkie 2009). Following estimation of the Kernel density distributions of diel activity for each species, an overlap term $\hat{\Delta}$ is calculated. The overlap term is the joint area under the two density functions, ranging from 0 to 1, where 1 indicates 100 % overlap. Ridout and Linkie (2009) performed a simulation study to test three of five previously suggested methods (Schmid & Schmidt 2006) for calculating the overlap term. I have followed their recommendations and used $\hat{\Delta}_4$ for large sample sizes ($n > 50$) and $\hat{\Delta}_1$ for small sample sizes ($n \leq 50$). Confidence intervals for the overlap term were bootstrapped with 1 000 bootstrap estimates, using the `Resample` and `bootEst` functions in the `overlap` package (Meredith & Ridout 2016). If the confidence interval contained 0.5, the amount of overlap was not considered different from random. As the bootstrap estimations might create a bias, the bias corrected quantiles confidence intervals were selected (Meredith & Ridout 2016). This procedure was performed for all species-pair and season (based on the subdominant species' year, Figure 3).

I mainly followed the approach of Wang et al. (2015) to test whether the degree of overlap in activity of two species differed between sites with different levels of human density. First, camera trap stations were divided into two groups; high and low human density. The break was set to 20 persons per 1 km²; the average human density in the study area (at the camera station level). Then, I estimated the overlap term between species A and species B, both in areas with high human density and in areas with low human density. I then obtained 1 000 bootstrap estimates of the overlap term between species A and B at high human density, and 1 000 estimates at low human density. To calculate the difference in activity overlap, the overlap term at low human density was subtracted from the overlap term at high human density, $\hat{\Delta}_{\text{difference}} = \hat{\Delta}_{\text{high density}} - \hat{\Delta}_{\text{low density}}$. These estimates were used to create a 95 % bootstrap confidence interval around the difference in overlap, following the same approach as for the season-specific overlap of species pairs. This procedure was performed for all species-pair with the subdominant species' season.

Originally, I wanted to use the Kernel density functions to test if one species' diel activity pattern differed between high and low human densities, as in Wang et al. (2015). However, my preliminary analysis revealed that even random designation to one of two groups could lead to significant

differences in overlap. This is probably due to the reported confidence intervals being too narrow when $\hat{\Delta}$ is close to one (Meredith & Ridout 2016). Instead, I used the difference in the estimated activity overlap between two species at high and low density (as described above) as the overlap estimates between two species will be farther away from one. To test if the same problem arise with this method, I divided the dataset in two by random and calculated the confidence interval and mean for the difference in activity overlap between the two randomly generated groups of camera traps. Most often the mean estimate was close to 0, but for the species pairs involving lynx there were larger deviations from 0, likely as a result of the low sample size (Meredith & Ridout 2016). However, all confidence intervals contained 0.

Results

In total, cameras were operational for 112 920 trap nights at 249 sites (mean = 453nights per camera; SD = 309). Eleven carnivore species were photographically captured; grey wolf (*Canis lupus lupus*), Eurasian lynx, red fox, arctic fox (*Vulpes lagopus*), badger (*Meles meles*), pine marten (*Martes martes*), American mink (*Neovison vison*), stoat (*Mustela erminea*), least weasel (*Mustela nivalis*), domestic dog (*Canis lupus familiaris*) and domestic cat (*Felis catus*). Of the study species, roe deer was most frequently captured, while lynx was captured the fewest times (Table 2). Human density and the number of human events per week at the camera trap site were uncorrelated (Pearson’s product-moment correlation $r = -0.064$, $p = 0.32$), implying that the effect of human density and human presence on camera sites could be separately analysed.

Table 2. Summary statistics for the four study species.

Species	Number of events	Cameras captured (out of 249)
Human	7500	179
Lynx	504	86
Red fox	5969	235
Roe deer	8327	210

Occupancy

Lynx occupancy was significantly higher at camera traps occupied by humans, during winter and spring (Table 3). Occupancy of red fox was significantly higher at sites occupied by humans in all seasons, except during the roe deer hunting season (Table 3). Human occupancy had a significant positive effect on roe deer occupancy in all seasons, except the winter (Table 3). During the winter, roe deer occupancy was significantly reduced by lynx occupancy (Table 3). Red fox occupancy had

a significant positive effect on roe deer occupancy in all seasons (Table 3). Figure 4 graphically display the log-odds effects of the co-occupancy parameters for the spring. For estimated effects of the other covariates on occupancy refer to Table S1.

Table 3. Mean estimates of the log-odds of the co-occupancy and effect of human density from the multi-species occupancy models. The parentheses give the 95 % percent confidence intervals. Significant results are shown in bold. Ψ denote occupancy.

Parameter	Winter	Spring	Breeding	Hunting
Human density effects on human Ψ	-0.510 (-1.152, 0.068)	-0.459 (-0.914, -0.114)	0.177 (-0.240, 0.781)	0.016 (-0.383, 0.632)
Human Ψ effects on lynx Ψ	1.677 (0.528, 1.848)	1.190 (0.303, 2.188)	0.780 (-0.654, 2.409)	0.956 (-0.279, 2.433)
Human density effects on lynx Ψ	-0.711 (-1.986, 1.284)	2.897 (1.220, 5.224)	1.032 (-2.114, 4.232)	-1.549 (-3.516, 2.021)
Human Ψ affecting fox Ψ	2.219 (1.180, 3.695)	1.185 (0.485, 1.959)	1.334 (0.632, 1.674)	0.499 (-0.207, 1.237)
Human density effects on fox Ψ	0.598 (-0.042, 1.594)	0.413 (-0.055, 1.163)	0.622 (0.033, 1.424)	-0.194 (-0.447, 0.095)
Lynx Ψ affecting fox Ψ	0.536 (-0.654, 1.804)	-0.403 (-1.498, 0.651)	-0.071 (-1.291, 1.674)	-0.165 (-1.270, 0.940)
Human Ψ affecting roe deer Ψ	0.397 (-0.362, 1.282)	0.799 (0.147, 1.464)	2.310 (1.186, 3.674)	1.392 (0.697, 2.172)
Human density effects on roe deer Ψ	0.246 (-0.228, 0.996)	0.741 (0.051, 1.635)	0.154 (-0.495, 1.250)	-0.048 (-0.321, 0.302)
Lynx Ψ affecting roe deer Ψ	-1.568 (-2.841, -0.377)	-0.403 (-1.666, 0.170)	-0.272 (-2.449, 2.226)	-0.244 (-1.510, 0.871)
Fox Ψ affecting roe deer Ψ	1.086 (0.275, 1.989)	1.043 (0.384, 1.721)	1.447 (0.634, 2.318)	1.218 (0.512, 1.963)

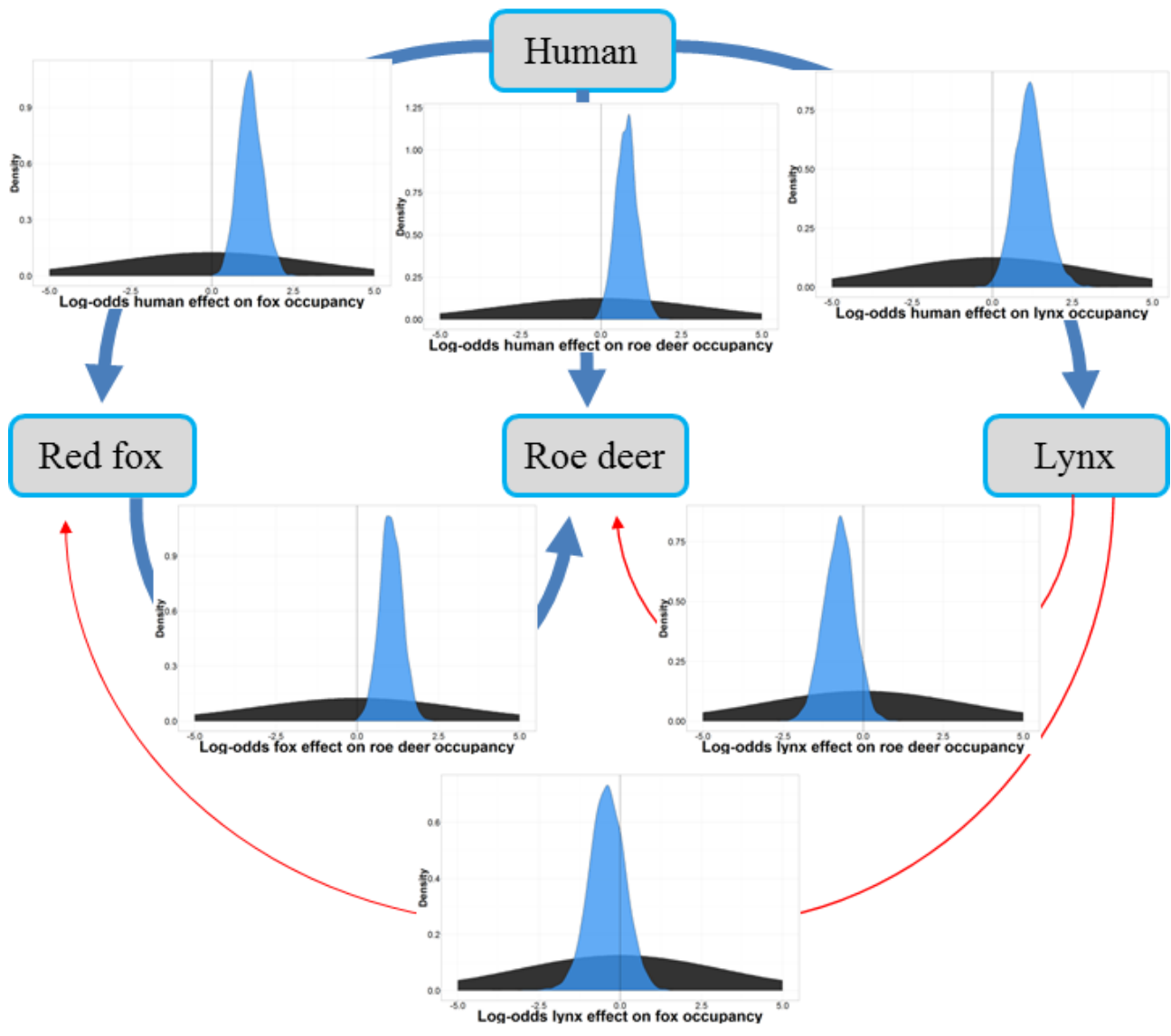


Figure 4. Results from the multi-species occupancy model during the spring, evaluating the study species effects on each other's occupancy. The plots in connection with a given arrow show the prior distribution (black) and the posterior distribution of the estimated effect of one species' occupancy on the other. Blue arrows indicate positive association and red arrows avoidance. Thick arrows represent significant effects ($p < 0.05$).

Temporal patterns

a. Humans

Human activity was diurnal, with a peak around 1200 (Figure 5C). The period of activity was narrowest during the winter and widest during the summer.

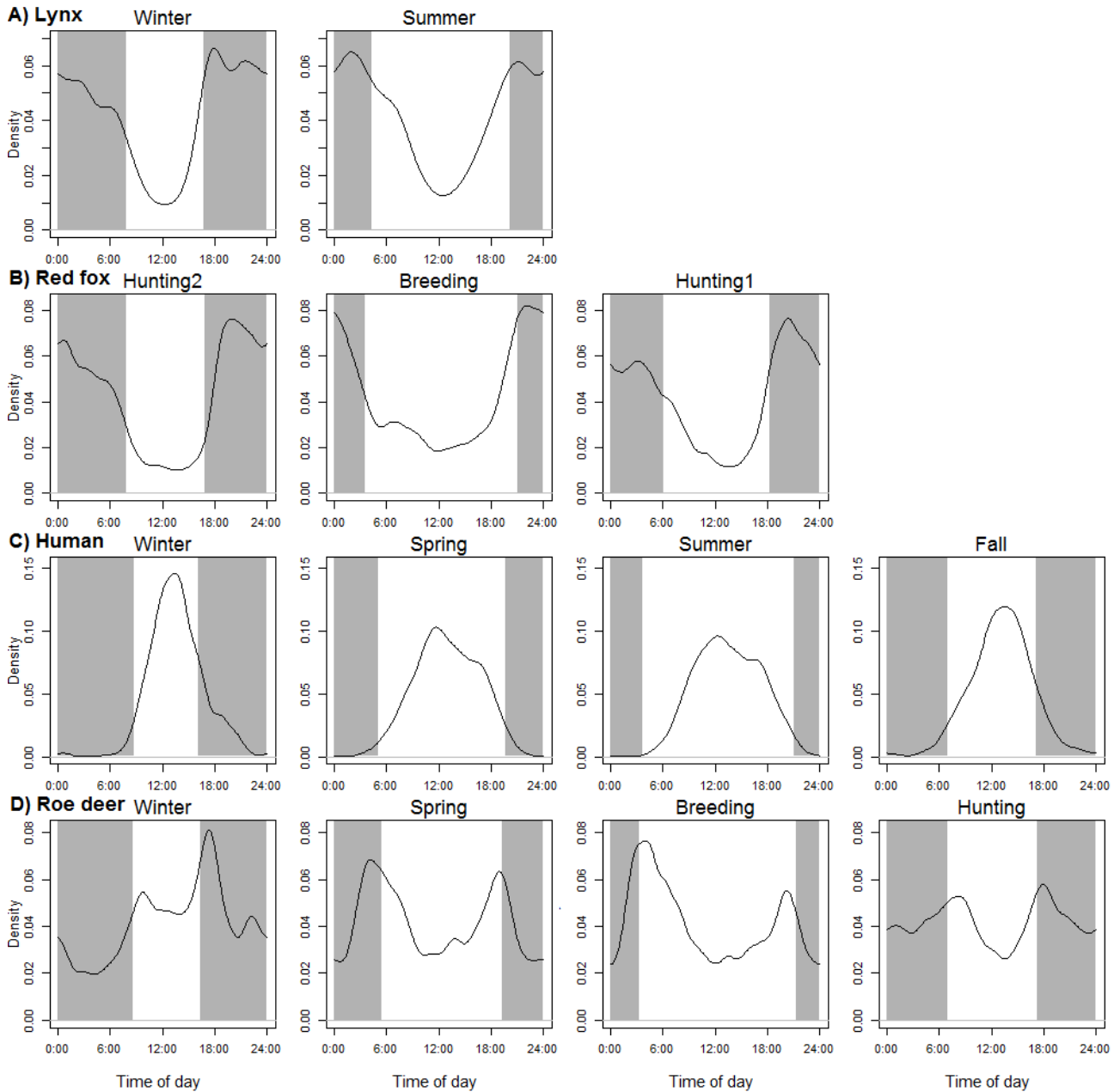


Figure 5. Season-specific activity patterns for lynx (A), red fox (B), humans (C) and roe deer (D). The shaded area represent the time between sunset and sunrise.

b. Lynx

Lynx activity peaked around dusk and dawn; activity remained comparatively high throughout the night, and was lowest at mid-day (Figure 5A). Lynx and human activity overlapped significantly less than expected by chance in both seasons (Figure 7A). During the summer, the activity overlap between lynx and humans was significantly (marginally) lower in areas with high human density, while there was no effect of human density in the winter (Figure 10 A). For graphic display of season-specific diel activity in lynx at high and low human density refer to Figure S1.

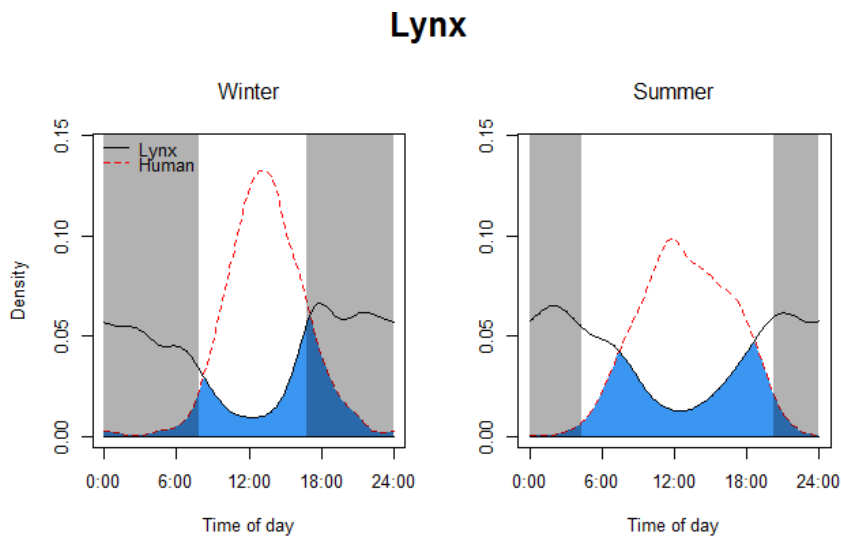


Figure 6. Season-specific activity overlap between lynx (focal) and humans. The shaded area represent the time between sunset and sunrise.

c. Red fox

Red fox activity peaked during first half of the night, with generally low activity in day time (lowest level around 1200) (Figure 5B). During their breeding season, red fox exhibited longer periods of low activity levels during daylight and peaks during the night. Fox activity overlapped less with human activity than predicted by random (Figure 7B). The amount of activity overlap between the two species was highest in the fox breeding season, intermediate in the first part of the fox hunting season and lowest in the last part of the hunting season. Fox activity and lynx activity showed a high degree of overlap, higher than expected by chance and with no apparent effect of season (Figure 7B). Human density significantly reduced the amount of overlap between activity of red fox and humans in the fox hunting seasons and I detected a trend of reduced overlap with human activity during the fox breeding season (Figure 10B). For graphic display of season-specific diel activity in red fox at high and low human density refer to Figure S2.

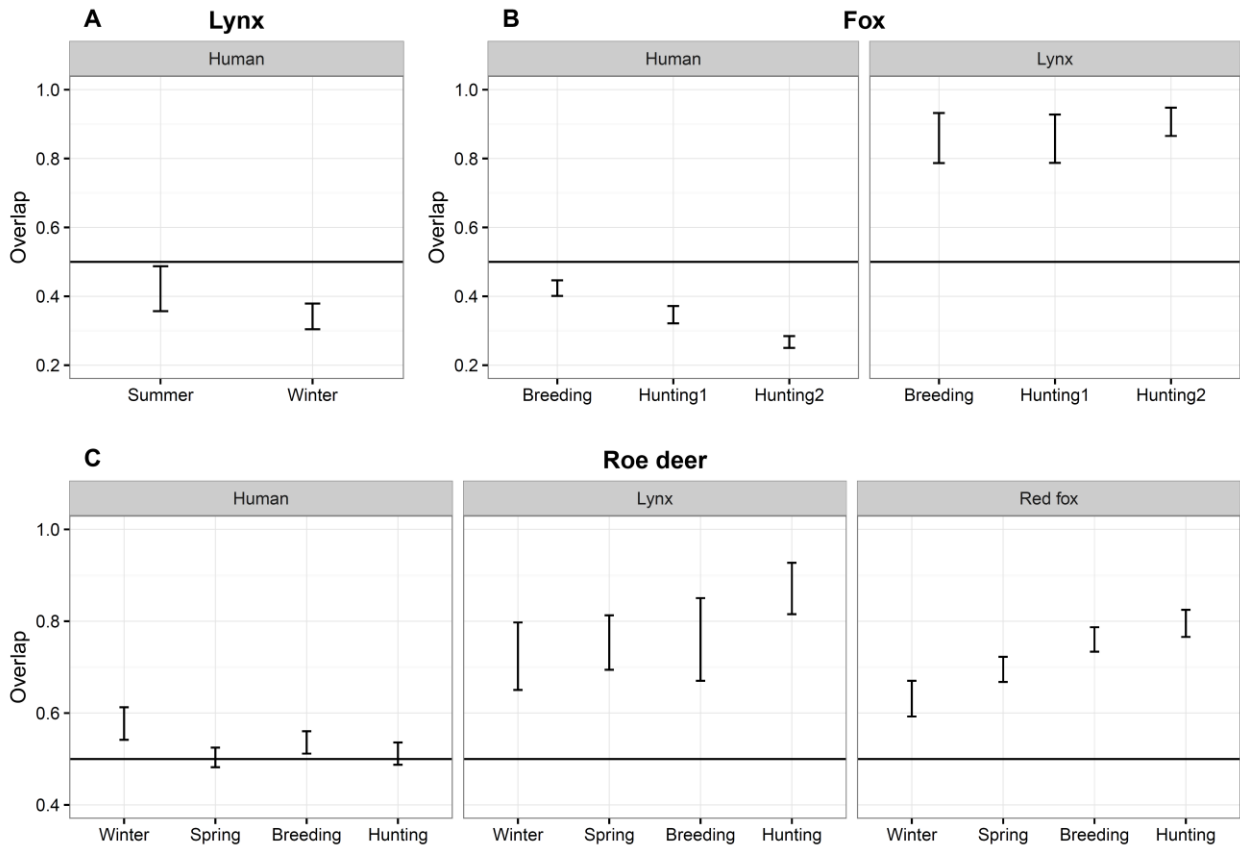


Figure 7. Confidence intervals (95 %) for the pair-wise overlap in diel activity. A) Activity overlap between lynx (focal) and humans. B) Activity overlap between fox (focal) and humans, and fox and lynx. C) Activity overlap for roe deer (focal) and all other study species. Seasons refer to periods based on the biology and management of the focal species in a given plot (see Figure 3). The horizontal line indicates the amount of activity overlap one would expect by chance (0.5).

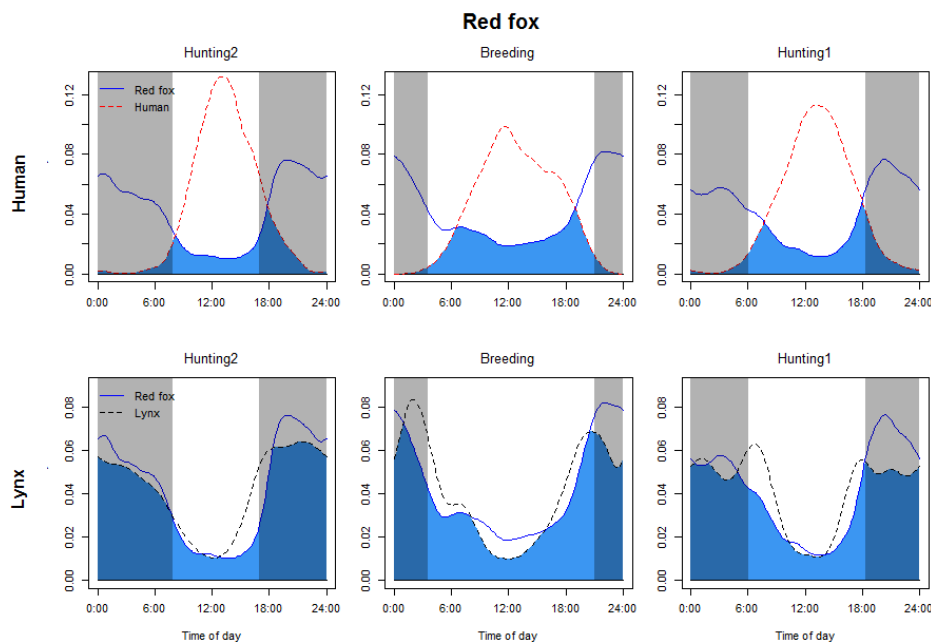


Figure 8. Fox (focal) activity and season-specific overlap with the activity of human and lynx. The shaded area represent the time between sunset and sunrise.

d. Roe deer

Roe deer activity peaked around dusk and dawn in all seasons (Figure 5D). Roe deer activity tended to be lowest around midnight and midday, except in the winter, where activity levels were comparatively high during day time. During the winter and breeding season, roe deer activity overlapped more with human activity than expected by chance (Figure 7C). Roe deer activity overlapped more than expected by chance with both lynx and fox activity, in all seasons (Figure 7C).

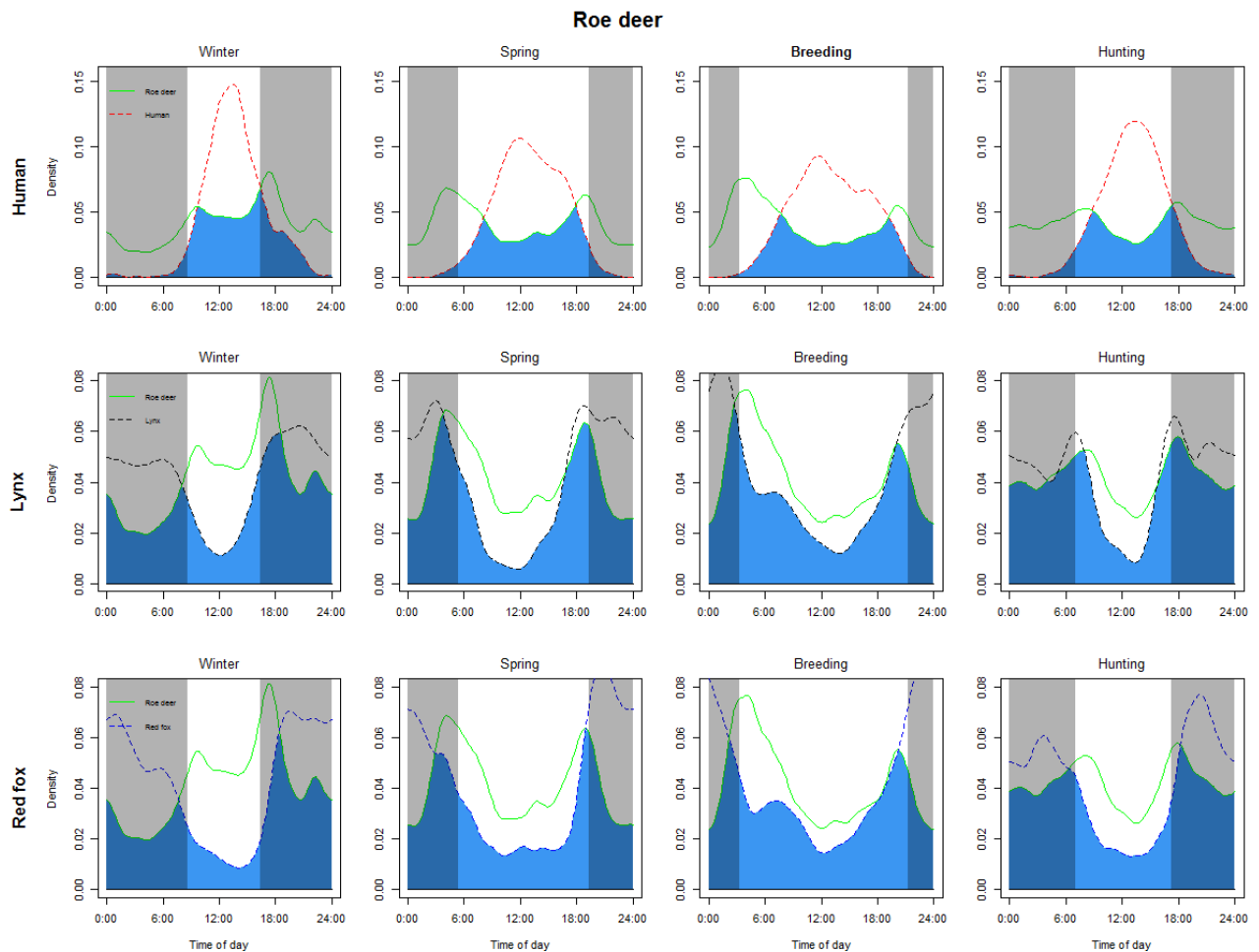


Figure 9. Roe deer (focal) activity and season-specific overlap with the activity of humans, lynx red fox. The shaded area represent the time between sunset and sunrise.

Human density significantly decreased activity overlap between humans and roe deer in all seasons, except the winter where it was a significant increase (Figure 10C). Activity overlap between roe deer and lynx did not show any significant response to human density (Figure 10C). Roe deer and fox activity overlapped significantly more at high human density in the spring and breeding, and significantly less during the winter (Figure 10C). Human density did not significantly affect the

amount of activity overlap between lynx and roe deer. For graphic display of season-specific diel activity in roe deer at high and low human density refer to Figure S3.

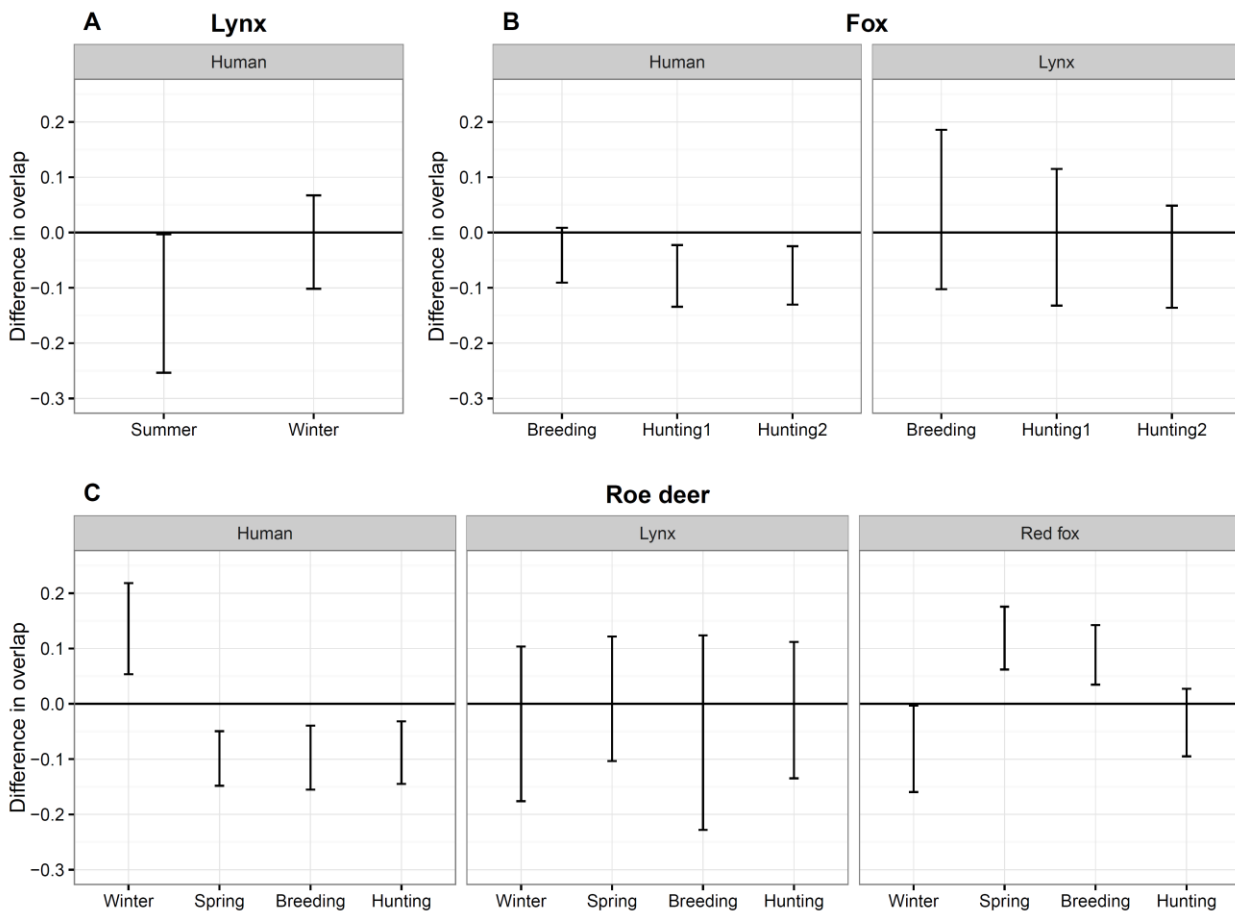


Figure 10. Confidence intervals (95 %) for the difference in pair-wise activity overlap at high and low human density. A) Difference between lynx (focal) and humans. B) Difference between fox (focal) and humans, and fox and lynx. C) Difference for roe deer (focal) and all other study species. Seasons refer to periods based on the biology and management of the focal species in a given plot (see Figure 3). Confidence intervals containing only positive values, indicates increased activity overlap at high human density.

Discussion

Spatiotemporal patterns in camera trap data revealed that anthropogenic influences do indeed play a role in shaping activity and interactions between predators and prey in my study system. Furthermore, use of space and time by roe deer, fox, and lynx was distinctly season-specific, as was the apparent interplay between species. Predator-prey interactions are complex, further compounded in my study system by seasonal differences and the involvement of four species (including humans) instead of only two. As a consequence, interpretation of the results from this study are far from clear-cut but did nonetheless yield valuable insights into anthropogenic effects on wildlife behaviour.

Association in space and avoidance in time

Occupancy of lynx, red fox and roe deer were for the most part positively influenced by occupancy of humans around camera trap stations. This finding is consistent with prediction P1.1. Other studies have revealed similar positive effects of humans or anthropogenic features (including agricultural fields) of the landscape on lynx (Basille et al. 2009; Basille et al. 2013; Belotti et al. 2012), red fox (Harris 1981; Harris & Rayner 1986) and roe deer (Bouyer et al. 2015a; Bunnefeld et al. 2006; Torres et al. 2012). Humans have settled in productive areas (Luck 2007) and through land transformations altered the habitat, which likely has increased the food supply for roe deer and red fox in relation to humans (Panzacchi et al. 2010b; Shapira et al. 2008). The proportion of agriculture positively influenced roe deer occupancy and red fox occupancy (Table S1), supporting this idea. Spatial association between lynx and humans could be a result of lynx selecting for areas with higher densities of their main prey, roe deer (Basille et al. 2009; Bouyer et al. 2015b).

I did not quantitatively account for the variations in day length, as I used Kernel density distributions to assess patterns in diel activity. However, activity plots suggest that the species in my study adjusted their activity patterns according to day length. My results are in accordance with previously reported activity patterns; lynx were crepuscular/nocturnal (Heurich et al. 2014; Podolski et al. 2013), fox were crepuscular/nocturnal (Díaz-Ruiz et al. 2015; Monterroso et al. 2014; Weber et al. 1994) and roe deer were mainly crepuscular with a tendency towards being more active at daytime during the winter, as reported by Pagon et al. (2013). However, one study has reported a peak in the activity of lynx around midnight (Schmidt 1999), which is slightly different from the lynx activity pattern reported here. In addition, the diel activity pattern in roe deer reported from one study in Sweden (Cederlund 1989), differs as well, where roe deer activity was reported to be more evenly distributed throughout the day. These deviations might be due to variations between study sites, or due to different methods. The activity patterns in Cederlund (1989) have been estimated with data from radio telemetry, Schmidt (1999) used in addition activity transmitters. Camera traps in my study captured 504 events of lynx, which probably gives less accurate estimates of the lynx' activity pattern, compared to the other study species. However, I consider the diel activity patterns reported here reliable, as they are mainly consistent with previous studies.

As predicted, lynx and red fox activity overlapped less with human activity than expected by chance (P1.2), indicating that for lynx and red fox, time is the most important dimension for avoiding humans. Spatial association and temporal avoidance in predators have been reported by several

studies (Carter et al. 2012; Riley et al. 2003; Schuette et al. 2013), suggesting that sympatric predators use temporal partitioning in order to co-exist (Monterroso et al. 2014). My results further support these patterns for avoidance of humans in lynx and red fox.

Lynx activity has been shown to follow that of its main prey in several study areas (Podolski et al. 2013; Schmidt 1999). Here, lynx activity followed that of the roe deer, and activity overlap estimates were generally high. Although, activity of roe deer overlapped as expected or more than expected by chance with human activity, lynx showed less activity overlap with humans than expected by chance, suggesting that the shape of the activity patterns of lynx is also influenced by people. Lynx in the northern part of Scandinavia, with polar days during summer and polar nights during winter, exhibited a bimodal patterns with lowest activity around 1200 (Heurich et al. 2014), although a previous study of activity of their main prey, reindeer (Pedersen et al. 1999), indicated week circadian activity and low social synchronization (van Oort et al. 2007). Assuming human activity shows the highest activity around 1200 also at higher latitudes, this would further support that human activity, in addition to the activity of the lynx' main prey, plays a role in determining the shape of diel activity patterns of lynx. Other factors could explain why lynx activity overlapped less than expected with humans, such as activity of other prey, or the vulnerability of roe deer.

Contrary to prediction P1.2, roe deer activity did not overlap less with human activity than expected by chance. Contrasting diel activity patterns of lynx and humans might explain this result; if roe deer decrease their activity overlap with humans, they would increase the activity overlap with lynx. This indicates that a further decrease in activity overlap with humans might not reduce the total predation risk for roe deer, as this probably would increase encounter rates with lynx. However, in the winter season, roe deer increased their daytime activity level, resulting in roe deer activity overlapping more than expected by chance with human activity. Pagon et al. (2013) suggested that variations in the activity levels of the roe deer mainly were due to thermoregulation. The authors explained the increased activity during daytime with lower energy expenditures of foraging at higher temperatures, combined with higher degree of inactivity at night which reduces heat loss. Effects of behavioural thermoregulation could also be seen in the light of predation risk; during the winter at northern latitude, when the risk of starvation is assumed to be high, roe deer might accept higher levels of predation risk (Ratikainen et al. 2007). Thus, in order to reduce energy expenditure roe deer have to increase their daytime activity and thereby exposing them towards humans. Lack of positive effects of human occupancy on roe deer occupancy during the winter, might then be explained by roe deer being forced to increase daytime activity, due to behavioural thermoregulation, making adjustments in space use necessary to reduce the encounter rate with

humans. Human occupancy was negatively affected by human density, suggesting that staying close to human settlements and avoiding people can be achieved simultaneously.

The breeding season and rutting period are associated with a higher degree of activity in some ungulates (Relyea & Demarais 1994). Higher activity overlap between roe deer and humans during the breeding season might then be explained by increased activity in roe deer, in combination with higher day length. Humans were also active for longer periods during this season, reducing the proportion of time available for roe deer to avoid humans. Pagon et al., (2013) suggest that thermoregulation is important throughout the year. During the breeding season, avoidance of warmest periods could minimize heat stress. Behavioural thermoregulation is likely confounded with temporal avoidance of humans, since the warmest period of the day will most probably occur around mid-day, when human activity peaks. However, future camera trap studies recording temperatures at the camera trap site will be useful to disentangle these effects. One could then test if roe deer are more likely to be more active at brighter periods during colder days.

Season-specific predator avoidance

Contrary to prediction P2.1, roe deer and red fox did not exhibit decreased activity overlap nor was roe deer occupancy negatively affected by occupancy of red fox during the roe deer' breeding season. Instead, overlap of roe deer and red fox activity was second highest during this season, and red fox occupancy positively affected roe deer occupancy throughout the year. Adult female red foxes have been shown to increase diurnal activity during the breeding season (Phillips & Catling 1991), and roe deer females will likely increase their foraging during lactation. Consequently, increased activity in both species might explain why roe deer and red fox increased activity overlap in this season. At high roe deer densities, fox predation on roe deer fawns has been shown to be closer to the functional response of a specialist (Panzacchi et al. 2010b). The hunting strategy that seemed most directed towards fawns was a sit and survey strategy over open areas, which also proved to be most successful (Jarnemo 2004). Hence, increased overlap could also be a result of red fox increasing activity in the search of roe deer fawns. Furthermore, Panzacchi et al. (2007) reported predation risk to increase with mother-fawn distance, and mother-fawn distance being dependent on habitat (visibility) and activity, age and sex of the fawn. Thus, a red fox observing an active roe deer doe could increase the predation risk on the fawns. My results, with red fox occupancy positively affecting roe deer occupancy and increased activity overlap between the two species, could indicate that the encounter rate between the two species is elevated during the breeding season. This suggests that roe deer fails to increase their avoidance of red fox. However,

avoidance of red fox in space and time might not be the best defence, as a roe deer doe manages to deter a red fox in 90 % of the times when the doe showed aggressive behaviour during an encounter (Jarnemo 2004). But, relatively few does exhibited aggressive behaviour (59 %) when considering the success rate of deterring the fox with aggressive behaviour.

Roe deer and humans showed least activity overlap in the spring and the hunting season, and human occupancy positively affected roe deer occupancy in the hunting season, contrary to prediction P2.2. However, the hunting season seemed to be the season with the highest level of nocturnal activity for roe deer, which might reflect a strategy of temporal avoidance of humans. Future analysis focusing specifically on nocturnal activity may help clarify whether or not nocturnal activity in roe deer could be used as an antipredator strategy towards hunters. It should also be noted that during the winter and hunting season, larger parts of the activity overlap occurred after sunset. Humans have relatively poor night vision and there is no legal hunting on roe deer during night, so overlap occurring after dusk could be of minor importance in a predation risk context for the roe deer. Although, my analyses did not reveal effects of hunting season on avoidance patterns in roe deer, other studies have shown season-specific anti-predator behaviour in roe deer (Benhaïem et al. 2008; Sönnichsen et al. 2013), which might be more important than season-specific spatial-temporal avoidance. Lone et al. (submitted manuscript) found that roe deer showed stronger avoidance of areas with high risk of hunting during the hunting season. In addition, roe deer used habitat with lower risk of hunting during the day and habitat with lower predation risk from lynx during the night. Such patterns might be harder to detect with camera traps, as the cameras generally are placed in the forest and likely are associated with lower variation in cover than available in roe deer home ranges. However, recording the degree of cover at the camera trap sites could have given more insight into the spatiotemporal avoidance patterns in roe deer, and should be considered as a part of the data collection protocol for the Scandinavian lynx project. Although the results did not follow my predictions from my second hypothesis (H2), the effect of human density on the activity overlap between roe deer and humans seems to be season-specific, which I will discuss further below.

Humans modulate spatiotemporal patterns of avoidance

The effect of human density was more complex than expected. Roe deer exhibited seasonal changes in their response to human density, while the effect of human density on the red fox was comparatively consistent; human density decreased the amount of activity overlap between red fox and humans. Decreased daytime activity in red fox closer to human settlements has previously been

reported in Spain (Díaz-Ruiz et al. 2015). Red fox are also known to be adaptable to humans, living at highest densities in urban areas (Harris 1981; Harris & Rayner 1986), resting inside human settlements (Janko et al. 2012) and respond to roads and traffic in order to reduce the risk of vehicle-induced mortality (Baker et al. 2007). My results indicate that higher temporal avoidance of humans might be important to facilitate co-existence of red fox and humans at high human density. Lynx activity was also following this pattern during the summer, with decreased activity overlap with humans at high human density. However, one should be careful when interpreting the results regarding the effect of human density on species-pairs containing lynx, due to statistical issues mentioned in the methods.

During the spring and breeding season, activity overlap of roe deer and red fox increased at high human density, consistent with prediction P3.1. Other studies have shown increased activity overlap between mesopredators at camera trap sites with high human activity (Wang et al. 2015). Here, I report the same pattern for the effect of human density on red fox and roe deer, during spring and breeding season. Such changes in the spatiotemporal activity patterns are likely to influence the interactions between red fox and roe deer. For instance, this might have implications for red fox predation on roe deer fawns at high human density. Red fox predation is higher in areas with high roe deer densities (Panzacchi et al. 2008) and roe deer density and human density have been shown to be correlated (Bouyer et al. 2015b). Thus, roe deer living at high human density are likely to suffer from increased fox predation on their fawns. Increased predation from red fox on fawns at high roe deer density, could then be partly explained by elevated activity overlap between roe deer and red fox, in those areas.

Contrary to prediction P3.1, roe deer and red fox activity overlap were lower at high human density in the winter, as a result of higher daytime activity of roe deer at high human density. Stomach and scat analysis have revealed increased roe deer content in the diet of red fox during severe winters (Cederlund & Lindström 1983). Hence, roe deer is likely to suffer from increased predation risk from the red fox during the winter. Consequently, a reduced temporal association between roe deer and red fox at high human density might reflect roe deer using humans as a shield against red fox in time. Alternatively, increased daytime activity of roe deer at high human density might be a result of starved roe deer habituating to humans at high human density. Nonetheless, human density changed the amount of activity overlap between roe deer and red fox, potentially affecting their interactions. These behavioural responses in roe deer and red fox to high human density is likely to have further implications on other species than the study species, which can be targeted by future studies.

Human density and the number of human pictures per week were not correlated. Furthermore, human density had a significant effect on human occupancy during the winter, where it negatively affected human occupancy. However, this result might be due to more camera traps being placed on trails and roads in areas with lower human density. Alternatively, hiking and high use of relatively remote areas for recreational purposes could also explain this result. Nonetheless, ecological studies should be cautious when using human density as a proxy for human activity.

Studying predator-prey interactions using camera traps

The use of camera traps for ecological studies has become increasingly popular during the past two decades (Rowcliffe & Carbone 2008), particularly for the study of elusive species, such as carnivores. Camera traps studies can be implemented cost-efficiently (Lyra-Jorge et al. 2008), and over large areas (Silveira et al. 2003). They also have the advantage of allowing the detection of multiple species and individuals, and are thus suitable to study interactions (Linkie & Ridout 2011; Wang et al. 2015). Modern camera traps can operate long periods without human disturbance, limiting invasiveness. Mammalian species, and especially Carnivora, have featured prominently in studies utilizing wildlife cameras (McCallum 2013).

Although camera trapping data can provide information on spatiotemporal activity patterns of sympatric species, there are limitations when it comes to interpreting predator-prey interactions from spatial distributions and diel activity patterns recorded only at camera trap locations. One issue is the lack of systematic direct observations of predation (although some cameras have recorded lynx carrying roe deer in their mouth and several incidences of red fox carrying roe deer fawns). Activity overlap between a predator and the prey does not need to reflect the importance of prey in the diet of the predator (Kamler et al. 2012). A prey might also use other behavioural responses (e.g. vigilance) to predators than avoidance in time and/or space (Sönnichsen et al. 2013), which camera trap studies are unable to capture. In addition, the predators may be able of killing inactive prey, which is the case of red fox predation on roe deer fawns in this study (Jarnemo 2004). Furthermore, this thesis analysed spatial and temporal aspects separately. Hence, a prey species which are both temporally and spatially associated with its predator, may still be able to achieve avoidance, because we cannot say whether or not they occupy the same site at the same time. Development of models considering space and time use simultaneously would, thus, give more insight into the complex anthropogenic effects on spatial and temporal aspects of predator-prey interactions. In this particular study, the undocumented use of lures at the camera traps stations is a drawback with the study design. Lures were applied during irregular periods and I have no record of

when, where or which type of lures had been applied. Lures have species specific effects on detectability (Bischof et al. 2014b), and may have influenced my results.

Conclusion

My results lend further support to the notion that sympatric predators use temporal partitioning in order to avoid humans in today's human-dominated landscapes. This pattern did not appear for the herbivore, which exhibited activity that overlapped more with humans than expected by chance. Further, patterns in wildlife responses to anthropogenic factors were more complex than I expected. Not only did use of space and time differ between species and species-pairs, but also between seasons. These results highlight the importance of considering seasonality when studying predator-prey interactions. Camera trapping presents a powerful tool for studying wildlife interactions in sympatric species. Development of models that consider both space and time use simultaneously, would provide new opportunities for exploring the complex spectrum of predator-prey interactions, and the possible impact of anthropogenic effects.

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Appendix

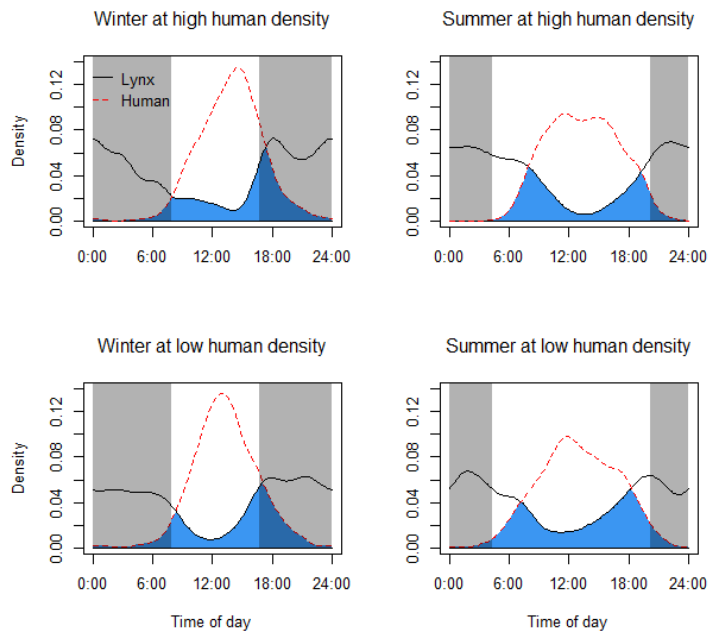


Figure S1. Seasonal activity overlap at high and low human density for the following lynx (focal) and humans. The shaded area indicates the time period between the sunset and sunrise for the season.

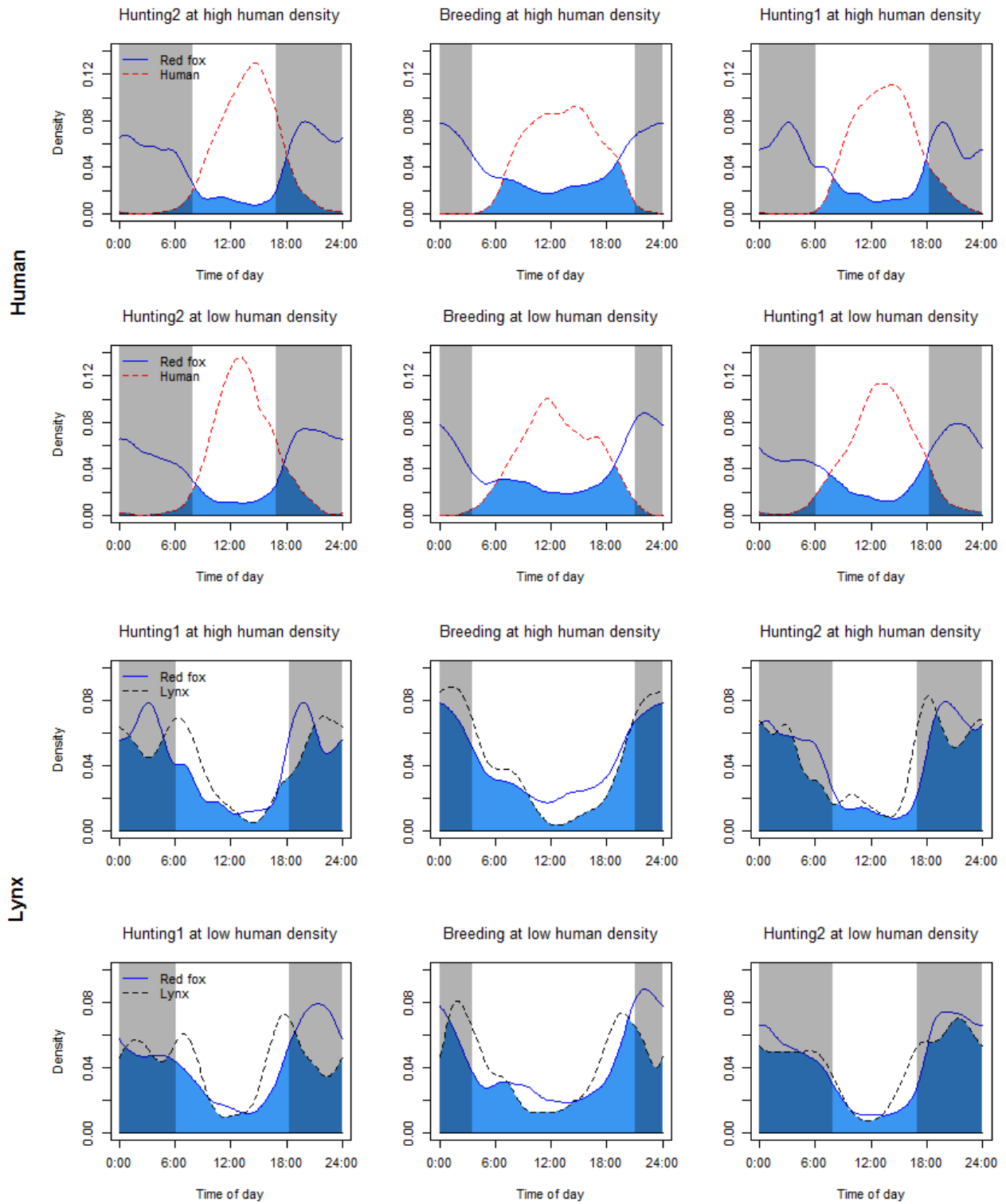


Figure S2. Seasonal activity overlap at high and low human density for the following species-pairs: red fox (focal) and humans, and red fox (focal) and lynx. The shaded area indicates the time period between the sunset and sunrise for the season.

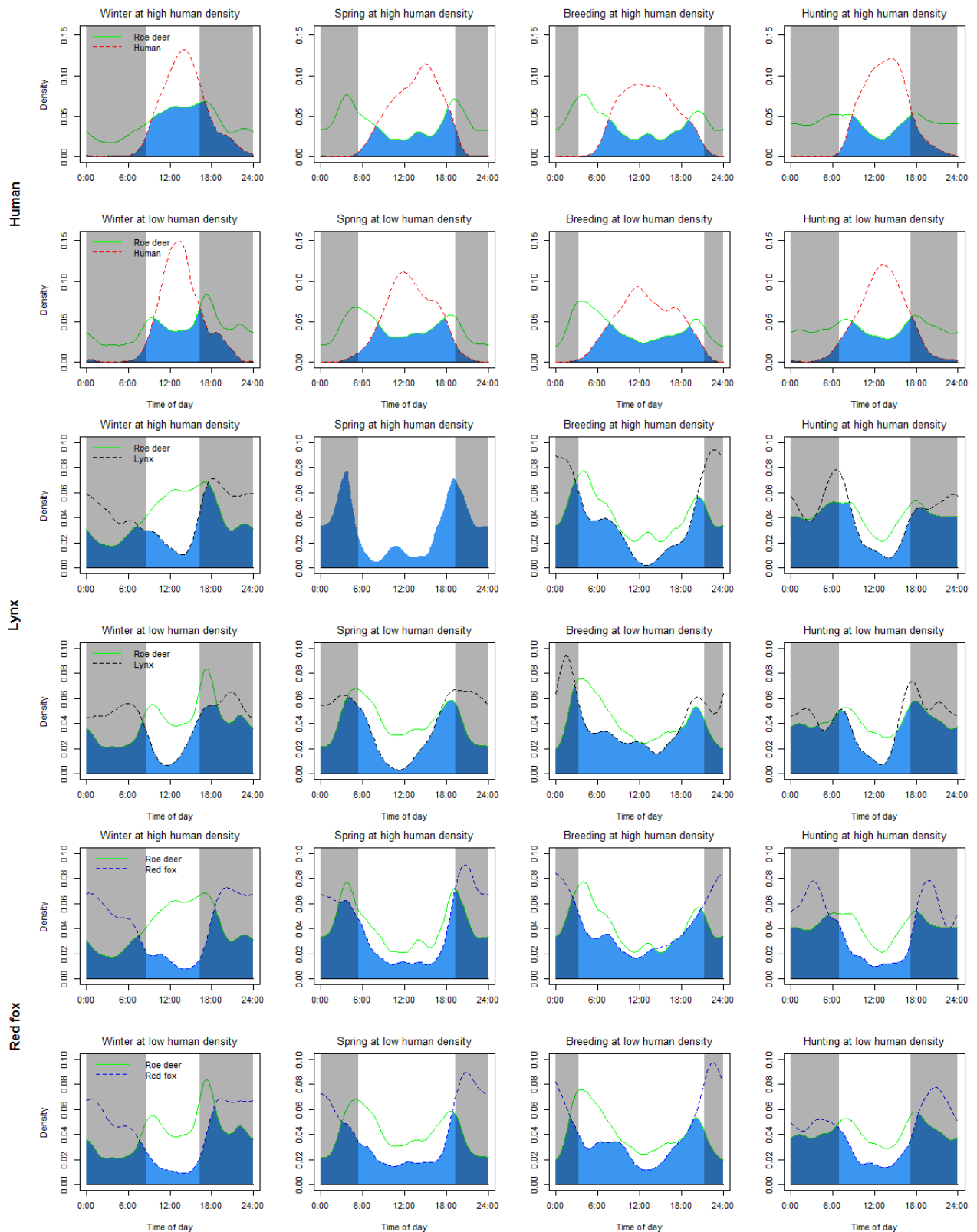


Figure S3. Seasonal activity overlap at high and low human density for the following species-pairs: roe deer (focal) and humans, roe deer (focal) and lynx, and roe deer (focal) and red fox. The shaded area indicates the time period between the sunset and sunrise for the season.

Table S1. Mean estimated log-odds effects of covariates on the occupancy of the study species, from the four occupancy models. 95 % confidence intervals are given in the parentheses. Significant effects are put in bold.

Parameter	Winter	Spring	Breeding	Hunting
Human				
Proportion of agriculture (1 km)	-0.081 (-0.365, 0.204)	-0.005 (-0.262, 0.283)	0.074 (-0.241, 0.781)	0.018 (-0.270, 0.330)
Elevation	-0.105 (-0.365, 0.204)	-0.132 (-0.371, 0.102)	0.060 (-0.228, 0.348)	0.035 (-0.262, 0.350)
Slope	-0.105 (-0.378, 0.178)	-0.076 (-0.335, 0.179)	0.200 (-0.056, 0.474)	-0.205 (-0.482, 0.071)
Lynx				
Proportion of agriculture (1 km)	2.085 (0.987, 3.665)	-0.535 (-1.152, 0.037)	-1.049 (-2.541, -0.060)	2.519 (0.889, 4.838)
Elevation	0.207 (-0.278, 0.714)	0.247 (-0.122, 0.616)	0.289 (-0.659, 1.980)	-0.374 (-1.068, 0.240)
Slope	1.300 (0.556, 2.165)	0.659 (0.137, 1.186)	0.949 (-0.339, 2.224)	0.615 (0.022, 1.259)
Red fox				
Proportion of agriculture (1 km)	0.118 (-0.340, 0.605)	0.551 (0.183, 0.973)	0.175 (-0.149, 0.553)	0.696 (0.194, 1.264)
Elevation	-0.252 (-0.571, 0.069)	0.543 (0.151, 0.987)	-0.299 (-606, 0.020)	-0.106 (-0.462, 0.265)
Slope	-0.194 (-0.592, 0.191)	-0.070 (-0.377, 0.252)	-0.086 (-0.496, 0.269)	0.052 (-0.285, 0.411)
Roe deer				
Proportion of agriculture (1 km)	1.301 (0.818, 1.879)	0.487 (0.153, 0.885)	0.428 (-0.104, 1.076)	0.582 (0.111, 1.099)
Elevation	-0.454 (-0.807, -0.124)	-0.289 (-0.607, 0.038)	-0.336 (-0.850, 0.098)	-0.380 (-0.744, -0.028)
Slope	-0.261 (-0.679, 0.170)	-0.199 (-0.513, 0.132)	-0.732 (-1.302, -0.202)	-0.354 (-0.707, -0.022)



Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway