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Seasonal and Diurnal Variation in Habitat Overlap of Roe Deer and Eurasian Lynx in a Human-Dominated Landscape

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MSc in Biology

Submission date: May 2015

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Summary

Predators affect prey directly (lethally), and indirectly (non-lethally), by altering their behaviour as they try to maximise habitat overlap with prey. Prey, on the other hand, are trying to minimise habitat overlap with predators by altering their spatial behaviour, often in a fine-scaled temporally-explicit manner. In a human-dominated world, humans also alter the landscape of fear of both predators and prey, whereas prey have to deal with predation risks from multiple sources. In southern Norway, roe deer is the main prey for lynx, and both roe deer and lynx face mortality risks from humans. Lynx are stalk-and-ambush predators that have highest activity at dusk and night, whereas mortality risks from humans and human hunters are higher by day in open areas with good visual sight. Thus, roe deer face mortality risks from multiple sources that are non-overlapping in space and time.

I examined how habitat overlap between roe deer and lynx varied in seasonal and diurnal temporal scales in southern Norway. Data was collected during the period 2005-2013 from Global Positioning System (GPS)-collars of 47 roe deer (27 females and 20 males) and 18 lynx (7 females and 11 males) with overlapping home ranges. I used an ecological niche factor analytical approach to obtain four uncorrelated environmental axes that explained most of the variation in the data. These axes were used as dependent variables in linear regressions to analyse habitat use and total niche distance between species in relation to seasons, photoperiods (day, night and twilight) and sex.

I found that total niche distance between roe deer and lynx was smallest by day (except in winter) and largest at twilight, in winter and between female roe deer and lynx compared to male roe deer and lynx. These findings suggests that diurnal variation in habitat overlap between roe deer and lynx seemed to be driven by predation risks as both species lowered their potential mortality risks by temporally shifting habitats with low and high risk, whereas fluctuations in high-quality food distribution seemed to drive changes in habitat overlap between seasons. These patterns were more pronounced in females compared to males, but in different ways which were dependent on the species-specific ecology. This study have documented seasonal and diurnal variation in habitat overlap of predators and prey in a human-dominated world.

Oppsummering

Predatorer påvirker byttedyr direkte (dødelig), og indirekte (ikke dødelig), ved å endre deres atferd når de prøver å maksimere habitatoverlappet med byttedyr. Byttedyr forsøker derimot å minimalisere habitatoverlappet med predatorer ved å endre deres atferd i tid og sted. I en menneskedominert verden endrer også mennesker landskapet av frykt for både predatorer og byttedyr, mens byttedyr må forholde seg til predasjonsrisiko fra flere kilder. I Sør-Norge er rådyr det viktigste byttedyret for gaupen, og både rådyr og gaupe møter dødelighetsrisiko fra mennesker. Gauper er natt- og skumringsaktive, snikende predatorer som er avhengige av vegetasjon ved jakt, mens dødelighet fra mennesker og jegere er høyere om dagen i åpne områder da de trenger langt synsfelt. Rådyr møter dermed dødelighetsrisiko fra flere kilder som ikke overlapper i tid og sted.

Jeg undersøkte hvordan habitatoverlappet mellom rådyr og gaupe varierte mellom sesonger og lysperioder i Sør-Norge. Data ble samlet inn under perioden 2005-2013 fra Globalt posisjoneringssystem (GPS)-halsbånd som var påfestet 47 rådyr (27 hunner og 20 hanner) og 18 gauper (7 hunner og 11 hanner) med overlappende leveområder. Jeg brukte en økologisk nisjefaktor analytisk tilnærming for å få fire ukorrelerte landskapsakser som forklarte mesteparten av variasjonen i dataene. Disse aksene ble brukt som avhengige variabler i lineære regresjoner for å analysere habitatbruk og total nisjeavstand mellom artene i forhold til årstider, lysperioder (dag, kveld og skumring) og kjønn.

Den totale nisjeavstanden mellom rådyr og gaupe var minst på dagen (bortsett fra om vinteren) og størst ved skumring, om vinteren, og mellom rådyr- og gaupehunner i forhold til rådyr- og gaupehanner. Disse funnene tyder på at døgnvariasjonen i habitatoverlapp mellom rådyr og gaupe ser ut til å være drevet av predasjonsrisiko da begge artene minsket sine potensielle dødelighetsrisikoer ved å skifte mellom habitater med lav og høy risiko i tid, mens sesongmessige variasjoner i habitatoverlapp ser ut til å være bestemt av fordelingen av høykvalitetsmat. For hunner var disse mønstrene tydeligere, men på forskjellige måter da det var avhengig av artsspesifikk økologi. I denne studien har jeg dokumentert hvordan habitatoverlapp for predatorer og byttedyr varierer mellom sesonger og lysperioder i en menneskedominert verden.

1. Introduction

The way animals utilise the landscape depends on the distribution of resources associated with different habitat types (Hall et al., 1997), such as food affecting their energy gain and mortality risk influencing the cost of being in a specific habitat type (McNamara and Houston, 1987, Sih, 2005, Lima, 1998). Optimal habitat use would allow an animal to gain energy in a food-rich habitat with a low risk of mortality, but such habitats are rare (Lima and Dill, 1990, Sih, 1980). Therefore, animals often have to trade-off energy gain for low mortality risk (Bjørneraas et al., 2011, Eldegard et al., 2012, Brown et al., 1988, Mysterud et al., 1999, Tolon et al., 2009). Such trade-offs are costly with respect to reducing the utilisation of high-quality food resources, and if the risk of starvation gets too high, animals might be forced to forage in habitats associated with higher mortality risk, for instance in areas with higher level of predation (Ratikainen et al., 2007, Lima, 1998, Lima and Bednekoff, 1999, Riginos, 2015).

Humans are one of the most important causes of mortality both for prey species and their predators, thus the presence of humans might affect animals negatively by depressing the utilisation of areas with high-quality food (Musiani et al., 2010, Andersen et al., 1994). Therefore, animals might associate human developments (e.g. agricultural fields, houses, roads) with increased mortality risk and respond by avoiding areas with high level of human-made landscape structures, and in particular in periods when human activity is high (Frid and Dill, 2002, Dyer et al., 2001, Eldegard et al., 2012, Lykkja et al., 2009, Basille et al., 2013, Nellemann et al., 2001). Human-dominated areas are increasing, and animals' natural habitats are altered by for instance urbanisation, agriculture and forestry. Hence, animals have to deal with fragmentation and reduced natural habitats, which increase disturbance (e.g. houses, roads, dogs) and may affect animals in respect to human-related mortality risk and to predators (e.g. due to lack of cover) (Hornseth et al., 2014, Hewison et al., 2001). On the other hand, some species may benefit from human-made landscapes as edge-habitats provide high-quality forage and great proximity to cover (Morellet et al., 2011, Brazaitis et al., 2014, Torres et al., 2011, Cederlund, 1983). In addition, some herbivores have been shown to use areas close to humans as "safe" areas because their predators show a greater avoidance of such areas (Berger, 2008, Hebblewhite and Merrill, 2009). Consequently, one can expect that a large part of animals' habitat use is shaped by their relationship to humans (Jiang et al., 2008, Ciuti et al., 2012).

Predators affect prey through the direct effect of killing them as well as through indirect ways by inducing fear. These indirect effects of predation can potentially affect animals to the same degree as lethal effects (Creel and Christianson, 2008, Preisser et al., 2005, Kotler, 1992). In a prey species' home range, the level of predation risk varies spatially according to habitat types and landscape features, as well as with season and time of day (Preisser et al., 2005, Iribarren and Kotler, 2012), creating a spatially and temporally heterogeneous pattern of varying predation risk called “the landscape of fear” (Laundre et al., 2001, Laundré et al., 2010). The fear of being killed may elicit behavioural antipredator responses that are costly in terms of avoiding high-quality food patches, even when there are no predators nearby (Brown et al., 1999, Nilsen et al., 2012), for example through alteration in group size, vigilance and habitat shift (Caro, 2005, Altendorf et al., 2001, Embar et al., 2011, Barja and Rosellini, 2008, Berger, 1991, Beier and McCullough, 1990, Latombe et al., 2014). For instance, elk prefer meadows with high-quality forage, but in the presence of wolves they increase the use of safer edge-habitats with more cover (Hernandez and Laundre, 2005, Muhly et al., 2010).

The landscape of fear can vary temporally because the benefits and costs that are related to a habitat type differ for instance between photoperiods and seasons (Sih, 2005, Lima, 1998, Preisser et al., 2005). Seasonal variation in quantity and quality of vegetation fluctuate greatly throughout the year and thereby affecting foraging species' distribution on a long temporal scale (Hansen et al., 2009, Morellet et al., 2013). For instance, moose (*Alces alces*) with young avoided open, food-rich habitats after their young were born in spring and summer, whereas male moose and females without young used such areas in the same time period (Bjørneraas et al., 2011). Snow cover is an important factor in Norway and can affect food availability and movement costs for some species (Parker et al., 1984), whereas other species, including many predators, are better adapted to snow rich climates and might benefit as prey that struggles in snow is easier to catch (Cederlund and Lindstrom, 1983).

The landscape of fear may differ within species (Coleman and Hill, 2014), for instance with age, sex and reproductive status (Bunnefeld et al., 2006, Winnie and Creel, 2007, Berger, 1991, McLellan and Shackleton, 1988). For instance, calving females reduce predation risk to their neonates by using habitat types that are safer, but sub-optimal, with respect to forage quality (Ciuti et al., 2006, Bjørneraas et al., 2011, Grignolio et al., 2007, Bleich et al., 1997, Dussault et al., 2005). Moreover, the landscape of fear might vary between species with respect to the specific predator(s) present as different predators have different hunting strategies (Altendorf et al., 2001, Thaker et al., 2011, Cresswell and Quinn, 2013, Ciuti et al.,

2012). In daytime, prey might be safer in forested habitat types providing cover as some day active predators use vision during hunts, whereas at night, the predation risk in the same habitat types might increase from nocturnal, stalking predators that need cover for successful hunting (Moreno et al., 1996, Lone et al., 2014).

There are several studies on how habitat use of one prey species is affected by a single predator, but in the real world, prey are often affected by multiple predators simultaneously. It is important to include this when we want to understand how animal's habitat use overlap with other species, especially of species in different trophical levels. Habitat use of predators is affected by the availability of prey and the costs of finding them, whereas a prey species habitat use is driven by the distribution of high-quality forage and the costs of avoiding mortality risks for instance from predators (Gorini et al., 2012). Thus, prey species want to minimise their habitat overlap with their predators, whereas predators try to maximise it (Sih, 2005). It is also important to realise that many predators may themselves be prey, either to larger predators or to human hunters, so that they may also face trade-offs concerning access to prey and risk of being killed.

My aim was to address the issue raised above in a study system with European roe deer (*Capreolus capreolus*) and its main predator, the Eurasian lynx (*Lynx lynx*), in an area experiencing large seasonal variation in the spatial distribution of food resources for roe deer. As a predator, lynx habitat use should be determined mainly by the distribution of its prey, whereas roe deer should use habitats dependent on availability of high-quality food and mortality risk factors.

The two factors generating the landscape of fear for roe deer are lynx and humans (Odden et al., 2006, Melis et al., 2010, Okarma et al., 1997, Krofel et al., 2014, Benhaiem et al., 2008, Bjørneraas et al., 2012b), while for lynx the only risk factor is mortality from humans (Andrén et al., 2006). Human hunters have highest activity during daytime, and they need to hunt in open areas with good visual sight. In contrast, lynx activity is highest at night and dusk and lowest at midday and as they are stalk-and-ambush predators, they need dense vegetation for successful hunting (Nilsen et al., 2009, Podolski et al., 2013, Belotti et al., 2013, May et al., 2008). Thus, the landscape of fear for roe deer is affected by double predation risks that do not overlap temporally or with respect to habitat types (Lone et al., 2014). It has been shown that roe deer use protective forested areas more in daytime and open areas providing high-quality forage at night (Bonnot et al., 2013), and that roe deer are more

nocturnal during autumn when hunting increases human-induced mortality (Krop-Benesch et al., 2013, Sönnichsen et al., 2013), compared to the year-round activity pattern with peaks at dusk and dawn (Pagon et al., 2013). However, human-dominated areas can also act as refuges for roe deer because lynx tend to avoid areas with high human abundance, giving roe deer the opportunity to exploit lynx's fear of humans by keeping close to such areas (Muhly et al., 2011, Basille et al., 2009). In addition, there may be a seasonal variation in the landscape of fear as the energy gain and costs associated to specific habitat types might differ more for roe deer than for lynx during a year. For instance, in winter, the availability of high-quality forage decreases with increasing snow depth (Mysterud et al., 1997), more energy is spent on thermoregulation (Holand et al., 1998), and also, the cost of locomotion is higher in deep snow (Parker et al., 1984).

In this study, I explored the temporal variation in habitat overlap of roe deer and lynx in a human-dominated area in southern Norway, and how it varied on long (seasonal) and short (diurnal) temporal scales. I focused particularly on habitat characteristics associated with human activity. Because humans are by far the most important mortality factor for lynx, I first expected that lynx would avoid areas associated with humans by utilising habitats with low levels of human disturbance (e.g. decreased density of and increased distances to houses and roads). In contrast, roe deer experience mortality both from lynx and humans, and may accept higher risks from humans to gain high-quality food in agricultural fields instead of utilising habitats with increased predation risk from lynx and poorer food quality (Abbas et al., 2011, Gill et al., 2001). However, roe deer should lower both predation risks by adjusting the use of open and covered habitat types. Moreover, I expected that roe deer and lynx will avoid human-associated areas in periods when human activity is high, and roe deer to not avoid such areas when lynx activity is high. Thus, I predicted the habitat overlap between roe deer and lynx to be greater when lynx activity is low and human activity is high, and smaller when roe deer and lynx are both active. Given that the relative mortality risks by humans are higher for lynx than for roe deer (Andrén et al., 2006), I expected such temporal patterns to be stronger for lynx compared to roe deer.

Secondly, because the spatial distribution of food varies greatly among seasons, and thus the gain of utilising habitats in relation to the landscape of fear also varies seasonally, I expected seasonal variation in how lynx and roe deer utilise habitats. However, whether this seasonal variation is strongest for lynx or for roe deer is not straightforward to predict. On the one hand, there are large variations in spatial distribution of vegetation offering high-quality

forage for roe deer. In summer, the vegetation is more evenly distributed, whereas in winter, high-quality forage is concentrated in agricultural fields and close to human settlements (for example at supplementary feeding sites) as snow reduces food availability elsewhere. This would involve a higher seasonal variation in habitat use of roe deer compared to lynx, and because humans may affect the landscape of fear of lynx more compared to roe deer, the habitat overlap should be smaller in winter when roe deer seek out human settlements for food. On the other hand, roe deer is the main prey species for lynx and seasonal changes in the spatial distribution of roe deer should be followed by changes in lynx distribution.

Finally, roe deer and lynx females live in family groups (mothers with young) throughout the year, thereby having higher mortality risks due to the vulnerability of their young. Therefore, I predicted that roe deer and lynx females should have smaller habitat overlap between each other and between roe deer and lynx males. Additionally, because lynx mostly kill female adult roe deer (Krofel et al., 2014), the habitat overlap should be more pronounced between roe deer females and lynx than roe deer males and lynx. I also expected that females of both species should avoid human-associated areas more than males and in particular when human activity is high. Female roe deer should modify their habitat use between open and covered areas to a higher degree than males, and female lynx should alter their spatial distribution by using habitats with lower levels of human impact (e.g. increased ruggedness that is associated with security) more frequently than males.

2. Materials and methods

2.1 Study area

The data were collected in southern Norway in the counties of Oppland, Buskerud, Telemark and Vestfold (Fig. 1), as a part of the Norwegian lynx and roe deer project (SCANDLYNX, 2015). The north-western part of the study area is dominated by coniferous forest and steep and rugged terrain, and it is marginally suitable for roe deer. The south-eastern part of the study area is more human-modified with broadleaved forest and cultivated land to a greater extent, and both human and roe deer occur at higher densities. Human activity (e.g. forestry, agriculture) takes place throughout the study area, but the majority of human activity occurs along valley bottoms where human settlements and agricultural land are typically found. For more details about the study area, see Gervasi et al. (2014).

Lynx are found all over the study area with a population size fluctuating between 60 and 70 individuals due to hunting harvest in winter (Linnell et al., 2010). The main prey for lynx in the study area is roe deer, and additionally free-ranging domestic sheep (*Ovis aries*) in summer (Odden et al., 2006, Gervasi et al., 2014). The main mortality cause for roe deer in the area is due to lynx predation, followed by human harvest and red fox (*Vulpes vulpes*) predation on neonates (Melis et al., 2013).

2.2 Study species' data

I obtained Global Position System (GPS) location fixes from GPS-collars that were attached to both roe deer and lynx. The collars were programmed to obtain a location at least every sixth hour (varying due to some periods with higher sampling frequency) and the mean lifetime of a collar was 12 months. For more information about animal capture and marketing, GPS-collars and the programming, see Arnemo et al. (2011), Lone et al. (2014), Mejlgaard et al. (2013) and Mysterud et al. (2012). The data were visually and statistically screened for erroneous fixes that could have occurred due to vegetation, topography, stressed animals after catch and release, position fix-rate or animal posture (Bjørneraas et al., 2010). I also removed observations from the first 24 hours after a GPS-collar was attached on an individual to avoid non-normal behaviour of stressed animals (Morellet et al., 2009).

Originally, I had data from 75 roe deer and 30 lynx. From the data sets I removed roe deer individuals with small number of observations and juveniles that were dispersing based on visual examination of their movement trajectory. To secure that data from roe deer and lynx were from the same area (i.e. that available habitat did not differ between the two species), I generated 95 % minimum convex polygon home ranges of all individuals (using the “adehabitatHR” package in R, Calenge (2006)), and I removed lynx individuals that had non-overlapping home ranges with roe deer, and roe deer that did not overlap with any lynx home ranges. The final dataset consisted of 47 roe deer (27 females and 20 males) and 18 lynx (7 females and 11 males) studied during the period 2005-2013.

2.3 Landscape variables

Habitat data were collected from the Norwegian Mapping Authority. This included vector-based data from the N50 digital map series. I used the following map layers: Buildings, public roads, private roads (including tractor roads) and habitat types (forest, bogs, agricultural areas, built-up areas and other open areas). I obtained complementary habitat types from a satellite

based vegetation map of Norway with a resolution of 30×30 meter (Johansen et al., 2009). I reclassified the 25 habitat types into eight habitat types: Coniferous forest, birch forests, broad leaved deciduous forests, tall herb deciduous forests, agricultural areas, bogs, built-up areas and open habitats (includes alpine ridges, heathlands, meadows, glaciers, water and other unclassified areas). To describe the topography, I used a digital elevation model (DEM) with a spatial resolution of 25×25 meter. From the DEM, I also calculated slope and terrain ruggedness based on a Vector Ruggedness Measure model (VRM) (Sappington et al., 2007).

As measures of human impact, I calculated the distance between animal observations to the closest private and public road and building. In addition, I measured the density of buildings and roads within a radius of 500 meters from each animal location. Locations that were inside human settlement polygons (built-up areas according to the habitat types) were all assigned a nominal fixed distance to buildings of 10 meters instead of the actual distance to the closest building as separate buildings were not included in the digital map data inside such areas. For all observations I also extracted habitat types and topographic parameters. As the elevation of a valley bottom is higher in the northern part of the study area compared to the southern part, I used relative elevation values which were 0 if animals were at a valley bottom in their area.

To obtain normally distributed data, I log transformed distance to private roads, public roads, buildings and I square root transformed density of private roads, public roads and buildings, and elevation, slope and terrain ruggedness.

2.4 Temporal parameters

I used seasons and photoperiods as temporal parameters in my analyses. As seasons differ due to climatic conditions, seasons were categorised as summer (June, July, and August), autumn (September, October and November), winter (December, January and February) and spring (March, April and May). The photoperiods were assigned by using the longitude and latitude coordinates of a central point in my study site and the solar angle to categorise the circadian rhythm by day, twilight and night. This was done with the function "solarpos" in package "maptools" (Bivand and Lewin-Koh, 2014) in R version 3.0.2 (R Core Team, 2013). Day was defined when solar elevation was above 0 degrees (i.e. above the horizon), twilight when solar elevation was between -6 and 0 degrees and night when solar elevation was below -6 degrees.

2.5 Statistical analyses

Habitat variables often correlate, for instance roads and buildings are typically found close to agricultural areas in flatter landscapes. I used an ecological niche factor analytical approach because I was not interested in each habitat variable *per se*, but rather how roe deer and lynx were located in an environmental niche that was constituted by a set of landscape variables. Accordingly, I decomposed the variables into environmental axes that were related to the landscape variables using a compositional analysis that can handle a combination of both categorical and continuous variables (function `dudi.mix` in package “`adehabitatHS`”, Calenge (2006)). I treated all observations as equally important and thus having equal weights in the analyses. This was justified due to the standardised sampling of observations from all individuals (see *Methods, Landscape variables*). Correspondingly, I assumed that my observations represented a random sample of the roe deer and lynx population in the study area. Each animal observation was assigned its value along the environmental axes from the compositional analysis. I then aggregated values on species, sex, season (summer, autumn, winter and spring), photoperiod (day, twilight and night), and day number (from January 1st). Years were pooled as I was not interested in annual variation in habitat overlap. These sets were then used to analyse how roe deer and lynx differed temporally in their environmental niches (see below).

I first assessed whether lynx and roe deer differed with respect to the values for each environmental axis, and if this difference varied between males and females, between seasons, and between photoperiods. I did this using linear regression with values along the environmental axis as dependent variables and species, sex, seasons and photoperiods as explanatory variables. I also included the two-way interactions between species and sex, species and season, species and photoperiod, sex and season, sex and photoperiod, and finally season and photoperiod. Additionally, one three-way interaction was included between species, sex and season because roe deer and lynx differ in their reproductive behaviour (e.g. territoriality in roe deer bucks and the time of mating periods) throughout a year (see Table 1 for model specification).

Next, I analysed the total niche distance between roe deer and lynx in relation to sex, season, and photoperiod. Moreover, I calculated the total distance between roe deer and lynx in an N-dimensional niche space, where N is the number of environmental axes that I kept from the compositional analysis (eigenvalue > 1). This was done by calculating the distances for each

day and photoperiod separately. I analysed this using linear regression with values along the total niche distance as dependent variables and sex, seasons and photoperiods as explanatory variables. I also included the two-way interactions between sex and photoperiod, sex and season, and season and photoperiod. I also separated between male and females, and the end data were, for each day number, photoperiod and season, the N-dimensional niche distances between male roe deer and male and female lynx, and female roe deer and male and female lynx. A high total distance between roe deer and lynx indicated low degree of habitat overlap, whereas if distance was low the species were located close to each other in the environmental space meaning that habitat overlap was high.

I used Akaike Information Criterion corrected for small sample size (AICc, Burnham and Anderson (2002)) to assess the importance of the explanatory variables and rank candidate models. All combinations of variables were allowed in candidate models, but if an interaction was included, main effects were always retained in the model. All statistical analyses were performed in R version 3.0.2 software (R Core Team, 2013).

3. Results

3.1 Correlation between landscape variables and environmental axes

Eigenvalues (Fig. 2) from the ecological niche factor analytical approach showed that four environmental axes (eigenvalues > 1) explained most of the variation in the data. The correlations between axes scores and the landscape variables are shown in Table 2. The first axis explained 23 % of the total variation in the data. This axis correlated negatively with distance to public roads, buildings, bogs and relative elevation, whereas it correlated positively with built-up areas and density of public roads and buildings. This corresponds to low and high human disturbance at low and high values of axis 1, respectively. Axis 2 correlated negatively with built-up areas and bogs, and positively with agricultural areas and density of private roads. Axis 3 correlated positively with terrain ruggedness and slope, and negatively with bogs and built-up areas. Axis 4 correlated negatively with slope, open areas, birch forest, bogs and relative elevation, and positively with agricultural areas and deciduous and coniferous forests.

3.2 Human disturbance

For Axis 1, which was related to human disturbance (e.g. density of and distance to public roads and buildings, Table 2), the highest ranked model according to AICc-values included species, sex, season and photoperiod, in addition to the two-way interactions species*sex, species*season, sex*season, sex*photoperiod, and the three-way interaction species*sex*season (model 1a, Table 1). Two alternative models had $\Delta\text{AICc} \leq 2$ (model 1b and 1c, Table 1), and included the interaction sex*photoperiod or species*photoperiod in addition to the terms included in the highest ranked model. I chose the simplest model (model 1a, Table 1) as the most parsimonious for explaining the variation in Axis 1. According to this model, roe deer had overall higher values along the first axis compared to lynx (Axis 1, Fig. 3), i.e. roe deer observations were closer to human developments and in areas with higher densities of public roads and buildings compared to lynx observations. Moreover, male lynx had higher values than female lynx, whereas the sex pattern was reversed for roe deer. Seasonal patterns were strongest for roe deer with higher values in spring and winter. Finally, for both species the values of Axis 1 were highest at night and lowest in daytime.

3.3 Built-up and agricultural areas and private roads

Axis 2 was related to built-up areas, density of and distance to private roads and agricultural areas (Table 2). According to AICc-values, the best model explaining the values of this axis was the full model (model 2a, Table 1). No alternative models received considerable support ($\Delta\text{AICc} \geq 5.066$). Roe deer had overall higher values along the second axis compared to lynx (Axis 2, Fig. 3), i.e. roe deer used more of agricultural areas with increased density of and shorter distance to private roads compared to lynx. Moreover, male roe deer had higher values than females in winter and spring, whereas females had higher values in summer (reversed at summer night) and autumn. Female lynx had higher values than male lynx, except for autumn night when males had higher values. Seasonal patterns were strongest for roe deer, with higher values in spring and lowest values in winter. Finally, for both species the values in Axis 2 were lowest by day and highest at night or twilight, depending on the sex and species. Roe deer and lynx males had similar diurnal patterns with lowest values at day and highest values at night in all seasons except winter with highest values at twilight. Females of both species also showed similar patterns with lowest values at day and highest at twilight, but female roe deer showed no pattern in summer.

3.4 Topographic characteristics

Axis 3 was related to high ruggedness and slope at high values (Table 2), and low ruggedness and slope at low values. The best supported model for explaining the variation in Axis 3, based on AICc-values, was the full model (model 3a, Table 1). No alternative models received considerable support ($\Delta\text{AICc} \geq 7.384$). The highest ranked model showed that lynx had overall higher values along the third axis compared to roe deer (Axis 3, Fig. 3), i.e. lynx used more rugged and steep terrain compared to roe deer. Moreover, roe deer and lynx males had higher values than females, but for lynx it was reversed in summer. Seasonal patterns were strongest for roe deer, with higher values during spring and winter and lowest values during summer. The diurnal pattern was strongest for lynx with highest values in daytime and lowest at night, except in spring when lowest values were at twilight. Roe deer showed similar pattern, but the difference between day and twilight was smaller.

3.5 Open and forested habitat types

Axis 4 was related to open and forested areas at low and high values (Table 2), respectively. The best supported model according to AICc-values included species, sex, season and photoperiod, in addition to the two-way interactions species*sex, species*photoperiod, species*season, sex*season, sex*photoperiod, and the three-way interaction species*sex*season (model 4a, Table 1). One alternative model also received support ($\Delta\text{AICc} = 0.885$, model 4b, Table 1), but I chose the simplest model (model 4a, Table 1) as the most parsimonious for explaining the variation in Axis 4. According to this model, the difference between males and females was most pronounced in winter and spring where females of both species had higher values than males, but with a reversed pattern in autumn (Axis 4, Fig. 3). Seasonal patterns varied between species with roe deer having lowest values during winter and lynx having highest values in autumn. Diurnal pattern was strongest for roe deer, but in autumn it was stronger for lynx. Roe deer had highest values of Axis 4 at night and lowest at twilight, except in autumn when highest values were in daytime. Lynx had the same pattern, but the highest values were at twilight in autumn.

3.6 Total habitat overlap

Habitat overlap, which was measured as the total distance between roe deer and lynx for all environmental axes in a four-dimensional niche space, was best explained by the full model that included sex, photoperiod and season, in addition to the 2-way interactions

sex*photoperiod, sex*season and season*photoperiod (model 5a, Table 1). No alternative models received considerable support ($\Delta AICc \geq 6.903$, Table 1). Overall, total distance was highest (i.e. low habitat overlap) during winter and lowest in summer and spring (Fig. 4). The total distance was also higher at twilight and lowest in daytime, except in winter when the distance was largest at night.

Roe deer females and lynx of both sexes had higher total distance than roe deer males and lynx in summer and autumn, and in winter and spring lynx females and roe deer had higher total distance than lynx males and roe deer (Fig. 4).

4. Discussion

Using an extensive dataset on habitat utilisation of a prey species and its predator sharing home ranges, I have documented the existence of long-term and short-term temporal variation in the level of habitat overlap between two species, and between males and females of a species.

The first part of prediction one, that roe deer and lynx should decrease the total niche distance between each other when human activity was high, was partly supported as total distance was smallest by day in all seasons except in winter with the smallest total distance at night (Fig. 4). In daytime when human activity was high, roe deer and lynx increased the use of areas with lower human disturbance and higher ruggedness, and used areas with higher level of human disturbance and lower ruggedness at twilight (Axis 1 and 3, Fig. 3). This is supported by many studies that have shown how animals avoid areas of human disturbance by modifying their habitat use (Dyer et al., 2001, Nellemann et al., 2001, Basille et al., 2009). Human settlements are normally found in flat landscapes, and flat hunting grounds are also likely to be preferred by human hunters, which reduces the potential mortality risk from humans in areas with high ruggedness. The pattern of higher use of rugged terrain by day was more pronounced for lynx than for roe deer, which may suggest that lynx habitat use was more affected by humans than that of roe deer. Humans are the most important mortality risk factors for lynx, mainly due to hunting and poaching activity (Andr n et al., 2006). At the same time, studies have shown that lynx have higher tolerance of human settlements than of humans *per se* (Sunde et al., 1998), and at night they do not avoid roads at all (Belotti et al., 2012). Higher tolerance might be due to lynx accepting higher risk for food probably because

of high roe deer abundance in such areas (Basille et al., 2009, Bunnefeld et al., 2006, Basille et al., 2013).

Overall, roe deer seemed to have higher tolerance of human settlements by consistently using areas with higher human disturbance and lower terrain ruggedness compared to lynx (Axis 1 and 3, Fig. 3), which is supported by other studies (Torres et al., 2012). In addition, as predators tend to follow the distribution and density of their prey (Gorini et al., 2012, Basille et al., 2009), the observed habitat shift between day and twilight might be explained by lynx tracking roe deer's diurnal pattern. Besides, the stronger diurnal pattern of lynx might be due to lynx having larger home ranges than roe deer, which makes it possible for lynx to avoid mortality risk to a higher degree compared to roe deer that are limited by their smaller home ranges.

Low total distance by day can also be explained by the species' activity patterns (Fig. 4). Lynx activity is lowest at midday (Podolski et al., 2013), but roe deer generally have activity periods throughout the day due to their short rumination cycle (Holand et al., 1998). During daytime, roe deer may forage in other habitats that have poorer food quality, suggesting a trade-off between food and safety from humans. Roe deer used more forested areas by day than at twilight (Axis 4, Fig. 3), which may suggest that roe deer move into woodlands when lynx are least active, making forests a safer habitat type for roe deer in daytime with respect to predation risk from both lynx and humans. In winter, the total distance between roe deer and lynx was lowest at night, and the use of forests areas was highest (Axis 4, Fig. 3). Roe deer are least active in this photoperiod as winter nights are the coldest periods throughout a year, increasing the costs of thermoregulation and use of cover (Krop-Benesch et al., 2013, Pagon et al., 2013, Mysterud and Østbye, 1995). This could also be explained by winter nights lasting temporally longer compared to night periods in other seasons, thereby extending the potential hunting period for lynx.

The second part of prediction one, that total distance between roe deer and lynx should be greater when both species' activity is high, was supported as the total distance between roe deer and lynx was highest at twilight in all seasons (Fig. 4). Interestingly, the diurnal pattern of lynx differed in autumn compared to other seasons. At twilight, lynx increased their use of areas with forests and lower level of human disturbance (Axis 1 and 4, Fig. 3). In the same photoperiod, roe deer showed a decreased use of open areas compared to other seasons (Axis 4, Fig. 3). As the roe deer hunting season (along with hunting seasons for moose, red deer and

small game) starts in autumn, lynx might be affected by the increased human presence in open areas, which also affects roe deer as they increase nocturnal activity and vigilance in this season (Krop-Benesch et al., 2013, Sönnichsen et al., 2013).

At twilight in other seasons than autumn, roe deer used open and agricultural areas more than lynx, and lynx seemed to follow the same pattern but to a lesser degree (Axis 2 and 4, Fig. 3). Roe deer are mostly found in edge-habitats between forests and fields where they can find both high-quality forage and cover (Cederlund, 1983), and studies have shown that roe deer modify the use of these habitat types between day and night to decrease predation risk from humans (Bonnot et al., 2013, Mysterud et al., 1999). Total distance between roe deer and lynx was possibly largest during this photoperiod because lynx do not use open areas while hunting, whereas roe deer use open areas for foraging on high-quality food (Hewison, 2009). Thus, open areas can be used to lower predation risk from predators that need cover to successfully stalk and hunt (Lone et al., 2014, Laundre and Hernandez, 2003), but in contrast, it might not be the case for roe deer in periods with high starvation risk or when they come under thermal stress (Ratikainen et al., 2007). Roe deer also benefit from using open areas as they decrease the cost of vigilance by gathering in larger groups as an antipredator behaviour (Barja and Rosellini, 2008, Caro, 2005), thus making detection of and escaping from predators quicker (Altendorf et al., 2001, McLoughlin et al., 2005). The pattern of roe deer using open habitats by twilight might be because they dare to forage in these areas when human activity is lower, in addition to decreased predation risk from lynx given that starvation risk for roe deer is low.

The second prediction of increased total distance between roe deer and lynx in winter was supported (Fig. 4), but lynx did not follow the seasonal pattern of roe deer. Roe deer used areas with highest human disturbance in winter compared to the other seasons (Axis 1 and 2, Fig. 3). High-quality forage is concentrated in, and around, agricultural fields and supplementary feeding sites, and as costs are high due to thermoregulation in cold weather and locomotion in deep snow (Parker et al., 1984, Pagon et al., 2013, Holand et al., 1998), roe deer cannot afford to avoid human settlements (Mysterud et al., 1997). In addition, when winters are harsh, predation by red foxes become more important (Panzacchi et al., 2009, Cederlund and Lindstrom, 1983), and several mortality risk sources can force them to accept higher risks in order to gain enough energy (Ratikainen et al., 2007, Gill et al., 2001).

Lynx, on the other hand, used areas with higher ruggedness in winter compared to the other seasons, but this pattern was less pronounced than the seasonal variation in human association of roe deer (Axis 1, 2 and 3, Fig. 3). This could suggest that lynx avoided humans more than roe deer as the availability of dense vegetation for hiding and stalking is smaller in winter compared to summer, which increase mortality risks for lynx. In addition, as lynx have larger home ranges compared to roe deer, they can more simpler adjust habitat use diurnally rather than seasonally as roe deer are easier to locate in winter because they concentrate close to human settlements (Barja and Rosellini, 2008).

The total distance between roe deer and lynx was smallest in summer and autumn (Fig. 4), which can be explained by roe deer migrating from low to higher elevations in summer, and *vice versa* in winter (Mysterud et al., 2012). In addition, roe deer home ranges during summer and autumn are smaller compared to the other seasons as they increase the use of forested areas due to more evenly spread food distribution between habitat types in these seasons (Cargnelutti et al., 2002, Morellet et al., 2013, Aiello et al., 2013). Also, lynx prey on other species which decrease their home ranges compared to other seasons with fewer significant prey species available (Odden et al., 2006). Higher habitat overlap in these seasons might result from both species decreasing their home ranges.

The third prediction of total distance between female roe deer and lynx being greater compared to male roe deer and lynx was supported (Fig. 4). This could be due to the combined effect of female roe deer using areas with higher level of human disturbance than males, and female lynx using areas with lower human disturbance compared to males (Axis 1, Fig. 3). Females with young are more vulnerable to predation resulting in higher awareness and use of safer habitat types with lower high-quality food (Ciuti et al., 2006, Bjørneraas et al., 2011, Grignolio et al., 2007, Bleich et al., 1997, Dussault et al., 2005), and earlier studies have shown that females in general use areas further away from human settlements than males, especially the first time after giving birth (Bunnefeld et al., 2006, Lykkja et al., 2009, Eldegard et al., 2012). This supports the observed habitat use in female lynx, but it seems not to be the case for female roe deer.

In addition to using areas with higher human disturbance, female roe deer used more built-up, agricultural and forested areas whereas males used more open areas, and this pattern was more pronounced in winter (Axis 2 and 4, Fig. 3). The winter pattern might be explained by high-quality forage becoming more important for female roe deer than males due to their

higher need of energy gain before giving birth in spring (Hewison, 2009). In spring and summer, male roe deer are territorial due to their reproductive behaviour (Liberg, 1998), while female roe deer hide their fawns and spend more time in edge-habitats that are safer due to the proximity of both cover and high-quality food (Tufto et al., 1996, Mysterud et al., 1999, Bjørneraas et al., 2012a, Panzacchi et al., 2010). The observed pattern might also be explained by female roe deer feeling safer close to humans as lynx mostly are found farther away from human-associated areas, making human settlements act as refuge areas from predation risk (Nowak et al., 2014, Basille et al., 2009, Berger, 2007). This may particularly apply for female roe deer that are hunted by lynx more frequently (Krofel et al., 2014). Finally, male lynx have larger home ranges than females and move longer distances in winter to find female lynx during mating periods, which may decrease the total distance with male roe deer additionally (Jedrzejewski et al., 2002, Herfindal et al., 2005).

In a landscape of fear, prey are often affected indirectly by predation risks which may elicit antipredator responses such as habitat shifts. While predators are trying to maximise habitat overlap with prey, prey are trying to minimise it (Sih, 2005). To understand habitat overlap between species, it is important to include all risk factors such as multiple predators (Gorini et al., 2012). This study demonstrated that habitat overlap between lynx and roe deer varied on long (seasonal) and short (diurnal) temporal scales with human hunting as an additional source of mortality risk. Diurnal variation in habitat overlap between the species seemed to be driven by predation risks as both species lowered their potential mortality risks by temporally shifting habitats with low and high risk (Lone et al., 2014), whereas variation in high-quality food distribution seemed to drive changes in habitat overlap between seasons. These temporal variations in habitat overlap were more pronounced in females compared to males, but in different ways which were dependent on the species-specific ecology. Thus, the landscape of fear varied temporally between both species and sex. As human-dominated areas are expanding, thus increasing mortality risks from humans in predators and prey, it is important to understand how anthropogenical alterations in natural habitats affect animal behaviour spatially, and especially as some species are challenged by multiple predators.

Acknowledgements

I would like to thank my supervisors Bernt-Erik Sæther (NTNU), Ivar Herfindal (NTNU) and John Linnell (NINA) for assistance and advice throughout this study. I am grateful for their collaboration, discussions and help with statistics and writing process, as well as being supportive and positive. Additionally, I would like to thank John Odden for inputs and interest in this project, Endre Grüner Ofstad for assistance, and finally I wish to thank my fellow student Ole Einar Butli Hårstad for sharing his terrain ruggedness model for my analyses.

At a personal level, I want to thank my boyfriend, family, friends and fellow students for encouragement and support.

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Tables

Table 1: AICc-based ranking of models explaining the variation in each of the four environmental axes and the total niche distance.

AXIS	MODEL	SPECIES	SEX	SEASON	PHOTOPERIOD	SPECIES × SEX	SPECIES × SEASON	SPECIES × PHOTOPERIOD	SEX × SEASON	SEX × PHOTOPERIOD	SEASON × PHOTOPERIOD	SPECIES × SEX × SEASON	AICc VALUES	ΔAICc	AICc WEIGHTS
1	1a	X	X	X	X	X	X		X		X	X	8296.95	0.000	0.399
	1b	X	X	X	X	X	X		X	X	X	X	8298.02	1.072	0.233
	1c	X	X	X	X	X	X	X	X		X	X	8298.13	1.182	0.221
	1d	X	X	X	X	X	X	X	X	X	X	X	8298.95	2.001	0.147
	1e	X	X	X	X	X	X		X		X		8326.75	29.795	0.000
2	2a	X	X	X	X	X	X	X	X	X	X	X	7572.40	0.000	0.916
	2b	X	X	X	X	X	X	X	X	X		X	7577.46	5.066	0.073
	2c	X	X	X	X	X	X	X	X		X	X	7581.28	8.885	0.011
	2d	X	X	X	X	X	X	X	X			X	7587.37	14.972	0.001
	2e	X	X	X	X	X	X	X		X	X		7590.16	17.760	0.000
3	3a	X	X	X	X	X	X	X	X	X	X	X	6608.91	0.000	0.975
	3b	X	X	X	X	X	X	X	X		X	X	6616.30	7.384	0.024
	3c	X	X	X	X	X	X	X	X	X		X	6623.06	14.141	0.001
	3d	X	X	X	X	X	X	X	X			X	6630.39	21.480	0.000
	3e	X	X	X	X	X	X	X	X	X	X		6649.01	40.093	0.000
4	4a	X	X	X	X	X	X	X	X		X	X	5231.74	0.000	0.608
	4b	X	X	X	X	X	X	X	X	X	X	X	5232.62	0.884	0.391
	4c	X	X	X	X	X	X	X	X		X	X	5247.08	15.336	0.000
	4d	X	X	X	X	X	X	X	X	X	X	X	5248.63	16.892	0.000
	4e	X	X	X	X		X	X	X		X	X	5252.86	21.115	0.000
Total niche distance	5a	-	X	X	X	-	-	-	X	X	X	-	9143.74	0.000	0.969
	5b	-	X	X	X	-	-	-	X		X	-	9150.65	6.903	0.031
	5c	-	X	X	X	-	-	-	X	X		-	9208.84	65.100	0.000
	5d	-	X	X	X	-	-	-	X			-	9213.95	70.207	0.000
	5e	-	X	X	X	-	-	-		X	X	-	9223.09	79.342	0.000

Table 2: The four most important environmental axes based on eigenvalues (EV) are shown with corresponding landscape variables. Values are axes scores (score, dudiobject\$co) and correlations (r^2/cr , dudiobject\$cr) that are extracted from the dudi.mix-analysis (see *Materials and methods, Statistical analyses*). Axes scores show where the landscape variables are located on the environmental axes, and correlations tell how important the landscape variables are for the environmental axes.

Landscape variables	AXIS 1 EV=3.67		AXIS 2 EV=1.81		AXIS 3 EV=1.42		AXIS 4 EV=1.20	
	score	r^2/cr	score	r^2/cr	score	r^2/cr	score	r^2/cr
(log) Distance to public roads	-0.869	0.755	0.151	0.023	-0.155	0.024	-0.048	0.002
(log) Distance to private roads	-0.219	0.048	-0.829	0.687	-0.084	0.007	0.047	0.002
(log) Distance to buildings	-0.826	0.682	-0.085	0.007	0.021	0.001	0.146	0.021
(sqrt) Density of public roads	0.853	0.024	-0.336	0.123	0.097	0.010	-0.016	0.000
(sqrt) Density of private roads	0.154	0.728	0.872	0.760	0.052	0.003	-0.057	0.003
(sqrt) Density of buildings	0.857	0.735	0.046	0.002	-0.040	0.002	-0.174	0.030
(sqrt) Slope	-0.129	0.017	-0.048	0.002	0.691	0.478	-0.425	0.181
(sqrt) Terrain ruggedness	-0.386	0.149	-0.022	0.001	0.623	0.388	0.173	0.030
(sqrt) Relative elevation	-0.558	0.311	-0.007	0.000	-0.237	0.056	-0.520	0.271
Habitat types		0.232		0.214		0.454		0.654
<i>Built-up areas</i>	2.433		-2.704		0.129		0.167	
<i>Agricultural areas</i>	0.543		0.871		-0.871		1.955	
<i>Coniferous and pine forest</i>	-0.231		-0.102		0.234		0.172	
<i>Broad leaved deciduous forest</i>	-0.081		0.183		0.480		0.779	
<i>Birch forest</i>	-0.126		-0.075		0.225		-0.577	
<i>Tall herb deciduous forest</i>	-0.094		0.027		0.106		-0.394	
<i>Bogs</i>	-1.663		-1.088		-4.610		-0.555	
<i>Open habitats</i>	0.555		0.251		-0.543		-1.297	

Figures

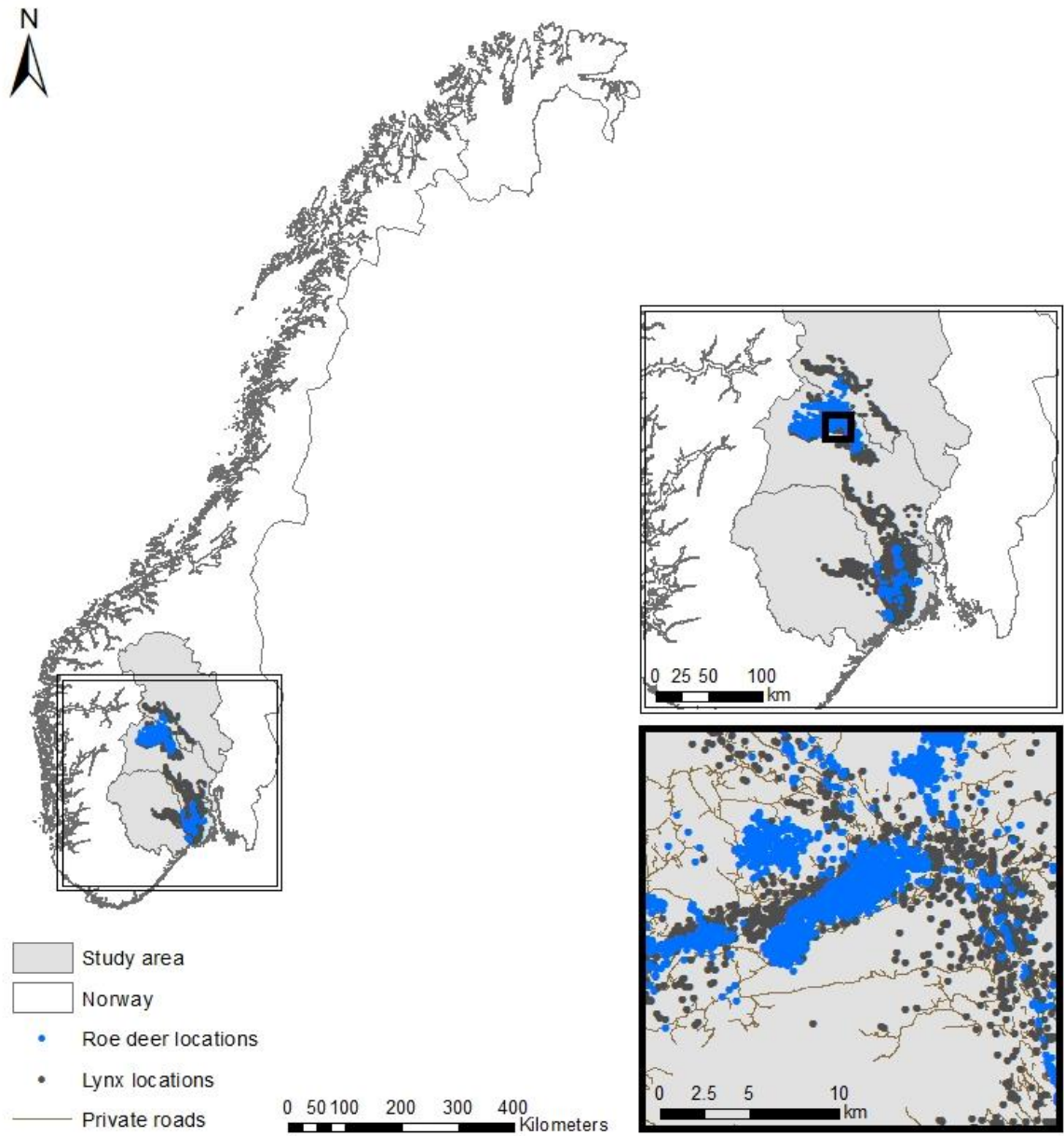


Figure 1: Study area (light grey) in the counties of Oppland, Buskerud, Telemark and Vestfold in southern Norway are shown. Main map and inset maps are showing roe deer (blue) and lynx (dark grey) locations, as well as private roads (brown line) in the inset map at the bottom right.

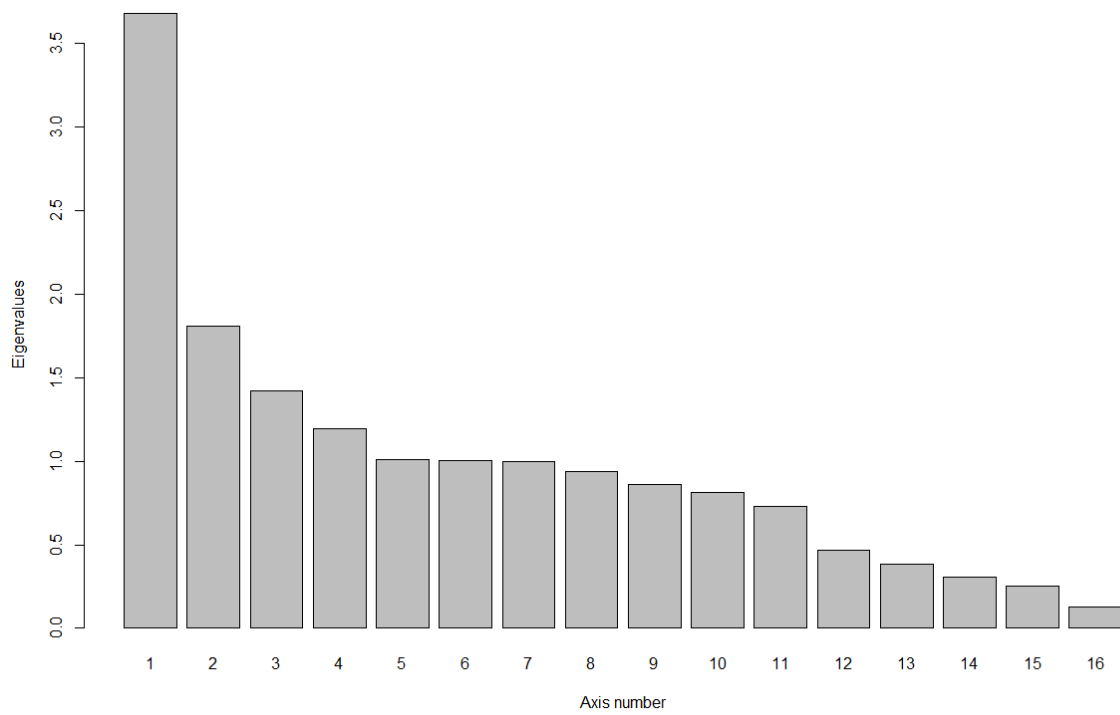


Figure 2: Bar plot of environmental axes according to eigenvalues from the environmental factor analysis approach.

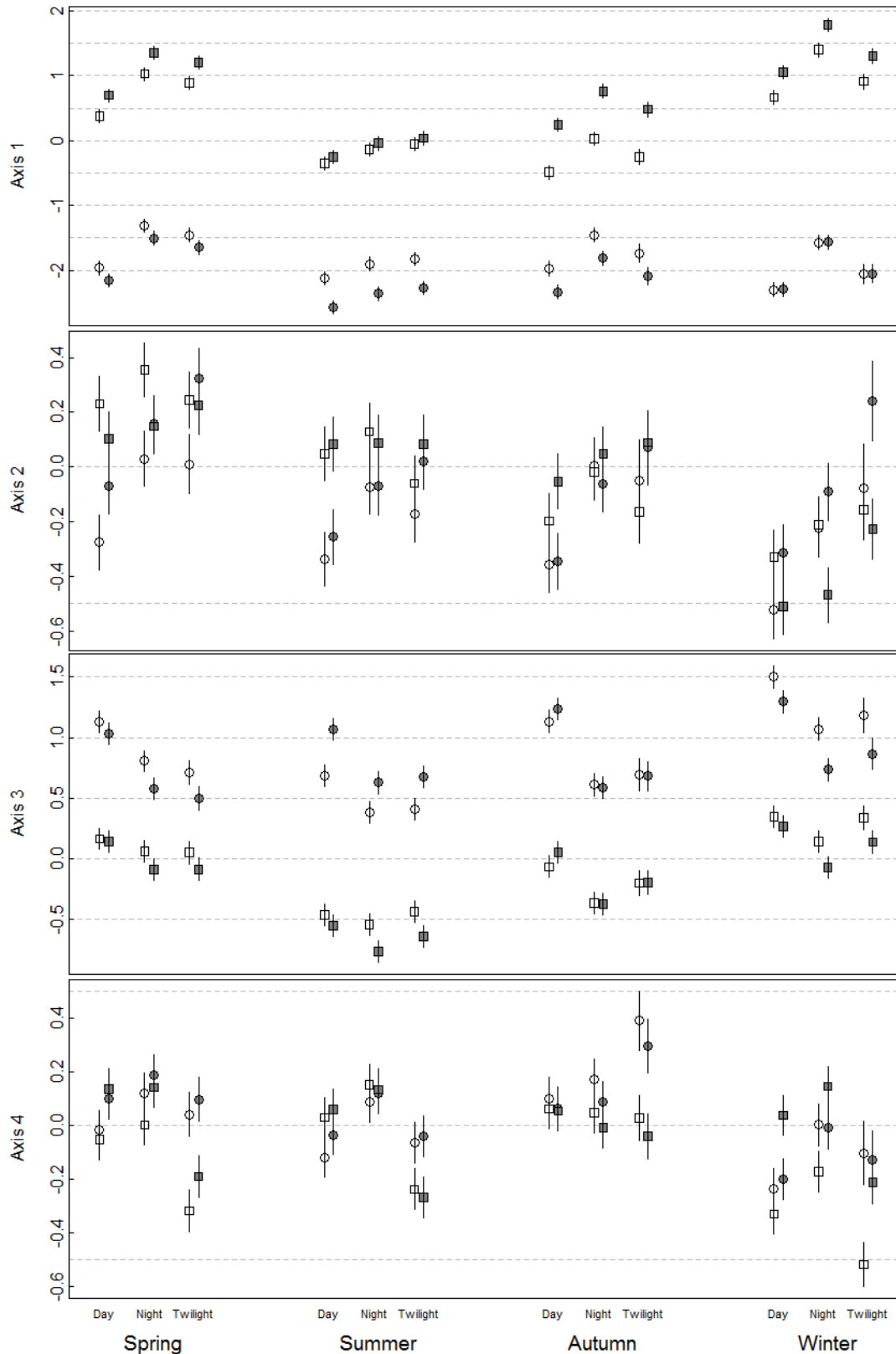


Figure 3: Seasonal and diurnal patterns of habitat use for male (white symbols) and female (filled symbols) roe deer (squares) and lynx (circles), based on the highest ranked models according to AICc-values (Table 1). For axes relationship to landscape variables, see Table 2. Bars represent 95% confidence intervals.

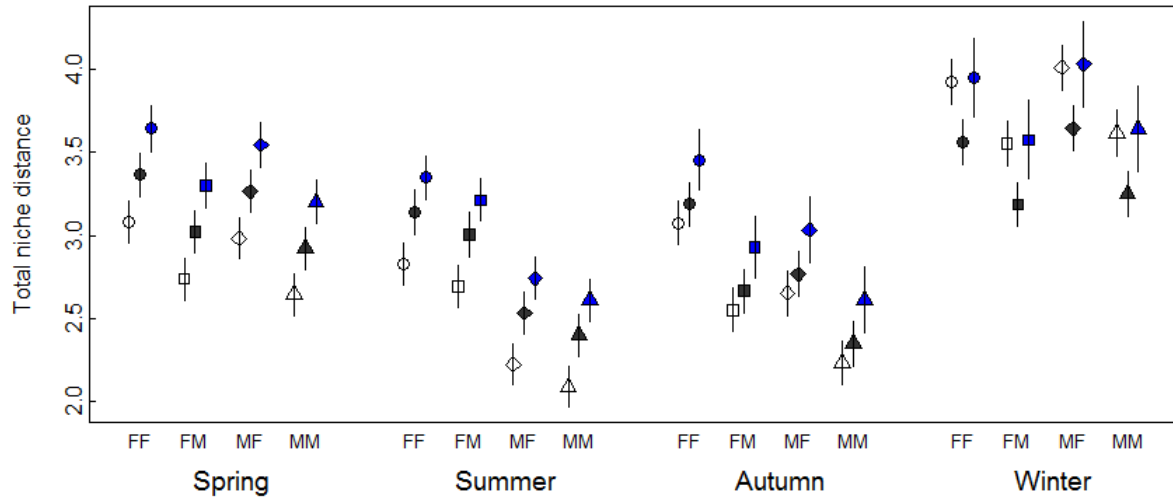


Figure 4: Seasonal and diurnal pattern in the total niche distance between roe deer and lynx, based on the highest ranked model according to AICc-values (Table 1). White, black, and blue symbols represent daytime, night and twilight, respectively. FF is female roe deer vs. female lynx, FM is female roe deer vs. male lynx, MF is male roe deer vs. female lynx, and MM is male roe deer vs. male lynx.