The establishment of reintroduced Eurasian lynx (*Lynx lynx*) in a forest-dominated low mountain range: habitat use and predation patterns

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for my beloved granddad

The establishment of reintroduced Eurasian lynx (*Lynx lynx*) in a forest-dominated low mountain range: habitat use and predation patterns

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Table of Contents

General Introduction

General Introduction

The distribution of lynx was once widespread throughout Europe (Sommer and Benecke 2006). However, by the end of the 19th and the early-20th century, lynx had been directly persecuted, resulting in a reduced population and distribution (Linnell et al. 2009; Breitenmoser et al. 1998; Breitenmoser and Haller 1993). In addition, strong deforestation was accompanied by the eradication of the ungulate population in Europe (Linnell et al. 2009; Linnell et al. 2005; Breitenmoser et al. 1998). The once large carnivore population was then severely reduced to local extinction (Linnell et al. 2005). Not only lynx but also brown bears (*Ursus arctos*) and wolves (*Canis lupus*) disappeared (Breitenmoser et al. 1998).
With the forest regeneration at the end of the 19th century, the ungulate population started to recover quickly (Breitenmoser et al. 1998). Favourable legislation, changes in public attitudes as well as management plans and policies turned the tide for lynx in Europe (Linnell et al. 2009; Linnell et al. 2005; von Arx et al. 2004; von Arx and Breitenmoser 2004) and started the recovery in northern and eastern Europe from the 1950s onwards (Breitenmoser et al. 2010). Large carnivores are today legally protected through the Berne Convention (Council of Europe 1979). From the 1970s, reintroductions of lynx in the Central and Western Europe started, resulting in a lynx population displaying an upwards trend compared with the mid-20th century (von Arx et al. (2004), **Fig. 1**). Reintroduction programs were conducted in Italy, Switzerland, Slovenia, Austria, Czech Republic, France and Poland (Linnell et al. 2005). In Germany, three reintroductions were initiated, the first in Bavaria in 1970–1975, followed by the Harz Forest in 2000 (Kramer-Schadt et al. 2005) and the latest in the Palatinate Forest ("Pfälzerwald") in 2016 (Foundation of Nature and Environment Rhineland-Palatinate - SNU-RLP (2018)). Five of the fifteen reintroductions that took place in eight European countries from the 1970 to 2007 appear to have been successful (Linnell et al. 2009). Linnell et al. (2009) highlight that many reintroductions were undertaken secretly, poorly planned and not followed up, and hence the learning effects gained from the failures were limited.

Reintroduction program in the Palatinate Forest

Along with the program in the Dinaric Alps (2017), the reintroduction of lynx in the Palatinate Forest is one of the latest rewilding programs in Europe (Rewildingeurope 2021). The reasons for the reintroduction of this large carnivore into the Palatinate Forest included establishing a metapopulation with the potential of distributing into the Northern Vosges and from a long-

term perspective creating a genetic exchange with the metapopulations in the Middle and Southern Vosges and further with the Jura and Alp populations (SNU-RLP 2020).
The reintroduction in the Palatinate Forest started in 2015 with public relations and integrational work of all directly affected groups, such as hunters and livestock breeders. The total number of lynx released in the Palatinate Forest should be sufficient in relation to some of the other reintroductions to achieve a viable population (Breitenmoser and Breitenmoser-Würsten 2008). Twenty individuals originating from Switzerland and Slovakia provided adequate genetic variation and were released over a time span of five years from 2016 to 2020 (SNU-RLP 2020). Reintroduced lynx are either wild catches or orphan lynx that were held for a certain time in captivity (SNU-RLP 2020). Each released individual was equipped with a GPS collar to observe the first year of movement in their new habitat (SNU-RLP 2020). One year after the reintroduction of lynx, the first lynx reproduction was detected, illustrating the success in the long-term return of this large carnivore in the Palatinate Forest. A systematic camera trapping session conducted throughout the Palatinate Forest from December to April 2019/2020 and 2020/2021 revealed seventeen and thirteen independent lynx, which corresponds to a population density of 0.65 and 0.51 lynx per 100 km² within the 1,800 km² study area, respectively (Port 2021; Port 2020).

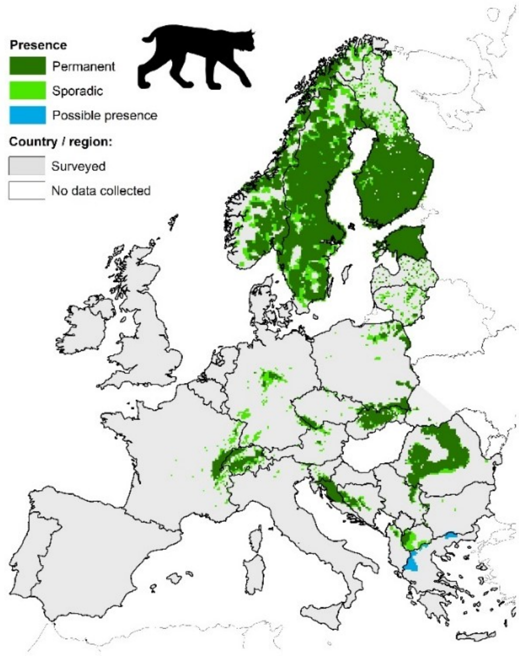

Fig. 1 Distribution of Eurasian lynx (*Lynx lynx*) in Europe with different presence levels (©LCIE 2021). The Iberian Lynx (*Lynx pardinus*), which occurs in small numbers in southern Spain, is not marked here on the map.

Lynx (Lynx lynx) – a large solitary felid

The Eurasian lynx (*Lynx lynx*) is the third largest carnivore in Europe, after the brown bear (*Ursus arctos*) and the grey wolf (*Canis lupus*) (Hočevar et al. 2020; Breitenmoser et al. 2000). In addition, it is the largest existing member of the Felidae family in Europe (Hočevar et al. 2020).

Lynx typically weigh around 12–35 kg, with males being larger than females (Breitenmoser et al. 2000). The total body length reaches 70–130 cm and the shoulder height can be up to 65 cm (Breitenmoser et al. 2000). Mating season occurs in February to mid-April (Breitenmoser et al. 2000) and brings forth a litter size of 1–5, with an average of 2–3 kittens (Breitenmoser and Breitenmoser-Würsten 2008; Breitenmoser et al. 2000; Kvam 1991). The fur coloration and pattering varies across the species' distribution range, showing a generally greyish coloration with various shadings (Breitenmoser et al. 2000). Breitenmoser et al. (2000) differentiate between three major coat patterns, namely spotted, striped and unspeckled. Each individual has its unique pattern (Hočevar et al. 2020; Breitenmoser and Breitenmoser-Würsten 2008; Breitenmoser et al. 2000), helping researchers to identify and distinguish the individuals.

The lynx is an ambush and stalking predator (Hočevar et al. 2020; Nilsen et al. 2009; Breitenmoser and Breitenmoser-Würsten 2008) specialised on medium-sized prey (Hočevar et al. 2020; Breitenmoser and Breitenmoser-Würsten 2008). In Europe, roe deer (*Capreolus capreolus*) is the main prey of lynx, but red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*) and rodents are also within their diet (Hočevar et al. 2020; Molinari-Jobin et al. 2007; Jobin et al. 2000; Jędrzejewski et al. 1993). In northern Europe, hare (*Lagopus* sp.) and reindeer (*Rangifer tarandus*) play a main role in the dietary pattern of lynx (Odden et al. 2006; Pedersen et al. 1999). All lynx are nocturnal and predominantly crepuscular active (Heurich et al. 2014; Podolski et al. 2013). Home range sizes of lynx vary between regions, also depending on the habitat type and density of prey, with lower prey densities leading to larger home ranges, and *vice versa* (Hočevar et al. 2020). Home ranges can range from 180–2,780 km² for males and 98–759 km² for females (Breitenmoser et al. 2000). The larger male home ranges can overlap with one or two female home ranges (Hočevar et al. 2020; Herfindal et al. 2005).

The return of the lynx and the conflicts

Around 9,000–10,000 lynx individuals are estimated to live in Europe nowadays (Status: excluding Russia and Belarus, Kaczensky et al. (2013)). With increasing numbers of lynx, conflicts with humans have arisen, especially with hunters and livestock breeders (Gervasi et al. 2020; von Arx and Breitenmoser 2004). Livestock breeders are afraid of losses in their herds, even though they are relatively low for lynx compared to other large predators. Compensation programs of the governments cover the financial loss, which should increase the acceptance towards this species (Gervasi et al. 2020; von Arx et al. 2004). Hunters perceive lynx as a direct competitor for the game animals (von Arx et al. 2004) and additionally they suspect the prey to change its behaviour, making it more difficult for hunters to be successful in the presence of this predator (von Arx and Breitenmoser 2004). Lüchtrath and Schraml (2015) found that the hunters' position towards lynx is influenced by their backgrounds (past experience), with forestry and nature conservation groups being positive towards lynx. Not only the direct competition for the prey but also the social identity as a hunter is questioned with the return of the lynx, leading to incomprehension among the hunters and in some cases illegal killing (Lüchtrath and Schraml 2015). Experts state that illegal killing is a major threat to the lynx population in Europe (Heurich et al. 2018; Breitenmoser et al. 2010; Andrén et al. 2006; von Arx and Breitenmoser 2004; Červený et al. 2002). Despite the legal protection, lynx in Scandinavia are regularly hunted (Sweden, Latvia, Estonia and Finland), and they even have annual hunting quotas in Norway (Hočevar et al. 2020). Additional threats to lynx include habitat loss and fragmentation (Kaczensky et al. 2013). In-breeding depression is a possible threat to small, isolated and/or introduced populations (Mueller et al. 2020; Port et al. 2020; Kramer-Schadt et al. 2005; Kramer-Schadt et al. 2004).

Population size / density estimation of prey species

Throughout recent decades, ungulates in Europe have experienced a strong increase in numbers and in some places they have even become overabundant (Carpio et al. 2020; Valente et al. 2020; Apollonio et al. 2010). The reasons for this include socio-demographic changes, habitat re-naturalisation with increased grazing availability for ungulates, restricted hunting laws, supplementary feeding, global warming, the declining number of hunters and the earlier reduction of natural predators such as wolf and lynx (Carpio et al. 2020; Valente et al. 2020; Melis et al. 2006). Naturally, there are positive effects for the ecosystem and society (Valente et al. 2020), although the high numbers of ungulates can also lead to a loss of plant diversity, decline in the population of other species, spread of diseases, increased number of wild ungulate-vehicle collisions and damage to agriculture and forestry, for example (Carpio et al. 2020; Valente et al. 2020; Warren 2011; Mysterud 2004).

For the efficient management of ungulate populations in Europe, it is necessary to understand the numbers and spatial variation in the ungulate density (Buckland et al. 2015; Wäber and Dolman 2015). Therefore, several sampling methods have been developed and tested in the past (Buckland et al. 2015). Many researchers have been studying the distribution and abundance of animals and their interaction with the environment (Buckland et al. 2001). Moreover, one of the most frequently asked questions in applied ecology is about the size (N) of a population and hence the population density (D) or even the rate of population change (Buckland et al. 2015). These parameters are dependent on time, space, species, sex and age (Buckland et al. 2001). The density and population size relationship is expressed by the parameter size (A), number per unit area (D) and the size of the population (N). The size of the study area (A) multiplied by the number per unit area reveals the size of the population (N) (Buckland et al. 2001).

Distance sampling (DS) can be a very effective approach to estimate the parameters D and N and therewith estimating the density or abundance of biological populations (Buckland et al. 2001). Borchers et al. (2002) describes distance sampling as a method that comprises several related methods involving the measurement or estimation of the distance to the detected animal from the line or point where the observer is positioned. DS has been widely used to determine ungulate populations (Focardi et al. 2013; Hemami et al. 2007; Focardi et al. 2005; Buckland et al. 2001; Focardi et al. 2001). Roe deer – the most common ungulate in Europe – have been successfully monitored with the distance sampling method under the application of thermal imagers (La Morgia et al. 2015; Wäber and Dolman 2015; Focardi et al. 2005; Smart et al. 2004; Ward et al. 2004). At night, the activity pattern of ungulates is higher, leading to a higher detectability during night than day (Franzetti et al. 2012). The use of thermal imagers for detecting wild ungulates at night is improving detectability (Focardi et al. 2013) and consequently the sample size for a given effort, i.e. the number of detected individuals per driven kilometre (Franzetti et al. 2012). In addition, DS is described as a cost-effective survey method (Franzetti et al. 2012; Smart et al. 2004; Ward et al. 2004; Gill et al. 1997). The method can be differentiated into line and point transect sampling (Buckland et al. 2015; Borchers et al. 2002; Thomas et al. 2002; Buckland et al. 2001). Line transect sampling in combination with thermal imagers is described to be a precise and effective method (Smart et al. 2004; Gill et al. 1997) even in denser habitats, and is more efficient in comparison with spotlight counts (Focardi et al. 2001). In the following, I will concentrate on line transect sampling due to its application in our data acquisition. In line transect sampling, the observer travels along lines searching for animals or animal clusters. The lines should be systematic grids or parallel lines and randomly placed within the study area to ensure uniform distribution of the animals with respect to the distance from the line (Borchers et al. 2002). The observer records the perpendicular distance χ from the line to each detected object or object group. In many cases, it is easier to record the radial distance τ and the angle Θ and then calculate the perpendicular distance by

$$\chi = r \sin(\Theta).$$

The recorded distance χ of the detected object is used to model the detection function $g(\chi)$, which predicts the probability of detecting an animal, given that it is at distance χ from the line (Buckland et al. 2015).

$$f(\chi) = \frac{g(\chi)}{\mu} \quad \text{for } 0 \leq \chi \leq \omega \qquad \text{(Buckland et al. 2015)}$$

μ = effective strip half-width, the half-width of the strip extending to either side of a transect centreline such that as many objects are detected outside the strip remain undetected within it (Buckland et al. 2001)

ω = truncation point

The animal density is then estimated by

$$\hat{D} = \frac{n}{2\,\omega\, L \hat{P}_a} \qquad \text{(Buckland et al. 2001).}$$

$\hat{D}$ = estimated density of objects based on the sample data
n = sample size, number of objects detected
ω = truncation point
L = total line length
$\hat{P}_a$ = probability that a randomly selected object in the survey area α is detected
(Thomas et al. 2002; Buckland et al. 2001).

This applied method assumes that all animals on or close to the transect line are detected by the observer ($g(0) = 1$) and even allows a proportion of objects in the distance ω of the line to be missed (Buckland et al. 2001). In addition, it is necessary that all detections are independent and that the detection probability decreases with increasing distance from the transect line (Buckland et al. 2015; Buckland et al. 2001). In many cases, line transect studies are conducted along roads, tracks or paths (Buckland et al. 2001), which are not randomly distributed in the study areas. Here, it is crucial to distinguish between density estimations based on evenly/randomly distributed transects and non-randomly distributed road transects, as the later may not be representative of the entire study area (Buckland et al. 2001).

Predator-prey interactions

Predation is defined as any kind of interaction in which energy flows from one organism (the prey) to another (the predator, Begon et al. (2006); Sih et al. (1985)). It can also be described as a special form of consumption by which one organism (predator) consumes another organism (prey) by actively searching for it and killing it (Hohmann, U., personal communication, 2021). Predation is also a “major selective force in the evolution of several morphological and behavioural characteristic of animals” (Lima and Dill 1990). Taylor (2013) describes predation as a behavioural act, an ecological process, or even a combination of both. The interaction between a predator and its prey inevitably leads to the removal of the prey individual (lethal effect), which can then have an impact on the prey population dynamics, the entire ecosystem and biodiversity (Creel and Christianson 2008; Ripple and Beschta 2004; Lima 1998). The interaction works across trophic levels, which can be controlled on a bottom-up or top-down basis (Miller et al. 2001). Based on the example of top-down-regulated interactions, the plant biomass is being reduced by herbivores, whereas they are held in check by carnivores (Begon et al. 2006).

Predators are not only affecting their prey by killing it (Creel and Christianson 2008; Lima 1998). Moreover, predation also triggers behavioural responses among prey, which elicit anti-predator strategies (Creel and Christianson 2008; Miller et al. 2001; Lima 1998). Anti-predator strategies can include changes in morphology or behaviour (Creel et al. 2007). Vertebrates mostly alter their behaviour as a result of predation risk (Creel et al. 2007; Lima 1998) to make it more difficult to be captured, detected or encountered by the predator (Lima 1998).

Predation risk is defined as the probability of being killed during some time unit (Lima and Dill 1990) and it is described with the following basic components:

$$P_{(death)} = 1 - \exp(-\,\alpha\, d\, T) \qquad \text{(Lima and Dill 1990)}$$

α = rate of encounter between predator and prey

d = probability of death given an encounter

T = time spent vulnerable to encounter (or attack)

Schmitz et al. (1997) indicated that the effects of predators on the behaviour of prey might be more important than the direct mortality in shaping patterns of herbivory. The authors postulate that predation risk can cause – for instance – reduced foraging time, followed by increased starvation risk and hence reduced impact on the lower trophic level, namely the plant ecosystem (Schmitz et al. 1997). To reduce predation risk, prey may alter their habitat preferences (avoiding risky habitats), group size, vigilance, time of activity and foraging patterns (Miller et al. 2001; Lima and Bednekoff 1999; Lima and Dill 1990).

For example, urine as olfactory cue of lynx causes a shift in the vigilance level in roe deer, even after a long absence of this predator within the ecosystem (Eccard et al. 2015). The results of Eccard et al. (2015) support the 'risk allocation hypothesis', according to which the prey increases anti-predator behaviour and at the same time reduces foraging behaviour during high pulses of predator presence, whereas with continuous pulses anti-predator behaviour decreases despite the risk (Eccard et al. 2015). On the other hand, Wikenros et al. (2015) found no difference in the vigilance level of roe and red deer when exposed to lynx scent (fresh scats), but they found a change in visitation duration at scat sites. Perhaps roe deer perceived lynx urine as an acute threat (Eccard et al. 2015), whereas fresh scats rather cause a change of foraging time at this site (Wikenros et al. 2015). Prey that reduce their exposure to predation risk due to the presence of a predator are described as being under the effect of 'ecology of fear' (Brown et al. 1999). Laundré et al. (2010) investigated an additional aspect of the fear in ecology, namely the landscape use of prey. They propose that the "spatial and temporal use of landscape is fear driven" (Laundré et al. 2010; Laundré et al. 2001) and they call the concept the 'landscape of fear' (Laundré et al. 2010). This concept aims to explain how animals that are trying to reduce predation risk use the landscape under the influence of fear (Laundré et al. 2010). The 'landscape of fear' theory caused by lynx predation has not been supported by current lynx studies (Eccard et al. 2015; Samelius et al. 2013). There is no evidence that roe deer avoid habitats with higher predation risk by lynx, and hence the recolonisation of lynx had limited impact on habitat selection by roe deer (Samelius et al. 2013). These findings are contrary to those found in Yellowstone National Park (North America), where elk responded in shifting habitat selection when wolf were reintroduced (Laundré et al. 2001). Samelius et al. (2013) suggest that the response of the prey to predation risk depends on ecosystems and the predator-prey constellation.

A large proportion of research studies in Europe have dealt with the interaction of lynx and their main prey in relation to population dynamics, kill rates and the impact of humans on the predator-prey system (Andrén and Liberg 2015; Heurich et al. 2012; Molinari-Jobin et al. 2002; Okarma et al. 1997). In Sweden, lynx were found to influence roe deer population dynamics along with density-dependent factors (Andrén and Liberg 2015). After lynx recolonization, the annual roe deer growth rate decreased, which was also related to roe deer density, from which Andrén and Liberg (2015) concluded that lynx predation was additive to other roe deer mortalities. Moreover, Melis et al. (2009) concludes that lynx predation seems to have a negative impact on the prey population. Lynx in the Swiss Jura killed around 9% of the roe deer spring population (Molinari-Jobin et al. 2002), whereas in Poland lynx reduced 21–36% of the spring numbers (Okarma et al. 1997). Similarly high impacts were measured in the north-western Alps in the mid-1990s, where lynx took 36–39% of the local roe deer population (Breitenmoser et al. 2010). Even temporary local extinctions of the prey within an area due to lynx predation have been documented (Swiss Turtmanntal, Haller (1992)). In the Bavarian Forest National Park, the survival of roe deer decreased due to a combination of severe winters and lynx predation (Heurich et al. 2012). In addition, Heurich et al. (2012) concluded that due to a low roe deer population density (1–5 roe deer / km²), the influence of the stalk-and-ambush predator on the prey population was very high. These results are in line with those of Jędrzejewska and Jędrzejewski (2005), finding a strong limitation of ungulate densities by predation in less productive environments. The importance of environmental productivity was clearly highlighted by Melis et al. (2009), who emphasized that it plays a crucial role in assessing the effect of the predator on its prey.

In general, lynx consume roughly one ungulate per week, adding up to around 55 ungulates per year (66 in presence of cubs, Breitenmoser and Haller (1987)). Within this thesis, predation rate is defined as the proportion of the prey population killed by predation per unit time (Gehr 2016; Andrén and Liberg 2015). Consumption rates of lynx vary depending on lynx sex, ranging from 3.8 kg for males and 3.1 kg for solitary females (Breitenmoser et al. 2010). In the Bohemian Forest, the main prey of lynx are roe deer, followed by red deer, hare (*Lepus europeus*), wild boar (*Sus scrofa*) and fox (*Vulpes vulpes*) (Mayer et al. 2012). Lynx preyed upon red deer more often in winter months than in summer, especially calves and adult females (Mayer et al. 2012). Kill series reveal that lynx on average spend 4–5 nights consuming an adult roe deer (Breitenmoser et al. 2010). Not only predation rates and the diet of lynx have been in the focus of the researchers in the last decade, but also the determination of foraging sites of lynx.

To date, foraging sites – hereafter called kill sites – have been investigated in the Bohemian Forest (Belotti et al. 2013), the Bialowieza Primeval Forest (Poland, Podgórski et al. (2008)), the Harz Mountains (Frauendorf 2012) and the Dinaric Mountains in Slovenia (Krofel et al. 2007). Habitat complexity, visibility (good stalking cover and good visibility) and rugged terrain seem to play a crucial role for a successful lynx hunt (Belotti et al. 2013; Podgórski et al. 2008; Krofel et al. 2007). The distribution of kill sites is independent of human infrastructure (public roads) and even positioned closer to tourist trails than random locations (Belotti et al. 2012). Sunde et al. (1998) concluded that lynx avoid the presence of humans but not the alteration of the habitat (roads, trails, houses). Thus, lynx use areas of high prey availability during the night when human activity is low, allowing these large carnivores to persist in human-dominated landscapes (Gehr et al. 2017).

Habitat selection of lynx

Habitat selection is an adaptive behaviour, where the organisms choose specific habitat attributes and food resources to maximise their fitness (Morris 2013; Thomas and Taylor 2006). To facilitate the return of lynx in Europe – an area where large parts of the landscape are human-dominated and disturbed – it is essential to understand the habitat requirements of the species (Niedziałkowska et al. 2006; Schadt, Revilla, et al. 2002). The co-existence of large carnivores and humans depends on successful management and conservation plans. Viable populations need to be established while the conflicts are kept to a minimum (Schadt, Revilla, et al. 2002). This requires knowledge about the species, its habitat preferences, dispersal habitat and tolerance towards human disturbance (Magg et al. 2015; Schadt, Revilla, et al. 2002). Habitat selection of lynx has been investigated under different setups and scales, and in different regions (Gehr et al. 2017; Bouyer, Gervasi, et al. 2015; Basille et al. 2013; Basille et al. 2009; Breitenmoser-Würsten et al. 2007; Breitenmoser et al. 2001).

Lynx appear to tolerate high levels of human disturbance and activity, provided that there is high forest density, high prey availability or good hiding cover (Gehr et al. 2017; Bouyer, Gervasi, et al. 2015; Sunde et al. 1998). Lynx face a trade-off between prey availability and the avoidance of human disturbance, and they respond by using either areas with high prey availability at times where human activity is low (Gehr et al. 2017) or by minimising the exposure to the most disturbed areas (Bouyer, Gervasi, et al. 2015). As a consequence the habitat selection of lynx differs between day and night time (Filla et al. 2017).

High prey availability is usually associated with fragmented landscapes that include open forest canopy structures, forest edges, agricultural fields, and numerous small patches of grassland (Filla et al. 2017; Torres et al. 2012; Basille et al. 2009). This could be the reason why lynx select a high proportion of fields and forests within their home ranges (Basille et al. 2013). On the other hand, the habitat selection analysis of lynx in the Vosges revealed the avoidance of agricultural areas and highways (Basille et al. 2008). Additionally, lynx in Norway avoid high road density within their home ranges, which poses an increased mortality risk from humans due to legal hunting (Basille et al. 2013; Bunnefeld et al. 2006). The parameters of altitude (elevation) and slope play a decisive role in the habitat selection of lynx (Bouyer, San Martin, et al. 2015; Basille et al. 2008; Krofel et al. 2007). Lynx in general prefer areas with high values of elevation, slope and rocks (Signer et al. 2019; Basille et al. 2008).

Overall, the research on lynx habitat selection provides us with an insight into the habitats that lynx require to establish their home ranges. For the re-establishment of the lynx in Europe, further in-depth studies are needed to decide which habitats and what home range sizes are suitable for this large predator.

Objectives and methodology

The aim of this thesis was to document the re-establishment of lynx by investigating the spatial habitat use of lynx and the effect on their main prey in a forest-dominated low mountain range in Germany.

The specific objectives of this study were to:

(1) investigate the roe deer population trend in the Palatinate Forest during the re-establishment of lynx;

(2) investigate the habitat structure of roe deer kill sites caused by the newly reintroduced lynx in the Palatinate Forest;

(3) investigate the habitat selection of newly reintroduced lynx in relation to anthropogenic structures in the Palatinate Forest between 2016 and 2019.

Lynx telemetry data used in this study were provided by the Foundation of Nature and Environment (SNU-RLP 2020) and collected in connection with the reintroduction program in the Palatinate Forest, where 20 lynx (12 females, 8 males) were fitted with GPS radio collars and released between 2016 and 2020 (SNU-RLP 2020).

Since 2016, we have been collecting count data of deer throughout the Palatinate Forest with thermal imaging cameras for population estimation calculations (**Fig. 2**). The data collected were then used to estimate the roe deer population in the entire Palatinate Forest prior to lynx reintroduction and during the establishment of lynx population in this area. Overall, we observed 4,671 roe deer during 120 nights on a 6,000 kilometre total transect line from 2016 to 2019.

We observed 123 kill sites from the GPS collared lynx within the study area over the period from 7th August 2016 to 27th August 2019 (SNU-RLP 2020). The kill sites were examined for their microhabitat structure and their location to human-dominated habitat features. GPS data of 14 lynx individuals over the period from 11th August 2016 to 31st December 2019 contained 18,038 locations for habitat selection analyses.

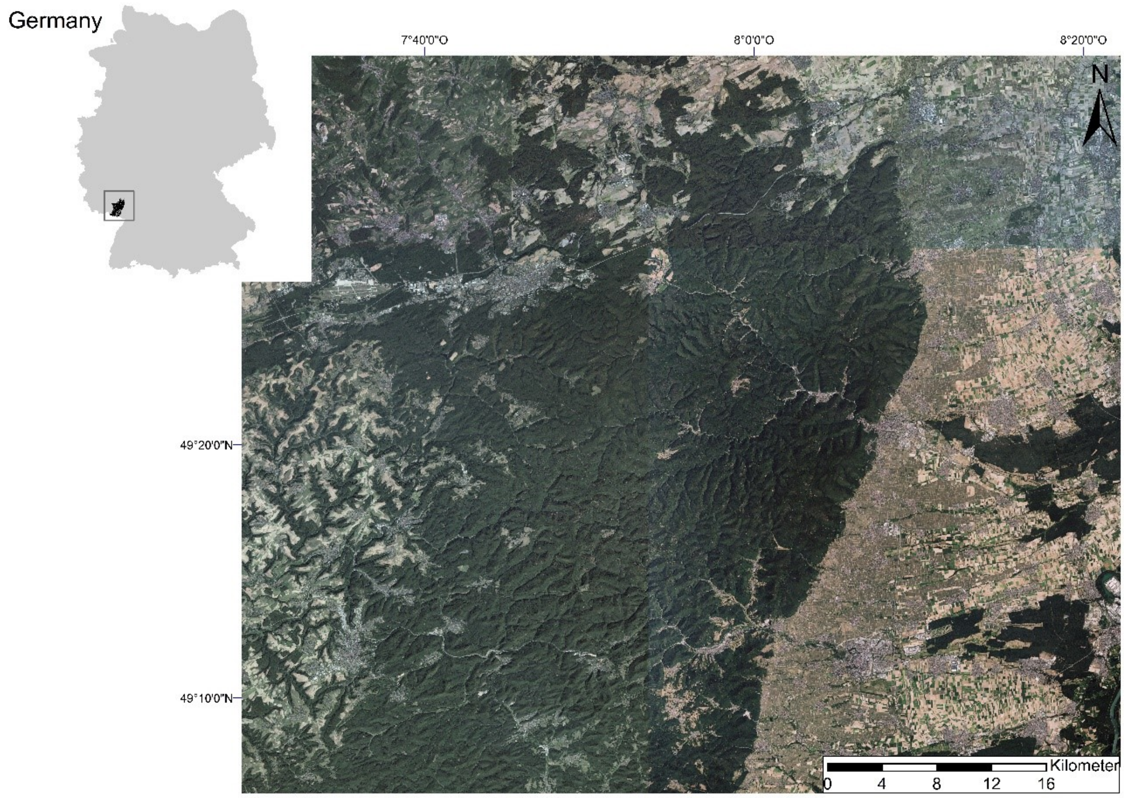

Fig. 2 Map of the study area, the Palatinate Forest, which is positioned in the southwestern part of Germany. The study area borders on to the Vosges du Nord in France.

References

Andrén H, Liberg O (2015) Large impact of Eurasian lynx predation on roe deer population dynamics. PloS One 10:e0120570

Andrén H, Linnell JD, Liberg O, Andersen R, Danell A, Karlsson J, Odden J, Moa PF, Ahlqvist P, Kvam T (2006) Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23-32

Apollonio M, Andersen R, Putman R (2010) European ungulates and their management in the 21st century. Cambridge University Press

Basille M, Calenge C, Marboutin É, Andersen R, Gaillard J-M (2008) Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. Ecol Modelling 211:233-240

Basille M, Herfindal I, Santin-Janin H, Linnell JD, Odden J, Andersen R, Arild Høgda K, Gaillard J-M (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography 32:683-691

Basille M, Van Moorter B, Herfindal I, Martin J, Linnell JD, Odden J, Andersen R, Gaillard J-M (2013) Selecting habitat to survive: the impact of road density on survival in a large carnivore. PloS one 8:e65493

Begon M, Harper J, Townsend C (2006) Ecology: from Individuals to Ecosystems. p 471–472 Blackwell. United Kingdom, Oxford

Belotti E, Červený J, Šustr P, Kreisinger J, Gaibani G, Bufka L (2013) Foraging sites of Eurasian lynx *Lynx lynx*: relative importance of microhabitat and prey occurrence. Wildlife Biol 19:188-201

Belotti E, Heurich M, Kreisinger J, Sustr P, Bufka L (2012) Influence of tourism and traffic on the Eurasian lynx hunting activity and daily movements. Animal Biodiversity Conservation 35:235-246

Borchers DL, Buckland ST, Zucchini W (2002) Estimating animal abundance: closed populations. Vol. 13. Springer Science & Business Media

Bouyer Y, Gervasi V, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. Animal Conservation 18:271-278

Bouyer Y, San Martin G, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. Biological Conservation 191:291-299

Breitenmoser-Würsten C, Zimmermann F, Molinari-Jobin A, Molinari P, Capt S, Vandel J-M, Stahl P, Breitenmoser U (2007) Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. Wildlife Biology 13:365-380

Breitenmoser C, Zimmermann F, Ryser A, Capt S, Laass J, Siegenthaler A, Breitenmoser U (2001) Untersuchungen zur Luchspopulation in den Nordwestalpen der Schweiz 1997 - 2000. KORA-Bericht, Nr. 9, Muri in Bern, 1-88

Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs. Salm Verlag, Wohlen/Bern, Switzerland: 1-537

Breitenmoser U, Breitenmoser-Würsten C, Capt S (1998) Re-introduction and present status of the lynx (*Lynx lynx*) in Switzerland. Hystrix - the Italian Journal of Mammalogy 10(1), 17– 30

Breitenmoser U, Breitenmoser-Würsten C, Okarma H, Kaphegyi T, Kaphegyi U, Wallmann U, Müller M (2000) Action plan for the conservation of the Eurasian lynx in Europe. Council of Europe, Nature and Environment, 112: 1-69

Breitenmoser U, Haller A (1987) Zur Nahrungsökologie des Luchses *Lynx lynx* in den schweizerischen Nordalpen. Zeitschrift für Säugetierkunde 52:168-191

Breitenmoser U, Haller H (1993) Patterns of predation by reintroduced European lynx in the Swiss Alps. Journal of Wildlife Management 57:135-144

Breitenmoser U, Ryser A, Molinari-Jobin A, Zimmermann F, Haller H, Molinari P, Breitenmoser-Würsten C (2010) The changing impact of predation as a source of conflict between hunters and reintroduced lynx in Switzerland. In: Macdonald, D.W.& Loveridge, A.J. (Eds.), Biology and Conservation of Wild Felids (pp. 493-506). Oxford: Oxford University Press.

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling. Estimating Abundance of Biological Populations. Oxford University Press, Oxford

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS (2015) Distance sampling: Methods and Applications. Vol. 431. New York, NY, USA: Springer

Bunnefeld N, Linnell JDC, Odden J, Van Duijn MaJ, Andersen R (2006) Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: Effects of sex and reproductive status. Journal of Zoology 270:31-39

Carpio AJ, Apollonio M, Acevedo P (2020) Wild ungulate overabundance in Europe: Contexts, causes, monitoring and management recommendations. Mammal Review 51:95-108

Červený J, Koubek P, Bufka L (2002) Eurasian lynx (*Lynx lynx*) and its chance for survival in central Europe: the case of the Czech Republic. Acta Zoologica Lituanica 12:428-432

Creel S, Christianson D (2008) Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194-201

Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. Science 315:960-960

Eccard JA, Meißner JK, Heurich M (2015) European roe deer increase vigilance when faced with immediate predation risk by Eurasian lynx. Ethology 123(1):30-40

Filla M, Premier J, Magg N, Dupke C, Khorozyan I, Waltert M, Bufka L, Heurich M (2017) Habitat selection by Eurasian lynx *(Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. Ecology and Evolution 7:6367-6381

Focardi S, De Marinis AM, Rizzotto M, Pucci A (2001) Comparative evaluation of thermal infrared imaging and spotlighting to survey wildlife. Wildlife Society Bulletin:133-139

Focardi S, Franzetti B, Ronchi F (2013) Nocturnal distance sampling of a Mediterranean population of fallow deer is consistent with population projections. Wildlife Research 40:437-446

Focardi S, Montanaro P, Isotti R, Ronchi F, Scacco M, Calmanti R (2005) Distance sampling effectively monitored a declining population of Italian roe deer *Capreolus capreolus italicus*. Oryx 39:421-428

Franzetti B, Ronchi F, Marini F, Scacco M, Calmanti R, Calabrese A, Paola A, Paolo M, Focardi S (2012) Nocturnal line transect sampling of wild boar (*Sus scrofa*) in a Mediterranean forest: long-term comparison with capture–mark–resight population estimates. European Journal of Wildlife Research 58:385-402

Frauendorf M (2012) Pilot Study on the microhabitat selection of the Eurasian lynx (*Lynx lynx*) concerning hunting sites in the Harz National Park, Germany. M.Sc. thesis. Van Hall Larenstein University, Sankt Andreasberg

Gehr B (2016) Predator-prey Interactions in a Human-dominated Landscape. Doctoral dissertation. University of Zurich, Switzerland

Gehr B, Hofer EJ, Muff S, Ryser A, Vimercati E, Vogt K, Keller LF (2017) A landscape of coexistence for a large predator in a human dominated landscape. Oikos 126:1389-1399

Gervasi V, Linnell J, Berce T, Boitani L, Cretois B, Ciucci P, Duchamp C, Gastineau A, Grente O, Hilfiker D (2020) Ecological and anthropogenic drivers of large carnivore depredation on sheep in Europe. bioRxiv doi:10.1101/2020.04.14.041160

Gill R, Thomas M, Stocker D (1997) The use of portable thermal imaging for estimating deer population density in forest habitats. Journal of Applied Ecology 34:1273-1286

Haller H (1992) Zur Ökologie des Luchses *Lynx lynx* im Verlauf seiner Wiederansiedlung in den Walliser Alpen.Mammalia depicta. Paul Parey, Hamburg, Berlin.

Hemami MR, Watkinson AR, Gill RMA, Dolman PM (2007) Estimating abundance of introduced Chinese muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* using portable thermal imaging equipment. Mammal Review 37:246-254

Herfindal I, Linnell JD, Odden J, Nilsen EB, Andersen R (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). Journal of Zoology 265:63-71

Heurich M, Hilger A, Küchenhoff H, Andrén H, Bufka L, Krofel M, Mattisson J, Odden J, Persson J, Rauset GR (2014) Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. PloS one 9:e114143

Heurich M, Möst L, Schauberger G, Reulen H, Sustr P, Hothorn T (2012) Survival and causes of death of European roe deer before and after Eurasian lynx reintroduction in the Bavarian Forest National Park. European Journal of Wildlife Research 58:567-578

Heurich M, Schultze-Naumburg J, Piacenza N, Magg N, Červený J, Engleder T, Herdtfelder M, Sladova M, Kramer-Schadt S (2018) Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. Biological Conservation 224:355-365

Hočevar L, Fležar U, Krofel M (2020) Overview of good practices in Eurasian lynx monitoring and conservation. INTERREG CE 3Lynx report. University of Ljubljana. Biotechnical Faculty, Ljubljana

Jędrzejewska B, Jędrzejewski W (2005) Large carnivores and ungulates in European temperate forest ecosystems: bottom-up and top-down control. In: Ray JC, Redford KH, Steneck RS, Berger J (Eds) Large carnivores and the conservation of biodiversity. Island Press (pp. 230-246),Washington DC.

Jędrzejewski W, Schmidt K, Miłkowski L, Jędrzejewska B, Okarma H (1993) Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. Acta Theriologica 38:385-403

Jobin A, Molinari P, Breitenmoser U (2000) Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. Acta Theriologica 45:243-252

Kaczensky P, Chapron G, von Arx M, Huber D, Andrén H, Linnell J (2013) Status, Management and Distribution of Large Carnivores – Bear, Lynx, Wolf and Wolverine in Europe. Part 1 IUCN/SSC Large Carnivore Initiative for Europe

Kramer-Schadt S, Revilla E, Wiegand T (2005) Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biol Conserv 125:169-182

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. Journal of Applied Ecology 41:711-723

Krofel M, Potočnik H, Kos I (2007) Topographical and vegetational characteristics of lynx kill sites in Slovenian Dinaric Mountains. Natura Sloveniae 9:25-36

Kvam T (1991) Reproduction in the European lynx, *Lynx lynx.* Zeitschrift für Säugetierkunde 56:146-158

La Morgia V, Calmanti R, Calabrese A, Focardi S (2015) Cost-effective nocturnal distance sampling for landscape monitoring of ungulate populations. European Journal of Wildlife Research 61:285-298

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401-1409

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1-7

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48:25-34

Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist 153:649-659

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640

Linnell JD, Breitenmoser U, Breitenmoser-Würsten C, Odden J, von Arx M (2009) Recovery of Eurasian lynx in Europe: what part has reintroduction played? . In: M. W. Hayward & M. J. Somers (Eds.), Reintroduction of top-order predators (pp. 72-91).Oxford:Wiley-Blackwell.

Linnell JD, Promberger C, Boitani L, Swenson JE, Breitenmoser U, Andersen R (2005) The linkage between conservation strategies for large carnivores and biodiversity: the view from the "half-full" forests of Europe. In: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.). Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, DC

Lüchtrath A, Schraml U (2015) The missing lynx - understanding hunters' opposition to large carnivores. Wildlife Biology 21:110-119

Magg N, Müller J, Heibl C, Hackländer K, Wölfl S, Wölfl M, Bufka L, Červený J, Heurich M (2015) Habitat availability is not limiting the distribution of the Bohemian–Bavarian lynx *Lynx lynx* population. Oryx 50(4):742-752

Mayer K, Belotti E, Bufka L, Heurich M (2012) Dietary patterns of the Eurasian lynx (*Lynx lynx*) in the Bohemian Forest. Säugertierkundliche Informationen 45:447–453.

Melis C, Jędrzejewska B, Apollonio M, Bartoń KA, Jędrzejewski W, Linnell JD, Kojola I, Kusak J, Adamic M, Ciuti S (2009) Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global Ecology and Biogeography 18:724-734

Melis C, Szafrańska PA, Jędrzejewska B, Bartoń K (2006) Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. Journal of Biogeography 33:803-811

Miller B, Dugelby B, Foreman D, del Rio CM, Noss R, Phillips M, Reading R, Soule ME, ETerborgh J, Willcox L (2001) The importance of large carnivores to healthy ecosystems. Endangered Species Update 18:202-210

Molinari-Jobin A, Molinari P, Breitenmoser-Würsten C, Breitenmoser U (2002) Significance of lynx *Lynx lynx* predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. Wildlife Biology 8:109-115

Molinari-Jobin A, Zimmermann F, Ryser A, Breitenmoser-Würsten C, Capt S, Breitenmoser U, Molinari P, Haller H, Eyholzer R (2007) Variation in diet, prey selectivity and home-range size of Eurasian lynx *Lynx lynx* in Switzerland. Wildlife Biology 13:393-405

Morris D (2013) Habitat Selection. Oxford Bibliographies in Ecology, New York: Oxford University Press

Mueller SA, Reiners TE, Middelhoff TL, Anders O, Kasperkiewicz A, Nowak C (2020) The rise of a large carnivore population in Central Europe: genetic evaluation of lynx reintroduction in the Harz Mountains. Conservation Genetics 21:577-587

Mysterud A (2004) Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. Wildlife Biology 10:203-211

Niedziałkowska M, Jędrzejewski W, Mysłajek RW, Nowak S, Jędrzejewska B, Schmidt K (2006) Environmental correlates of Eurasian lynx occurrence in Poland – Large scale census and GIS mapping. Biological Conservation 133:63-69

Nilsen EB, Linnell JD, Odden J, Andersen R (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. Journal of Animal Ecology 78:741-751

Odden J, Linnell JDC, Andersen R (2006) Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. European Journal of Wildlife Research 52:237-244

Okarma H, Jedrzejewski W, Schmidt K, Kowalczyk R, Jedrzejewska B (1997) Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeral Forest, Poland. Acta Theriologica 42:203-224

Pedersen VA, Linnell JD, Andersen R, Andrén H, Lindén M, Segerström P (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. Wildlife Biology 5:203-211

Podgórski T, Schmidt K, Kowalczyk R, Gulczyńska A (2008) Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica 53:97-110

Podolski I, Belotti E, Bufka L, Reulen H, Heurich M (2013) Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx lynx* in relation to availability of kills. Wildlife Biology 19:69-77

Port M (2020) Systematisches Fotofallenmonitoring des Luchses im Pfälzerwald. FAWF Mitteilungen. Institute for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Trippstadt

Port M (2021) Systematisches Fotofallenmonitoring des Luchses im Pfälzerwald 2019/20 und 2020/21, unpublished report. Institute for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Trippstadt

Port M, Henkelmann A, Schröder F, Waltert M, Middelhoff L, Anders O, Jokisch S (2020) Rise and fall of a Eurasian lynx (*Lynx lynx*) stepping-stone population in central Germany. Mammal Research 66(1):1-11

Rewildingeurope (2021) Return of the missing lynx. rewildingeurope.com. Accessed 02.01. 2021

Ripple WJ, Beschta RL (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766

Samelius G, Andrén H, Kjellander P, Liberg O (2013) Habitat selection and risk of predation: re-colonization by lynx had limited impact on habitat selection by roe deer. PLoS ONE 8:1-8

Schadt S, Revilla E, Wiegand T, Knauer F, Kaczensky P, Breitenmoser U, Bufka L, Červený J, Koubek P, Huber T (2002) Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecology 39:189-203

Schmitz OJ, Beckerman AP, O'Brien KM (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388-1399

Signer J, Filla M, Schoneberg S, Kneib T, Bufka L, Belotti E, Heurich M (2019) Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. Wildlife Biology 2019 (1):1-5

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269-311

Smart JC, Ward AI, White PC (2004) Monitoring woodland deer populations in the UK: an imprecise science. Mammal Review 34:99-114

SNU-RLP (2018) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed Januar 18, 2018

SNU-RLP (2020) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed 15.11.2020

Sommer R, Benecke N (2006) Late Pleistocene and Holocene development of the felid fauna (Felidae) of Europe: a review. Journal of Zoology 269:7-19

Sunde P, Stener SØ, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. Wildlife Biol 4:177-183

Taylor RJ (2013) Predation. Springer Science & Business Media, New York NY, USA

Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324-336

Thomas L, Buckland S, Burnham K, Anderson D, Laake J, Borchers D, Strindberg S (2002) Distance sampling. In: ElShaarawi, A.H. and Piegorschs, W.W. (Eds). Encyclopedia of Environmetrics. pp. 544–552. John Wiley & Sons: Chichester, UK

Torres RT, Virgós E, Panzacchi M, Linnell JD, Fonseca C (2012) Life at the edge: Roe deer occurrence at the opposite ends of their geographical distribution, Norway and Portugal. Mammalian Biology 77:140-146

Valente AM, Acevedo P, Figueiredo AM, Fonseca C, Torres RT (2020) Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. Mammal Review 50:353-366

von Arx M, Breitenmoser-Würsten C, Zimmermann F, Breitenmoser U (2004) Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. KORA-Bericht, Nr. 19. Muri in Bern, 1-319

von Arx M, Breitenmoser U (2004) Reintroduced lynx in Europe: their distribution and problems. ECOS: A Review of Conservation 25(3/4):64-68

Wäber K, Dolman PM (2015) Deer abundance estimation at landscape-scales in heterogeneous forests. Basic and Applied Ecology 16:610-620

Ward AI, White PC, Critchley CH (2004) Roe deer *Capreolus capreolus* behaviour affects density estimates from distance sampling surveys. Mammal Review 34:315-319

Warren R (2011) Deer overabundance in the USA: recent advances in population control. Animal Production Science 51:259-266

Wikenros C, Kuijper DP, Behnke R, Schmidt K (2015) Behavioural responses of ungulates to indirect cues of an ambush predator. Behaviour 152:1019-1040

Outline of the thesis

The work presented here focuses on the establishment of a recently-introduced predator, the Eurasian lynx (*Lynx lynx*) and the interaction with its main prey, the European roe deer (*Capreolus capreolus*) in the Palatinate Forest, an ecosystem where prey did not experience a natural predator for a longer time. The thesis is structured into three manuscripts. In these three manuscripts, I explore the roe deer population trend after the reintroduction of lynx, the successful hunting sites, and the general habitat selection of lynx within the study area.

Manuscript I:
Carolin Tröger, Diress Tsegaye, Ulf Hohmann (in Press), Roe deer population trend after reintroduction of Eurasian lynx within the Palatinate Forest: a first insight into a long-term study, European Journal of Ecology

In the first manuscript, I examine how the roe deer population trend in the Palatinate Forest developed under the newly established presence of a large carnivore. In particular, I started to monitor the roe deer population prior to lynx reintroduction and under the presence of lynx. Roe deer hunting bag and lynx spatial habitat use were linked to investigate possible (short-term) effects of this new predator on its prey population in the first years after reintroduction.

Manuscript II:
Carolin Tröger, Diress Tsegaye, Johannes Signer, Ulf Hohmann, unpublished, Microhabitat influences the kill sites of recently-introduced lynx within the Palatinate Forest in Germany

In the manuscript 2, I was interested in exploring lethal effects, and more specifically the habitat in which the direct interaction between the predator and prey occurs. The investigation of microhabitats at kill sites should reveal habitats in which lynx successfully hunts roe deer and where roe deer experience increased mortality risk. To answer this research question, clusters of lynx GPS locations were used to locate potential kill sites. Confirmed kill sites were then related to the habitat structure at different scales and compared with random and lynx GPS locations.

Manuscript III:

Carolin Tröger, Diress Tsegaye, Sylvia Idelberger, Ulf Hohmann, unpublished, The effect of anthropogenic structures on habitat selection of newly reintroduced Eurasian lynx (*Lynx lynx*) in the Palatinate Forest, Southwest Germany

In the manuscript 3, I investigate the habitat selection of the newly reintroduced lynx in the Palatinate Forest regarding anthropogenic structures. The lynx GPS data was related to different temporal settings, as well as being compared with the habitat offer at the same scales. Habitat selection analysis of newly introduced lynx considered habitat parameters such as distance from human settlements, infrastructure, and grazing areas.

Manuscript I

Roe deer population trend after reintroduction of Eurasian lynx within the Palatinate Forest: a first insight into a long-term study

Carolin Tröger, Diress Tsegave, Ulf Hohmann

Status of Manuscript: Published in European Journal of Ecology

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Manuscript II

Microhabitat influences the kill sites of recently-introduced lynx in the Palatinate Forest in Germany

Carolin Tröger, Diress Tsegave, Johannes Signer, Ulf Hohmann

Status of Manuscript: unpublished

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Microhabitat influences the kill sites of recently-introduced lynx within the Palatinate Forest in Germany

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Abstract

Kill sites are often used to understand the interaction between predator and prey considering habitat structures. The aim of this study was to analyse the microhabitat of roe deer (*Capreolus capreolus*) kill sites caused by Eurasian lynx (*Lynx lynx*), which have been reintroduced since 2016 within the Palatinate Forest in the southwestern part of Germany. We identified 123 roe deer kill sites caused by thirteen radio-tracked lynx (6 female, 7 male) over a total period of four years (2016–2019).

We tested seasonal differences of microhabitat features at kill sites and their influence on the kill probability of roe deer in the Palatinate Forest. Kill sites were compared with habitat availability, represented by random locations, and with habitat use by considering lynx GPS locations. Random locations were generated within lynx home ranges. We found that 95% of all kill sites were related to ground cover and that summer kill sites displayed a significantly lower percentage of canopy cover than winter kill sites. We detected a higher probability of a roe deer kill in proximity to forestry roads, paved public roads, grassland areas and at low elevations. On the other hand, we found a significantly lower probability of kill closer to human settlements (villages). Comparing the kill sites with lynx habitat use (based on lynx GPS positions), we also found a higher kill probability in proximity to grassland areas and partly to not truck-drivable roads. Our kill site monitoring underlines that the interaction of roe deer and lynx follows a known pattern, indicating that this newly returned predator has quickly adapted to new conditions while occupying unfamiliar surroundings. Nevertheless, further in-depth investigations of kill sites within the Palatinate Forest are recommended to gain a better understanding of the interaction between the predator and its main prey with respect to the long-term consequences for the prey population.

Keywords: Eurasian lynx, *Lynx lynx*, roe deer, predator-prey interaction, microhabitat

Introduction

By the late-1960s, the European lynx (*Lynx lynx*) population had recovered in Europe due to favourable legislation and increasing habitat quality in most European countries (Linnell et al. 2005; Linnell, Andersen, et al. 2001). In addition, reintroduction programmes were initiated in several European countries, including Italy, Switzerland, Slovenia, Austria, Czech Republic, France and Poland (Linnell et al. 2005). In Germany, three reintroductions were conducted, the first in Bavaria in 1970–1975, followed by Harz Forest in 2000 (Kramer-Schadt et al. 2005) and more recently in the Palatinate Forest in 2016 (SNU-RLP 2018). The return of this predator into human-dominated landscape raises the question of how ungulates – particularly roe deer – respond to a predation risk by a predator that has long been absent in its environment (Sand et al. 2006). In particular, it holds interest to distinguish in which habitat the predation risk of the prey increases when large carnivores are present in the area.

As a stalking and ambush predator (Breitenmoser and Breitenmoser-Würsten 2008), lynx habitat selection is driven by prey accessibility and mortality risk (hunting, poaching and traffic collision, Basille et al. (2009)). Many studies have focused on habitat selection by lynx (Signer et al. 2019; Belotti et al. 2018; Filla et al. 2017; Belotti et al. 2012; Rozylowicz et al. 2010; Basille et al. 2009; Herfindal et al. 2005). Filla et al. (2017) suggested that lynx select open habitats at night, linking this to high prey density, whereas during the day lynx select habitats with dense understory cover on rough terrain and with a low risk of human disturbance. On the other hand roe deer are known to favour closed habitats with a higher degree of complexity during the day and a more open habitat with higher grazing quality during twilight and night (Mysterud, Larsen, et al. 1999). Basille et al. (2009) verified that lynx stay in areas with high roe deer abundance and they additionally documented a trade-off between habitats with intermediate roe deer abundance and intermediate human disturbance. Hence, lynx avoid habitats with maximum prey density, which is usually linked to high human density (Basille et al. 2009). By contrast, Belotti et al. (2012) observed that lynx do not avoid roads and tourist trails. Small and less frequented gravel roads are most likely used by carnivores to move quickly and conserve energy (Creel et al. 2002; Sunde et al. 1998). Moreover, it can be presumed that at night paths are rarely used by humans, whereby lynx is able to use them without fearing any disturbance.

Although many studies have explored the habitat use of lynx and roe deer in general, more knowledge about lynx hunting habitat and hunting success is still required to understand the direct interaction between a predator and its prey, especially after the long absence of the large carnivore within an area. Our study focused on gaining a better understanding of the interaction between a recently-reintroduced predator and its main prey by observing kill sites and their microhabitats in the Palatinate Forest. Only a few studies to date have investigated microhabitats by looking at kill sites (Belotti et al. 2013; Frauendorf 2012; Podgórski et al. 2008; Krofel et al. 2007).

Krofel et al. (2007) examined thirteen kill sites in the Slovenian Dinaric Mountains and concluded that lynx do not necessarily need dense vegetation and rugged terrain, but it may influence their hunting success. Successful documented hunts mainly took place in areas with steep slopes and rugged terrain (Krofel et al. 2007). Dolines – a special karst structure in the Dinaric Mountains – might be of great importance for hunting (Krofel et al. 2007). Krofel et al. (2007) assume, that roe deer prefer the downwards escape when fleeing. When reaching the bottom of the doline, the only chance is to run upwards, which slows the roe deer down (Krofel et al. 2007). Here, it is important to remember that lynx are sight-hunting predators that ambush and stalk their prey (Squires et al. 2010), whereas wolf are chasing predators with distances of around 237 m for roe deer and 76 m for moose (Wikenros et al. 2009). On the other hand, lynx will use the 'surprise' moment for the prey and jump with two to three steps to reach the prey (Breitenmoser and Breitenmoser-Würsten 2008).

Podgórski et al. (2008) found that lynx in Białowieża Primeval Forest successfully hunted in habitats of high complexity and low visibility. The number of useful stalking structures like branches, logs, root plates and bushes characterised high complexity within their analyses (Podgórski et al. 2008). They found no selection for any type and/or age class of the forest when observing 116 hunting sites (Podgórski et al. 2008). Additionally, in summer they found more hunting sites in the vicinity (0–50 m) of forest glades than expected from their availability (Podgórski et al. 2008). This could indicate that these habitats represent good stalking cover for lynx and rich foraging grounds for ungulates (Podgórski et al. 2008). Visibility at hunting sites was significantly lower than at random sites but higher at kill sites than caching sites (Podgórski et al. 2008). Furthermore, Belotti et al. (2013) showed that lynx in the Bohemian Forest killed roe deer in winter in habitats with good stalking cover but also good visibility. In addition, they found significant differences between kill locations and those of alive ungulates in winter seasons, suggesting that the positions of kill sites are not only based on the habitat use of ungulates (Belotti et al. 2013).

Using roe deer kill sites based on a GPS dataset of reintroduced lynx in the Palatinate Forest, we tested the following predictions:

1) Lynx successfully hunt roe deer in areas with higher vegetation/ground cover on a fine landscape scale.

2) Lynx successfully hunt roe deer in areas with increased probability of encountering prey, like grasslands areas, meadows, open forests and along travel corridors (roads).

3) Lynx successfully hunt roe deer in areas where there is a low risk of disturbance (e.g. away from human settlements).

4) The season influences the relative importance of the different habitat features of kill sites.

Material and Methods

Study area

The study was conducted in the Palatinate Forest in the southwestern part of Germany, which lies in the temperate zone between the Atlantic and continental climate (49°12'N, 7°45'N). Elevation in the Palatinate Forest ranges from 210 m to 609 m a.s.l.. The Palatinate Forest contains only small settlements and little infrastructure (Hohmann et al. 2018; Simon and Kotremba 2016). Approximately 90% of the area is covered by forest (MUEEF RLP 2012), which mainly comprises of *Fagus sylvatica* and *Pinus sp.*. Dense and steep carved valley systems and various hill formations characterise the Palatinate Forest, a variegated mountain range (MUEEF RLP 2012). Annual precipitation is about 700–800 mm and annual average temperature is 10–11.5 °C (2015–2020, Rheinland-Pfalz Kompetenzzentrum für Klimawandelfolgen (2021)). The Palatinate Forest is one of Germany's largest contiguous forest areas with over 1790 km² and borders in the south on the Vosges du Nord. Since 1998, the Vosges du Nord and the Palatinate Forest have been the first transboundary biosphere reserve in Europe (Naturpark Pfälzerwald 2018), covering about 3018 km². Our study concentrated on the German part of the biosphere reserve, the Palatinate Forest (**Fig. 1**). The primary species of wild ungulates are roe deer, red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*). In the northern part of the forest, mouflon (*Ovis musimon)* occur in small numbers. All ungulates above are hunted within the whole study area, with one exception of a 25 km^2 area in the centre of the forest.

Lynx reintroduction and population

In 2015, an EU-LIFE project – supervised by the Foundation of Nature and Environment (SNU) Rhineland-Palatinate – initiated the reintroduction of lynx within the Palatinate Forest (Idelberger et al. submitted). From 2016 onwards, the first lynx were released in the Palatinate Forest (SNU-RLP 2018). Over the course of five years, a total of 20 lynx were reintroduced, with lynx (*Lynx lynx carpathicus*) originating from Slovakia (Carpathian Mountains) and Switzerland. Reintroduced lynx are either wild catches or orphan lynx that were held for a certain time in captivity. In 2017, the first lynx offspring was documented within the Palatinate Forest. In the first half of 2019, twelve independent (adult and subadult) lynx were verified (at least temporary) within the central Palatinate Forest.

All lynx were released in the central part of the Palatinate Forest. Two large motorway (two to four lanes) splits the forest into a northern, a central and a southern part. GPS collars were fitted on all reintroduced lynx with an approximate battery life of around one to two years. The frequency of GPS measurements was programmed differently depending on the status and requirements of the reintroduction project. One individual received an additional collar prior to the battery expiry date of the original one, resulting in longer GPS datasets. Data of GPS collared lynx provided information about possible prey kill sites, which were verified by research teams (Gaß 2018; SNU-RLP 2018; Schukraft 2017). The dataset is a random, non-systematic sample of kill sites in the period from 7th August 2016 to 27th August 2019 and resulted in 123 roe deer kill sites within the centre of the Palatinate Forest (**Fig. 1**). Kill sites located in the southern and northern part of the Palatinate Forest were considered outliers and removed from the dataset due to different habitat structures in the boundary areas of the Palatinate Forest.

Habitat data / Explanatory variables

We applied two different approaches to the 123 roe deer kill sites found in the Palatinate Forest. **I:** Descriptive habitat features of different diameters are recorded in the field at the kill sites, and hereafter called microhabitat features. We applied these features to the first 75 kill sites within the period from 2016–2018. Data acquisition took place between August 2017 and April 2018. In 2017, we recorded habitat features for the confirmed kill site at this point with a time offset (from kill to habitat recording) of several months and up to a year within the same vegetation season. In 2018, we were able to record habitat features directly after the lynx abandoned the site, around 3–5 days after killing its prey. The exact position of the kill site – especially those registered in the previous years (2016–2017) – was determined by GPS positions, general habitat descriptions and photographs of the kill site and its surrounding. We tried to find the exact position to verify that the habitat structure had remained the same.

II: GIS-based habitat features were applied to all kill sites (n = 123) and additional random points (see paragraph below), hereafter called geographic habitat features.

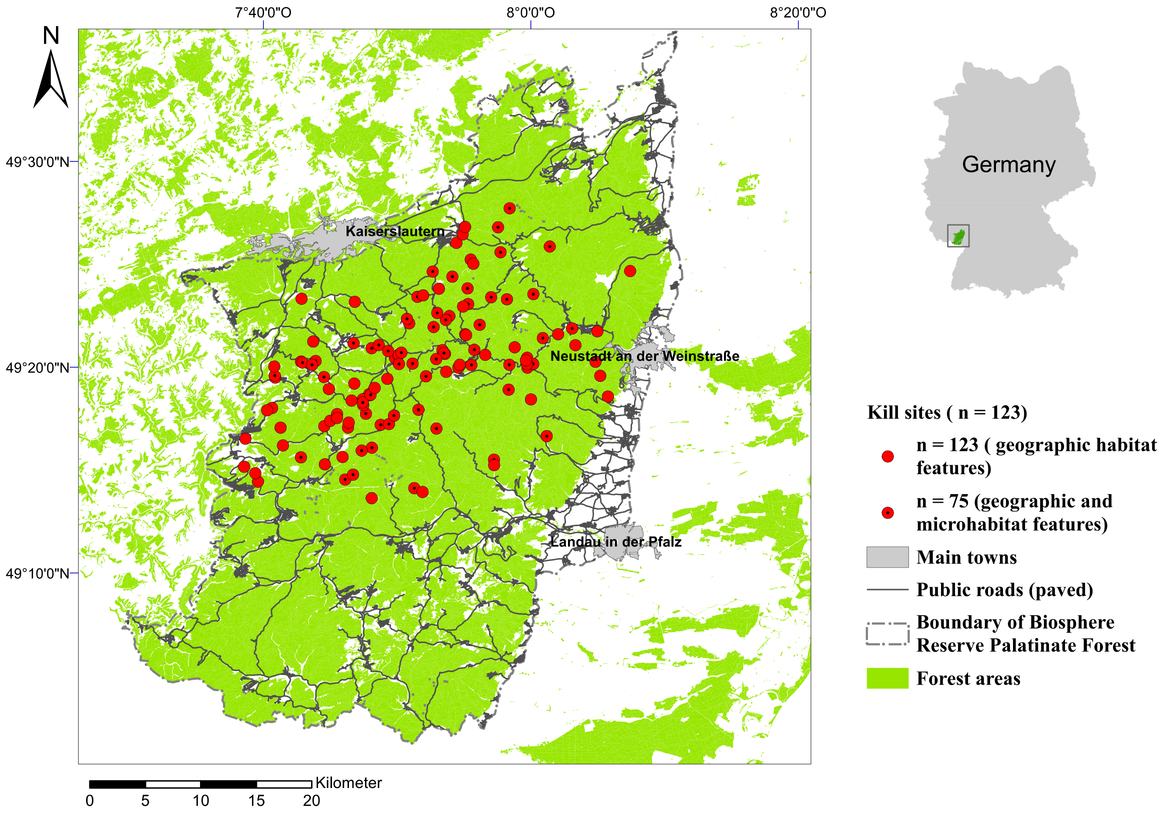

Fig. 1 Distribution of 123 roe deer kill sites caused by thirteen lynx individuals within the Palatinate Forest, Germany. Kill sites were observed between 2016 and 2019. Microhabitat features were observed at only 75 kill sites, whereas geographic habitat features are available for all 123 kill sites.

I: Microhabitat features

We focused on seasonal differences in those microhabitat features around the kill sites that may have influenced predation, i.e. forage quality with respect to deer, habitat concealment with respect to lynx or human infrastructure (traffic-related disturbance). Within a 5 m radius of the kill site, detailed forest characteristics (mature stand, mature stand in generation change, young timber, pole wood, thicket, regeneration, open area or forestry and paved roads) were recorded. Kill sites positioned directly on forestry roads were registered as 'roads' in line with the forest characteristics.

Additionally, we estimated habitat concealment, ground cover and canopy cover within a 20 m radius of the kill site. Canopy cover was classified into four groups (categories: “1” 0–25%, “2” 26–50%, “3” 51–75% and “4” 76–100%). In order to quantify the possibility of a lynx hiding and stalking up on its prey, we applied the ‘pole method’ (Belotti et al. 2013; Pierce et al. 2004). Based on this method, we registered habitat features within a radius of 20 m around the kill sites, representing the mean distance over which lynx might move carcasses from the original kill site (Podgórski et al. 2008; Jędrzejewski et al. 1993).

For the pole method, we used a 2 m-high wooden pole divided into ten different coloured segments, each 20 cm in width. We positioned the pole in the middle of the kill site. At a distance of 20 m in each cardinal direction, the observer kneed at a height of 1 m and registered the number of segments, which were > 50% hidden (Belotti et al. 2013). For an in-depth investigation of the kill site, we used the ground cover index according to Belotti et al. (2013), which describes the "number of cardinal directions in which the three lowest segments of the wooden pole were completely hidden". In our case, we defined ground cover as the number of cardinal directions in which the three lowest segments were > 50% hidden (**Table 1**). Additionally, we used the habitat concealment index of Belotti et al. (2012), adapted to the lowest three segments of the pole, e.g. the lowest 60 cm ('habitat concealment < 60 cm', **Table 1**). Finally, we documented tree species composition (leaf, needle and mixed forest, open areas and meadows) within a 50 m radius of a kill site.

II: Geographic habitat features

Geographic habitat features were calculated for kill sites, random positions within lynx home ranges, as well as lynx GPS positions. This enabled us to compare certain habitat features at the kill sites with their availability. The forest taxation database of Rhineland-Palatinate was linked to all aforementioned positions (Landesforsten RLP Forest Taxation 2020; LVermGeoRP 2020). For the analyses, we considered the geographic habitat features of slope, elevation (digital elevation model with 5 m resolution), exposition and nearest distance to grassland edge, meadows, roads (three categories) and villages. These features were applied for each site (kill site, random positions, lynx GPS positions) using corresponding GIS layers in R 3.5.3 (R Core Team 2020).

We categorised roads into 'paved public roads', 'truck-drivable forestry roads' and 'not truck-drivable forestry roads (only 4WD car)'. Meadows were defined as small grazing areas within the forest (wild meadows, glades), maintained mostly by hunters sowing seed mixtures to attract ungulates and small mammals (hares). Sizes of meadows within the range of kill sites varied from a minimum < 0.01 km^2 to a maximum 0.026 km^2.

In contrast to meadows, we defined grassland as grassed areas that are not utilised as a farmland crop. The sizes ranged from a minimum < 0.01 km^2 to a maximum of 0.28 km^2. Based on the size difference and characterisation, we separated meadows and grassland areas within the analyses.

As defined by the German Weather Service, we classified roe deer kills in two seasons, whereby we refer to hereafter as summer (from 1st April to 31st September) and winter kills (from 1st October to 31st March). Belotti et al. (2013) used similar season dates (15th April – 14th October for summer, 15th October – 14th April for winter). With habitat shifts of red deer in summer and winter seasons (Mysterud et al. 2001), lynx diet also differ by season (Odden et al. 2006) and hence habitat features change between the two seasons (Belotti et al. 2013), justifying the setting of our season dates.

A) For the comparison of the 123 kill sites with random sites, we derived the following data subsets:
We selected lynx GPS locations, including the locations two weeks before each individual's first roe deer kill and ending with each individual's last registered roe deer kill. In order to be included in the analysis, each lynx individual had to contribute with a minimum of five roe deer kills. A minimum convex polygon (MCP 100%) for each of the thirteen individual lynx was then produced based on the clipped GPS locations of each individual. Within each of the thirteen MCPs, we generated 1,000 random locations (R package *sp*, Bivand et al. (2013); Pebesma and Bivand (2005)), resulting in 13,000 random locations within the home ranges of the thirteen lynx individuals.

B) For the comparison of kill sites with lynx GPS locations, we included only lynx GPS locations of the thirteen individuals from the first detected roe deer kill (07th August 2016) to the last recorded roe deer kill (27th August 2019). This resulted in 19,167 GPS locations, of which 13,000 GPS locations were then randomly selected (package dplyr, Wickham et al. (2020)). The aforementioned geographic habitat parameters were also calculated for the random locations and the randomly-chosen lynx GPS locations. For both, we did not record microhabitat features at these locations (**Tab. 1**). All analyses were carried out using R version 3.5.3 (R Core Team 2020).

Statistical analyses

We used a chi-squared test to examine probable differences between seasons in habitat parameters (ground cover, habitat concealment < 60 cm, canopy cover) of kill sites (n = 75). Kernel density plot was applied for visualising the distribution of habitat concealment < 60 cm (R Core Team 2020; Wickham 2016).

Prior to the final analysis, we checked multicollinearity with the variance inflation factors using the *car* package (Fox and Weisberg 2011). We could not find any multicollinearity between our geographic habitat features. We randomly assigned season (summer/winter) and lynx ID to random locations.

A) Model: kill sites with random sites

We applied a generalised linear mixed-effects model (GLMM). Lynx ID was used as a random effect to encounter for individual variation. Model evaluation was undertaken by using Akaike information criterion (AIC) for a small sample size to select the most parsimonious model (Burnham and Anderson 2002). The response variable of the GLMM was binomial (1 = kill sites and 0 = random locations). The 'season' parameter was used as an interaction term in the model. To allow the model to converge, the variables were scaled (i.e. standardised by shifting the centre to their means, and scaling with the respective standard deviation).

B) Model: kill sites with lynx GPS positions

For the comparison of GPS lynx locations with kill sites (n = 123 kill sites), the data of the same lynx individuals that caused the 123 kill sites (thirteen lynx individuals) was selected. Three analysis considering I) all lynx GPS locations (day and night) including lynx ID as random effect (n = 13,000 lynx GPS points), II) only lynx GPS locations at night (dawn, dusk and night included) including lynx ID as random effect (n = 7,052 lynx GPS locations) and III) only lynx GPS points at night (dawn, dusk and night included) without random effect (n = 7,052 lynx GPS locations) were performed. Individual lynx ID was included as random effects in two model setups (I and II) to account for individual variation. The models were evaluated using AIC for a small sample size to select the most parsimonious model (Burnham and Anderson 2002). The response variable of the GLMM was binomial (1 = kill sites and 0 = lynx GPS locations). To allow the model to converge, the variables were scaled (i.e. standardised by shifting the centre to their means, and scaling with the respective standard deviation). All analyses were conducted in R version 3.5.1 (R Core Team 2020).

Tab. 1 Habitat features recorded at lynx kill sites in the Palatinate Forest, Germany. Microhabitat measurements are based on a radius of 5–50 m around each kill site. Geographic habitat features were calculated using ArcGIS for the each kill site location. Indices modified after Belotti et al. (2013); Belotti et al. (2012).

	Radius around kill site	Comparison to random points	Seasonal comparison	Unit	Description
Microhabitat features (n = 75 kill sites)					
Forest characteristics	5 m	No	Yes	-	mature stand, mature stand in generation change, young timber, pole wood, thicket, regeneration, open area, path
Ground Cover modified after (Belotti et al. 2013)	20 m	No	Yes	Index (0 - 4)	Number of cardinal direction in which the three lowest segments of the pole were > 50% hidden (three segments = 60 cm)
Habitat concealment < 60 cm modified after Belotti et al. (2012)	20 m	No	Yes	Index (0 – 3)	Index of the presence of hiding places at the kill site (Belotti et al. 2012) Mean of four values registered in the 20 m radius plot using 'pole method' counting the number of segments (lowest 3) of the pole, which were > 50% hidden of vegetation value 0 (open habitat), value 3 (closed habitat)
Canopy Cover	20 m	No	Yes	Index (0 - 4)	Index 1: 0–25% cover Index 2: 26–50% cover Index 3: 51–75% cover Index 4: 76–100% cover
Tree composition groups	50 m	No	Yes	-	leaf, needle and mixed forest, open areas / meadows
Geographic habitat features (n = 123 kill sites)					
slope, elevation, exposition, distance to grassland / meadow / road / village	Point of kill site	Yes	No	Distances [m] Slope [°] Elevation [m above sea level]	Information was gained out of associated ArcGIS layers (Landesforsten RLP Forest Taxation 2020; LVermGeoRP 2020)

Results

For the microhabitat feature analysis, we examined 31 summer and 44 winter roe deer kill sites (n_{total} = 75 roe deer kills) in the Palatinate Forest. Microhabitat feature mapping revealed that lynx kill sites were mostly in forested areas (~ 95%, n_{forest} = 71, $n_{open/rest}$ = 4). In summer, a larger number of kill sites were positioned directly on forestry roads (n = 7, ≙ 23%) whereas in winter this was true for only one kill site (≙ 2.3%). In summer and winter, similar numbers of kill sites were found within complex and structure-rich habitats, represented by regeneration, thickets and mature forest in generation change (n_{summer} = 17, ≙ 54.8%, n_{winter} = 16, ≙ 36.4%, Mann-Whitney-U-Test, p = 0.8). Ground cover was found at 95% of all kill sites ($n_{ground\ cover}$ = 71 kill sites), whereby 43% of all 75 kill sites exhibit ground cover in all four cardinal directions (n = 32, 45.5% in winter, 38.7% in summer). Only four kill sites (two in each season) showed no ground cover at all, thereby representing 5.3% of all kill sites. Ground cover of summer and winter kill sites showed no significant differences (p = 0.88, X^2 = 1.21; chi-squared test), nor did habitat concealment < 60 cm (p = 0.6, X^2 = 1.86; chi-squared test, **Fig. 2 A**). Canopy cover at summer kill sites was significantly lower than at winter kill sites (p = < 0.001, X^2 = 19.861, chi-squared test, **Fig. 2 B**). In both seasons, kill sites tend to be located in a setting of high habitat concealment and ground cover scores. Thus, unlike in summer, correlation of habitat concealment and ground cover scores with canopy cover was less pronounced in winter (**Fig. 3 A & B**). Only in winter kill sites with higher habitat concealment and ground cover were also found in places with a higher canopy cover (category 3: 51–75% and category 4: 76–100%, **Fig. 3 A & B**).

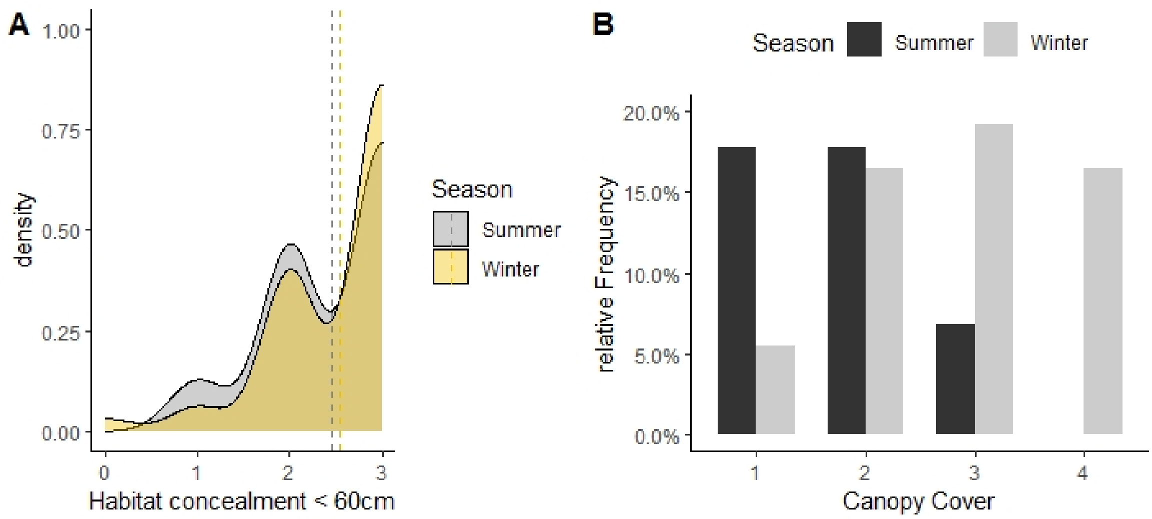

Fig. 2 A Density distribution of habitat concealment < 60 cm on 75 kill sites in summer and winter seasons in the Palatinate Forest. Habitat concealment is defined as an index of the presence of hiding places at the kill site (Belotti et al. 2012), which in this case is based on a height level of 0 – 60 cm. Values range from 0 (open habitat) to 3 (closed habitat). **B** Relative frequency distribution of canopy cover on 75 roe deer kill sites in winter and summer seasons in the Palatinate Forest. Categories: "1" 0–25%, "2" 26–50%, "3" 51–75% and "4" 76–100% canopy cover.

In terms of geographic habitat features, we produced several models with a level of support similar to the best-supported model (**Supplementary material Appendix 1 Tab. 1,** Δ AIC < 2). The best-supported model displayed a significantly higher relative probability of a roe deer kill in close distance to truck-driveable forestry roads, paved public roads and not truck-drivable forestry roads in comparison with random locations (**Fig. 4, Tab. 2)**. The relative probability of a roe deer kill was higher at lower elevation (p = 0.072, estimate = -0.179) and significantly higher closer to grassland edges (p = 0.004, estimate = -0.379, **Fig. 5, Tab. 2**). In addition, we found a significant lower probability of a roe deer kill in close distances to villages (p = 0.031, estimate = 0.239, **Fig. 4, Tab. 2**).

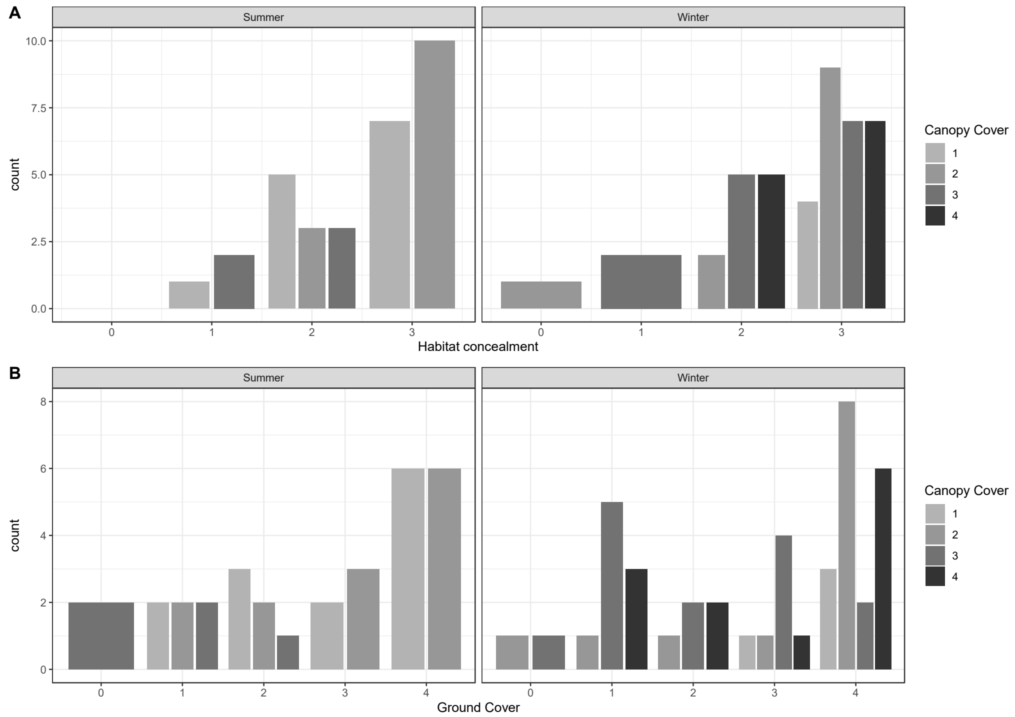

Fig. 3 A Relationship between habitat concealment < 60 cm and canopy cover in summer and winter seasons at roe deer kill sites (n = 75) in the Palatinate Forest. Habitat concealment ranges from 0 to 3, representing open and closed habitat, respectively. **B** Relationship between ground cover and canopy cover in summer and winter seasons at roe deer kill sites (n = 75) in the Palatinate Forest. Ground cover is the number of cardinal directions in which the three lowest segments of a 2 m pole (pole method) were > 50% hidden (lowest three segments = 60 cm). Canopy cover categories: "1" 0–25%, "2" 26–50%, "3" 51–75% and "4" 76–100% canopy cover.

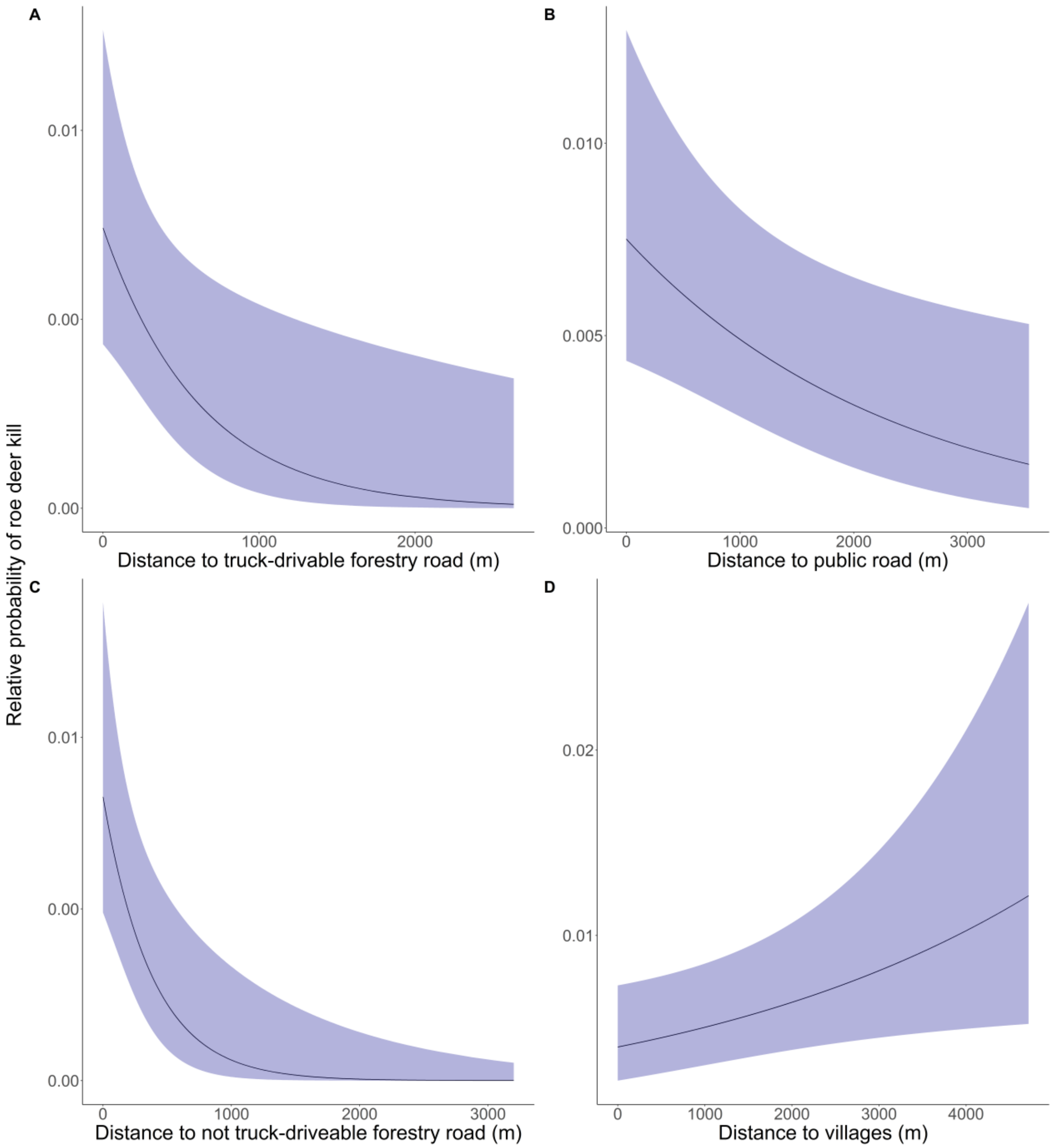

Fig. 4 Relationship between the relative probability of a roe deer kill and the nearest distance to paths (truck-driveable forest path, not truck-driveable forest path and public roads) and nearest distance to human settlements (villages) based on a GLMM analysis of lynx kill sites (n = 123) and random sites (n = 13,000) in the Palatinate Forest, Germany.

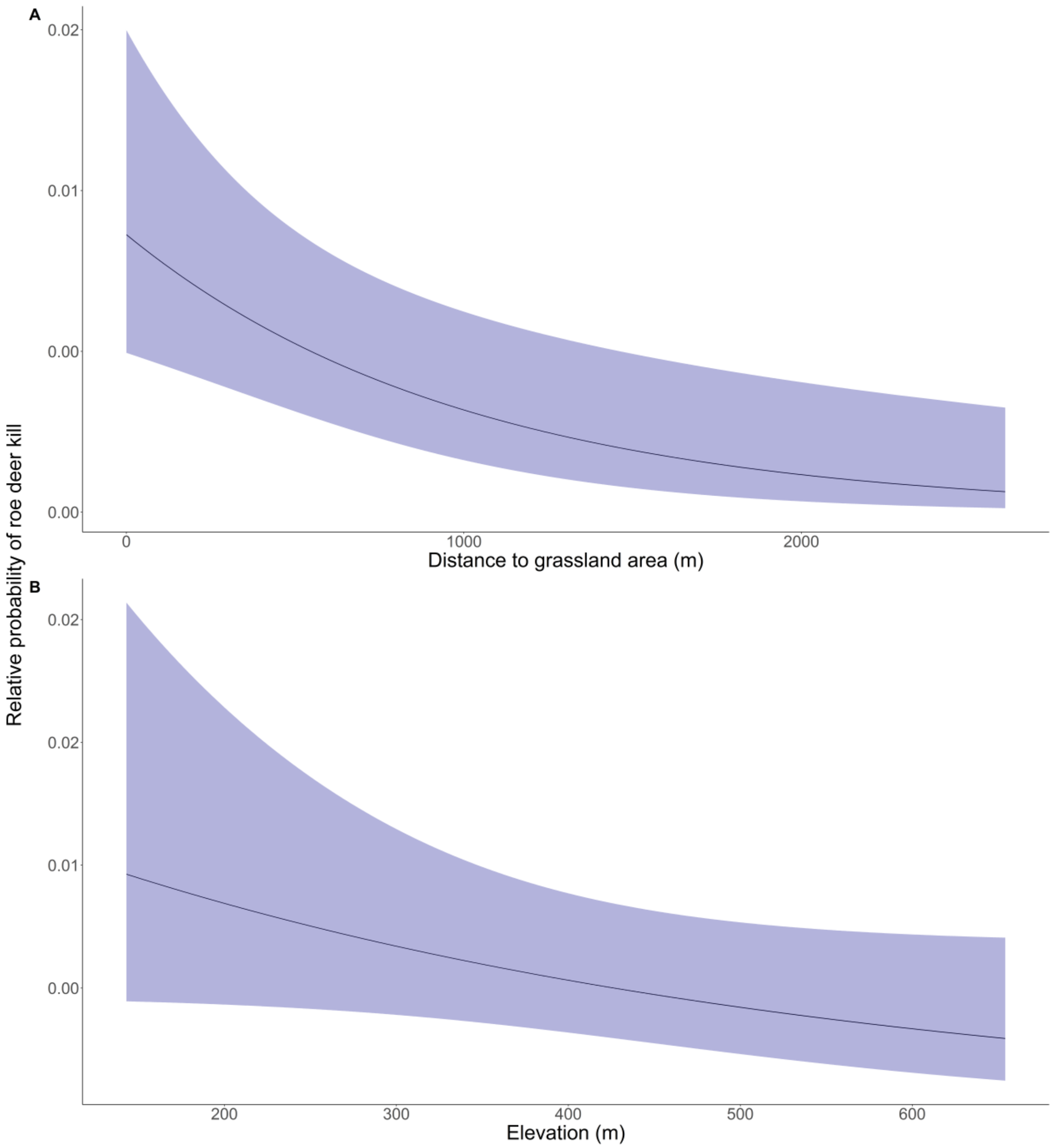

Fig. 5 Relationship between relative probability of a roe deer kill and the nearest distance to grassland areas (A) and elevation (B) based on a GLMM analysis of lynx kill sites (n = 123) and random sites (n = 13,000) in the Palatinate Forest, Germany.

Tab. 2 Effect of the explanatory variables on the predicted probability of lynx predation for roe deer in the Palatinate Forest, Germany. Correlation and multicollinearity for all explanatory variables was checked. A GLMM model with individual Lynx ID as random effect was applied. A binomial set up (kill sites / random site) was used. All predictor variables were scaled in order to allow model conversion. Significant factors are marked in boldface. Predictor variables roads, village and grassland present each the nearest distance from kill site / random site to these predictors.

	Estimate	**Std. Error**	**z value**	**Pr (>|z|)**
(Intercept)	-5.187	0.260	-19.95	**< 0.001**
Elevation	-0.179	0.100	-1.799	0.072
Road truck-driveable	-0.315	0.137	-2.296	**0.022**
Road public roads	-0.268	0.114	-2.358	**0.018**
Road not truck-drivable	-0.586	0.206	-2.847	**0.004**
Villages	0.239	0.111	2.161	**0.031**
Grassland	-0.379	0.132	-2.861	**0.004**

Comparing lynx GPS locations with kill sites, in all three-model setups (I, II, III) we found significant differences regarding the distance to grassland edges and partly significant differences for not truck-drivable forestry roads (**Tab. 3**). For model setup I (day and night lynx GPS locations), the relative probability of a roe deer kill was significantly higher at lower slopes ($p = < 0.001$, **Tab. 3**) and in proximity to not truck-drivable forestry roads ($p = 0.027$) and grassland edges ($p = 0.014$) when compared with lynx live locations. For model setup II (night – inclusive dawn and dusk – lynx GPS locations with lynx ID as a random effect), the relative probability of a roe deer kill was significantly higher closer to grassland edges ($p = 0.012$, **Tab. 3**). Slope and distance to not truck-drivable roads remained in the best model, but did not show significant values (**Tab. 3**). For model setup III (lynx GPS locations at night, dawn and dusk without random effect), the relative probability of a roe deer kill compared with lynx live locations was significantly higher closer to not truck-drivable forestry roads ($p = 0.04$) and grassland edges ($p = 0.006$, **Tab. 3**).

Tab. 3 Effect of the explanatory variables on the predicted probability of lynx predation for roe deer in relation to lynx movement in the Palatinate Forest, Germany. A binomial set-up (1 = kill sites / 0 = lynx GPS locations) was applied. A GLMM model with individual Lynx ID as random effect was applied for model set-up I and II. Model set-up III did not have a random effect included in the GLM model. All predictor variables were scaled in order to allow model conversion. Significant factors are marked in boldface. Predictor variables road, village and grassland present each the nearest distance from site (kill sites / lynx GPS points) to these predictors.

	Estimate	Std. Error	z value	Pr (>|z|)
Model set-up I (lynx GPS locations for day and night with random effect lynx ID)				
(Intercept)	-4.808	0.153	-31.498	**< 0.001**
Elevation	-0.156	0.099	-1.571	0.116
Slope	-0.354	0.094	-3.771	**< 0.001**
Road not truck-drivable	-0.265	0.120	-2.208	**0.027**
Grassland	-0.292	0.119	-2.447	**0.014**
Model set-up II (lynx GPS location at night with random effect lynx ID)				
(Intercept)	-4.158	0.136	-30.528	**< 0.001**
Slope	-0.140	0.092	-1.532	0.125
Road not truck-drivable	-0.232	0.121	-1.922	0.055
Grassland	-0.286	0.114	-2.502	**0.012**
Model set-up III (lynx GPS points at night without random effect)				
(Intercept)	-4.168	0.104	-40.070	**< 0.001**
Slope	-0.145	0.092	-1.583	0.113
Road not truck-drivable	-0.245	0.119	-2.054	**0.040**
Grassland	-0.309	0.113	-2.743	**0.006**

Discussion

Ground cover and seasonal differences at kill sites

Our results indicated that in order to hunt successfully, cover and habitat concealment on the ground is important for lynx in the Palatinate Forest. In addition, places with ground vegetation are attractive forage sites for deer. Hence, hunting in structure-rich and complex habitats may increase encounter probability and the possibility to sneak up on its prey. This conclusion is in line with other studies showing that lynx almost never hunt roe deer in places with no ground cover (Belotti et al. 2013; Podgórski et al. 2008; Krofel et al. 2007). Although Belotti et al. (2013) found more kill sites in open habitats, the term "open" is misleading due to including habitats where the strong vegetation growth may have 'homogenised' the habitat features in the 20 m radius plots. Like in our study, Podgórski et al. (2008) only found lynx kill sites in forested areas, a result that mainly reflects the similarity with the landscape of the Bialowieza Primeval Forest, where "forest stands are quite continuous with only a few glades occupied by villages, marshes and open river valleys" (Podgórski et al. 2008). Our study area is also mainly characterised by forested areas, where open structures like grassland are common within valleys and close to villages. The results of our analysis showed that the majority of kill sites are found in forested areas and around 45% of the sites exhibit ground cover in all cardinal directions. Krofel et al. (2007) state that lynx in Slovenia do not necessarily need total dense vegetation and rugged terrain for hunting. However, lynx in the Palatinate Forest also hunted successfully when cover only existed in one cardinal direction, which again partly supports Krofel et al. (2007) hypothesis.

Comparing microhabitat features at kill sites with each other, we found seasonal differences, whereas when analysing geographic habitat features at kill sites with random sites we were unable to find seasonal differences (for the best-supported model). Belotti et al. (2013) found habitat differences in visibility between summer and winter kill sites and concluded that in summer predation risk is dependent on prey occurrence rather than habitat variables. We could not find any seasonal differences in vegetation cover at kill site (habitat concealment < 60 cm height and ground cover), but we found seasonal differences in canopy cover when analysing our data on a fine scale. In winter, kill sites showed a higher and in summer a lower percentage of canopy cover. We found that summer kill sites with low canopy cover revealed high ground cover as well as habitat concealment values, whereas winter kill sites had a larger variety with respect to both habitat features. We conclude that in summer less canopy cover is required for a successful hunt, due to better vegetation structures on the ground (habitat concealment < 60 cm height). Low canopy cover usually leads to regeneration or the establishment of light favouring plants like raspberry and blackberry, hence offering an optimal foraging habitat for roe deer. This leads to dense ground cover with complex vegetation structures, which in turn reduces the visibility, so that a stalking predator can easily approach its prey (Podgórski et al. 2008). In summer, lynx might profit from seasonally-dependent vegetation structures, whereas in winter other habitat parameters might be favourable for a successful hunt. This premise supports the hypothesis posited by Belotti et al. (2013) that predation risk in winter depends on habitat variables rather than prey density. We assume that the kind but not really the amount of ground cover changes over season. Cover in the form of regeneration, deadwood, uproot trees, stones and rocks are probably more important in winter than summer. Podgórski et al. (2008) found a higher degree of complexity and lower visibility at hunting site than random sites. We believe that a high amount of ground cover might lead to more successful lynx hunting attempts in the Palatinate Forest. However, lynx are not dependent on the presence of ground cover in all cardinal directions to hunt successfully.

Habitat parameters of kill sites and random sites

When comparing kill sites with random sites regarding their geographical parameters, we found a higher kill probability in close proximity to grassland areas, reflecting an example of naturally attractive foraging grounds for ungulates. The edge habitat of grassland areas offers high plant diversity and different kinds of shrubs, hence providing ideal habitat (food and cover) for roe deer (Gill et al. 1996) and consequently good habitat cover for lynx. At night, grassland areas present little disturbance for both roe deer and lynx, and thus could lead to a higher probability of a roe deer kill in close distances to grassland areas. Gehr et al. (2017) found a lynx trade-off between prey availability and the avoidance of human disturbance by using prey-rich areas at night when human activity is low. This supports our results, which show that lynx hunt successfully near grassland areas during a time when human disturbance is naturally low. We assume that due to the low numbers of roe deer kills directly on the grassland areas, lynx kill their prey in the vicinity of the grassland, where cover helps the predator to ambush or stalk up on its prey. Molinari-Jobin et al. (2004) demonstrated that roe deer in the Jura Mountains were mainly preyed upon while ruminating. When doing so, roe deer normally bed down close by the grazing ground. Roe deer usually rely on their good sense of hearing and smell (Stubbe 1997), but while ruminating their sense of hearing might be inactive and they mainly rely on their sense of smell (Molinari-Jobin et al. 2004; Raesfeld 1985). Thus, the risk of a predator approaching undetected increases. Grassland areas in the Palatinate Forest are often situated in valleys, which could explain the increased kill probability at lower elevations.

Our findings demonstrate that in close vicinity to linear infrastructures, roe deer experience a higher predation probability regardless of classification (paved public roads, truck- and not truck-drivable forestry roads). Earlier studies suggested that lynx use forestry roads and hiking trails (Kunz et al. 2020; Pesenti and Zimmermann 2013; Weingarth et al. 2012) for energy-efficient travel, scent marking, quick travel from one place to another and dispersal (Mathisen et al. 2018; Vogt et al. 2014). We assume that lynx might use these linear structures additionally for hunting, due to the oversupply of forestry roads in the Palatinate Forest. With 50–90 m/ha (Simon and Kotremba 2016), the forestry road network in the Palatinate Forest is very high and hence possibly influences the habitat use of lynx. Not only lynx use this infrastructure, but also ungulates use human-made structures to benefit from this road edge environment (Meisingset et al. 2013). Roads provide gaps in forested environments, increase the light regime, change water and nutrient availability and generate soil disturbance (Coffin 2007). Taken together, this might lead to a different vegetation composition alongside roads, generating attractive grazing grounds for ungulates. For both lynx and roe deer, roads are highly attractive and therefore the kill probability for roe deer close to roads is higher.

Besides human-made infrastructure, human disturbance in the form of distance to settlements (villages) might also influence the kill probability of roe deer in the Palatinate Forest. In our study, we analysed the effect of villages on the kill probability of roe deer by lynx. Our findings demonstrate that with increasing distance to villages, an increased kill probability occurred. This could lead to the assumption that the predator or the prey might avoid human-disturbed areas. However, roe deer are known to cope with human disturbance near settlements better than – for instance – red deer (Jiang et al. 2008), and additionally roe deer use the more open habitat and feeding possibilities in the proximity of settlements, especially at night (Mysterud, Lian, et al. 1999). Additionally, lynx trade-off between prey availability and human disturbance (Bouyer, Gervasi, et al. 2015; Basille et al. 2009), and are able to tolerate intermediate human disturbance (Basille et al. 2009). Contrary to this, our results rather support the avoidance theories. Further detailed analyses of lynx GPS data in the study area did not reveal any avoidance of settlements in the Palatinate Forest (unpublished data, manuscript 3). However, the establishment of lynx in the Palatinate Forest is still at its beginning, leaving still-free home ranges within the area to be occupied by lynx, and hence possibly creating bias in our kill site analyses regarding human settlements, which are sparsely distributed in the Palatinate Forest.

The tolerance of lynx to human disturbance depends on its intensity, which was shown by Belotti et al. (2012), where lynx chose their day-resting place further away when having a prey close to tourist trails. In southern Norway, the home range of 49 lynx has been studied regarding their tolerance to human-modified landscapes (Bouyer, Gervasi, et al. 2015). They authors found that increasing human disturbance generates a home range adjustment of lynx “to minimize exposure to most disturbed areas” (Bouyer, Gervasi, et al. 2015). In addition, Bouyer, San Martin, et al. (2015) and Basille et al. (2009) found that lynx select areas with medium levels of human modification and an avoidance of most-disturbed areas (Basille et al. 2009). For the Palatinate Forest the most-disturbed areas (eastern part of the forest) are not yet occupied by lynx, which probably confirms the results of Basille et al. (2009). Future investigations within this specific subject will possibly offer more insights into how lynx utilised their territory for hunting, especially when it comes to the proximity of human settlements.

Habitat parameters of kill sites and lynx GPS locations

Comparing lynx live locations with kill sites of roe deer in the Palatinate Forest we found further evidence that kill probability increases in closer distance to the grassland edge. Lynx also use other habitat structures like the proximity of forestry roads for hunting. Both forestry roads and grassland edges are habitats where prey density and prey encounter rate is presumably high (prey habitat selection). For a successful hunting attempt, the terrain inclination could be advantageous for lynx in the Palatinate Forest (predator site selection). Habitat structure like elevation and slope also play a crucial role for the habitat selection of lynx in other study areas (Signer et al. 2019; Bouyer, San Martin, et al. 2015; Basille et al. 2008; Krofel et al. 2007). Rock formations seem to be important criteria for lynx resting sites (Signer et al. 2019), possibly explaining our difference in the degree of slope when comparing lynx locations with kill sites.

Conclusions

The findings of this study highlight the fact that interactions between lynx – a stalking predator – and roe deer – its main prey – depend on those landscape features that increase both the nocturnal encounter rate (public and forestry roads, grassland areas) as well as approach and ambush opportunities (ground cover and concealment). Apart from our study, few other studies to date have dealt with a reintroduced predator into a habitat in which prey had not experienced this predator over a long period. The alleged avoidance of human settlements should be subject to further investigations. Our results contribute to the understanding of how large carnivores like lynx re-establish within a new environment, and how their prey adapt to a new and additional predation risk. Nevertheless, further investigations of kill sites in the Palatinate

Forest should be continued over longer periods of time to better understand the interaction between lynx and roe deer, and thus the long-term consequences for the prey population in the forest.

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References

Basille M, Calenge C, Marboutin É, Andersen R, Gaillard J-M (2008) Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. Ecol Modelling 211:233-240

Basille M, Herfindal I, Santin-Janin H, Linnell JD, Odden J, Andersen R, Arild Høgda K, Gaillard J-M (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography 32:683-691

Belotti E, Červený J, Šustr P, Kreisinger J, Gaibani G, Bufka L (2013) Foraging sites of Eurasian lynx *Lynx lynx*: relative importance of microhabitat and prey occurrence. Wildlife Biol 19:188-201

Belotti E, Heurich M, Kreisinger J, Sustr P, Bufka L (2012) Influence of tourism and traffic on the Eurasian lynx hunting activity and daily movements. Animal Biodiversity Conservation 35:235-246

Belotti E, Mayer K, Kreisinger J, Heurich M, Bufka L (2018) Recreational activities affect resting site selection and foraging time of Eurasian lynx (*Lynx lynx*). Hystrix 29:181-189

Bivand RS, Pebesma EJ, Gómez-Rubio V (2013) Applied Spatial Data Analysis with R. Springer Science, New York

Bouyer Y, Gervasi V, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. Animal Conservation 18:271-278

Bouyer Y, San Martin G, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. Biological Conservation 191:291-299

Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs. Salm Verlag, Wohlen/Bern, Switzerland: 1-537

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach (2nd edition). Springer-Verlag, New York

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transport Geography 15:396-406

Creel S, Fox JE, Hardy A, Sands J, Garrott B, Peterson RO (2002) Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809-814

Filla M, Premier J, Magg N, Dupke C, Khorozyan I, Waltert M, Bufka L, Heurich M (2017) Habitat selection by Eurasian lynx *(Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. Ecology and Evolution 7:6367-6381

Fox J, Weisberg S (2011) An R companion to applied regression. Sage Publications, Los Angeles

Frauendorf M (2012) Pilot Study on the microhabitat selection of the Eurasian lynx (*Lynx lynx*) concerning hunting sites in the Harz National Park, Germany. M.Sc. thesis. Van Hall Larenstein University, Sankt Andreasberg

Gaß R (2018) Habitatkartierung von Luchsrissorten im Pfälzerwald im Projekt „Interaktion von Luchs und Reh im Pfälzerwald". M.Sc. thesis. Hochschule für Forstwirtschaft Rottenburg

Gehr B, Hofer EJ, Muff S, Ryser A, Vimercati E, Vogt K, Keller LF (2017) A landscape of coexistence for a large predator in a human dominated landscape. Oikos 126:1389-1399

Gill R, Johnson A, Francis A, Hiscocks K, Peace A (1996) Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. For Ecol Manag 88:31-41

Herfindal I, Linnell JD, Odden J, Nilsen EB, Andersen R (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). Journal of Zoology 265:63-71

Hohmann U, Hettich U, Ebert C, Huckschlag D (2018) Evaluierungsbericht zu den Auswirkungen einer dreijährigen Jagdruhe in der Kernzone „Quellgebiet der Wieslauter" im Wildforschungsgebiet „Pfälzerwald" (Langfassung). vol Nr. 84/18. Forschungsanstalt für Waldökologie und Forstwirtschaft FAWF, Mitteilungen aus der Forschungsanstalt für Waldökologie und Forstwirtschaft FAWF

Idelberger S, Krebühl J, Back M, Ohm J, Prüssing A, Sandrini J, Huckschlag D (submitted) Reintroduction of Eurasian lynx (*Lynx lynx carpathicus*) in the Palatinate Forest, Germany

Jędrzejewski W, Schmidt K, Miłkowski L, Jędrzejewska B, Okarma H (1993) Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. Acta Theriologica 38:385-403

Jiang G, Zhang M, Ma J (2008) Habitat use and separation between red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi* in relation to human disturbance in the Wandashan Mountains, northeastern China. Wildlife Biol 14:92-100

Kramer-Schadt S, Revilla E, Wiegand T (2005) Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biol Conserv 125:169-182

Krofel M, Potočnik H, Kos I (2007) Topographical and vegetational characteristics of lynx kill sites in Slovenian Dinaric Mountains. Natura Sloveniae 9:25-36

Kunz F, von Rotz J, Breitenmoser-Wörsten C, Breitenmoser U, Zimmermann F (2020) Fang-Wiederfang-Schätzung der Abundanz und Dichte des Luchses in der Zentralschweiz West IIIa im Winter 2018/19. KORA Bericht, Nr. 94, Muri in Bern, 1-18

Landesforsten RLP Forest Taxation (2020).

Linnell JD, Andersen R, Kvam T, Andren H, Liberg O, Odden J, Moa P (2001) Home range size and choice of management strategy for lynx in Scandinavia. Environ Manage 27:869-879

Linnell JD, Promberger C, Boitani L, Swenson JE, Breitenmoser U, Andersen R (2005) The linkage between conservation strategies for large carnivores and biodiversity: the view from the "half-full" forests of Europe. In: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.). Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, DC

LVermGeoRP, GeoBasis-DE (2020) dl-de/by-2-0. lvermgeo.rlp.de.

Mathisen K, Wójcick A, Borowski Z (2018) Effects of forest roads on oak trees via cervid habitat use and browsing. Forest Ecology and Management 424: 378–386

Meisingset EL, Loe LE, Brekkum Ø, Van Moorter B, Mysterud A (2013) Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77:181-191

Molinari-Jobin A, Molinari P, Loison A, Gaillard JM, Breitenmoser U (2004) Life cycle period and activity of prey influence their susceptibility to predators. Ecography 27:323-329

MUEEF RLP (2012) Klimawandel-Informationssystem RLP: Regionale Informationen - Pfälzerwald. Ministry of Environment, Energy, Food and Forestry Rhineland-Palatinate. kwis-rlp.de/de/anpassungsportal/regionale-informationen/pfaelzerwald/. Accessed 15.01.2018

Mysterud A, Langvatn R, Yoccoz NG, Chr N (2001) Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 70:915-923

Mysterud A, Larsen PK, Ims RA, Østbye E (1999) Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Can J Zool 77:776-783

Mysterud A, Lian L-B, Hjermann DØ (1999) Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. Can J Zool 77:1486-1493

Naturpark Pfälzerwald (2018) Biosphärenreservat Pfälzerwald-Nordvogesen. Naturpark Pfälzerwald pfaelzerwald.de/naturpark-pfaelzerwald/. Accessed 15.01.2018 2018

Odden J, Linnell JDC, Andersen R (2006) Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. European Journal of Wildlife Research 52:237-244

Pebesma E, Bivand RS (2005) S classes and methods for spatial data: the sp package. R news 5:9-13

Pesenti E, Zimmermann F (2013) Density estimations of the Eurasian lynx (*Lynx lynx*) in the Swiss Alps. J Mammal 94:73-81

Pierce BM, Bowyer RT, Bleich VC (2004) Habitat selection by mule deer: forage benefits or risk of predation? The Journal of Wildlife Management 68:533-541

Podgórski T, Schmidt K, Kowalczyk R, Gulczyńska A (2008) Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica 53:97-110

R Core Team (2020) R: A language and environment for statistical computing.R Foundation for Statistical Computing.Vienna.

Raesfeld F (1985) Das Rehwild. Paul Parey, Hamburg, Berlin

Rheinland-Pfalz Kompetenzzentrum für Klimawandelfolgen (2021). www.kwis-rlp.de. Accessed 01.04 2021

Rozylowicz L, Chiriac S, Sandu RM, Manolache S (2010) The habitat selection of a female lynx (*Lynx lynx*) in the northwestern part of the Vrancea Mountains, Romania. North West J Zool 6:122-127

Sand H, Wikenros C, Wabakken P, Liberg O (2006) Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? Proc Royal Soc B 273:1421-1427

Schukraft R (2017) Luchs-Riss-Habitatkariterung im Projekt "Interaktion von Luchs und Reh im Pfälzerwald".M.Sc. thesis. Hochschule für Wirtschaft und Umwelt Nürtingen-Geislingen.

Signer J, Filla M, Schoneberg S, Kneib T, Bufka L, Belotti E, Heurich M (2019) Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. Wildlife Biology 2019 (1):1-5

Simon O, Kotremba C (2016) Lebensraumgutachten Rotwild in der Hegegemeinschaft Pfälzerwald-Süd KdöR - Lebensraumanalyse und Maßnahmenempfehlungen 2014/2015. Unveröffentlichtes Gutachten. Auftraggeber Rotwildhegegemeinschaft "Pfälzerwald-Süd", 1-70, Institut für Tierökologie und Naturbildung.

SNU-RLP (2018) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed Januar 18, 2018

Squires JR, Decesare NJ, Kolbe JA, Ruggiero LF (2010) Seasonal resource selection of Canada lynx in managed forests of the Northern Rocky Mountains. The Journal of Wildlife Management 74:1648-1660

Stubbe C (1997) Rehwild: Biologie, Ökologie, Bewirtschaftung. Parey Buchverlag, Berlin, 568 pp.

Sunde P, Stener SØ, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. Wildlife Biol 4:177-183

Vogt K, Zimmermann F, Kölliker M, Breitenmoser U (2014) Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behav Processes 106:98-106

Weingarth K, Heibl C, Knauer F, Zimmermann F, Bufka L, Heurich M (2012) First estimation of Eurasian lynx (*Lynx lynx*) abundance and density using digital cameras and capture–recapture techniques in a German national park. Anim Biodivers Conserv 35:197-207

Wickham H (2016) ggplot2: Elegrant graphics for data analysis.Springer International Publishing. 2nd edn., Cham, Switzerland

Wickham H, François R, Henry L, Müller K (2020) dplyr: a grammar of data manipulation. R package version 0.8. 0.1, CRAN.R-project.org/package=dplyr

Wikenros C, Sand H, Wabakken P, Liberg O, Pedersen HC (2009) Wolf predation on moose and roe deer: chase distances and outcome of encounters. Acta Theriologica 54:207-218

Supporting Information Appendix 1

Appendix 1 Tab. 1 Results of model fitting for the probability of a roe deer being killed by lynx in the Palatinate Forest. Within the model we included individual lynx ID as random effect. Models were compared based on the number of parameters and the Akaike´s Information Criterion corrected for sample size and the difference from the best-fitting model (Δ AIC). Only the models Δ AIC < 2 are presented.

Model	AIC	Δ AIC
Elevation + Road Truck-driveable + Road public + Road not-Truck driveable + Village + Grassland	1308.3	0
Season + Elevation + Road Truck-driveable + Road public + Road not-Truck driveable + Village + Grassland + Season * (Road public)	1309.0	0.7
Season + Elevation + Road Truck-driveable + Road public + Road not-Truck driveable + Village + Grassland	1310.2	1.9

Manuscript III

The effect of anthropogenic structures on habitat selection of newly reintroduced Eurasian lynx (*Lynx lynx*) in the Palatinate Forest, Southwest Germany

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The effect of anthropogenic structures on habitat selection of newly reintroduced Eurasian lynx (Lynx lynx) in the Palatinate Forest, Southwest Germany

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Abstract

Germany is characterized in large parts by an anthropogenic dominated landscape. Understanding habitat requirements of large carnivores within this human dominated landscape is necessary for a successful return of such species. We therefore investigated the habitat selection of recently-reintroduced lynx in the Palatinate Forest in relation to anthropogenic structures. In general, we predicted that newly reintroduced lynx do not avoid the surroundings of human settlements, but their habitat selection varies in relation to time of day (day vs. night) and environmental variables. We used GPS data from 14 lynx (equal sex distribution) in the Palatinate Forest over the time span of 2016 to 2019. We compared lynx (1) locations vs. random locations and (2) time of the day (daytime vs. night-time) in relation to anthropogenic and environmental variables by applying a generalized linear model (GLM) or generalized linear mixed model (GLMM). Our results reveal that lynx did not avoid human settlements and even chose to remain in areas near them at night. Roads play an important role in the habitat selection of lynx in the Palatinate Forest, as lynx select areas close to them and prefer public roads and small forest roads even more at night-time than during daytime. At night, lynx chose lower terrain ruggedness (lower elevation and lower slopes) and closer distances to grassland areas than during the day. Our study results contribute to the current knowledge of habitat requirements of large carnivores in Europe and can be used to improve future management plans related to lynx.

Keywords: Eurasian Lynx, habitat selection, anthropogenic structures, reintroduction

Introduction

The Eurasian lynx (*Lynx lynx*) is slowly recovering in Germany and across Europe (Schadt, Revilla, et al. 2002) due to changes in public attitudes towards wildlife (Filla et al. 2017; Kramer-Schadt et al. 2005) and favourable conservation choices regarding large carnivores (Filla et al. 2017; Linnell, Swenson, et al. 2001). This shift in awareness has led to lynx presence in 23 European countries in 2014 (considering all continental European countries excluding Belarus, Ukraine and Russia). These can be divided into 11 populations, 6 of which are based on reintroduction programmes (Chapron et al. 2014). According to Chapron et al. (2014), around 9,000 lynx are assumed to be located in Europe. In Germany alone, there were three lynx reintroduction programmes, including the Bohemian-Bavarian ecosystem (Heurich et al. 2012), the Harz Mountains (Chapron et al. 2014) and the Palatinate Forest (SNU-RLP 2018). In 2015, a reintroduction programme was initiated in the Palatinate Forest, as the Vosges lynx population was declining (status 2014) and only a few occasional lynx proofs were confirmed on the German side. Reintroducing lynx into their original habitat is often accompanied by conflicts with and apprehension by hunters and farmers (Filla et al. 2017; Lüchtrath and Schraml 2015; Červený et al. 2002; Breitenmoser et al. 2000), and it has raised debate on suitable spaces for viable populations (Chapron et al. 2014) within our agricultural and otherwise modified landscape (Bouyer, San Martin, et al. 2015). The spatial requirements of large carnivores exceed the capacity of European protected areas, which are usually small and contiguous areas with little human modification (Filla et al. 2017; Chapron et al. 2014). To enable the coexistence of carnivores and humans in Europe, we need a better understanding of habitat requirements, movements and acceptance of lynx towards human settlements (Filla et al. 2017; Chapron et al. 2014; Zimmermann and Breitenmoser 2007; Zimmermann et al. 2005). For this reason, we investigated movement data of recently-reintroduced lynx to examine their habitat selection in the Palatinate Forest, Germany.

Habitat selection is defined as a hierarchical process involving inherent and learned behavioural decisions made by an individual in order to choose a habitat at different environmental scales (Hutto 1985). Additionally, it is described as an adaptive behaviour for maximising an individual's fitness (Thomas and Taylor 2006). Only a limited number of studies have investigated lynx habitat selection at a finer scale (Belotti et al. 2013; Podgórski et al. 2008), and have shown the importance of habitat visibility and heterogeneity for lynx to hunt successfully. Habitat selection on a large scale has been investigated in different areas of Europe (Herrero et al. 2020; Signer et al. 2019; Filla et al. 2017; Bouyer, San Martin, et al. 2015; Basille et al. 2013; Basille et al. 2009) and has revealed a variety of outcomes.

For example at night, lynx in the Bohemian Forest Ecosystem chose for open habitats, such as meadows, which are associated with higher ungulate abundance, whereas during the day, habitats with dense understory cover and rugged terrain away from human infrastructure were preferred (Filla et al. 2017). Other studies revealed no avoidance of human disturbed areas but showed that lynx differentiate regarding the level of human activity (Bouyer, San Martin, et al. 2015; Basille et al. 2009). For instance, Bouyer, San Martin, et al. (2015) state that lynx choose habitats with medium human modification and avoid low and very high degrees of modification (Basille et al. 2009). Conversely, lynx showed tolerance towards high human activity within their range as long as dense habitat cover is present (Sunde et al. 1998). Ruggedness and elevation seem to be two important factors allowing lynx to withstand highly modified areas (Bouyer, San Martin, et al. 2015). Trade-offs between prey and disturbance seem to be proved through several studies (Gehr et al. 2017; Gehr 2016; Basille et al. 2009). Resting sites of lynx are selected in close proximity to rock formations (Signer et al. 2019; Weingarth et al. 2012) and in Norway even away from human settlements and roads (Sunde et al. 1998). It is also known that lynx, especially for natal den sites, use rugged terrain, low road- and human density (White et al. 2015). It appears that roads and streams are important for shaping the home range and habitat use of lynx (Donovan et al. 2011). Thus, lynx like to travel on established, easily accessible routes like forestry roads, hiking trails and cross-country ski-tracks in order to move fast and save energy (Weingarth et al. 2015; Weingarth et al. 2012; Sandrini 2010; Breitenmoser and Breitenmoser-Würsten 2008; Zimmermann and Breitenmoser 2007; Koehler and Brittell 1990). Koehler and Brittell (1990) also found that lynx like to travel along roads of less than 15 meters' width and with cover on both sides. They use these linear structures to move between areas within their large home range (Vogt et al. 2014) and to scent mark for territoriality and communication (Vogt et al. 2014).

Until now, the habitat selection of Eurasian lynx shortly after reintroduction and its differences regarding the phases of the day have not been fully investigated yet (Filla et al. 2017). We therefore will seek to link the outcomes of this study to other European research results regarding the habitat selection of a large carnivore in our human-dominated landscape. Our research might contribute to improve management actions of Eurasian lynx, especially when considering reintroduction programmes. In this study, we investigated the habitat selection of newly reintroduced Eurasian lynx in relation to anthropogenic structures, habitat parameters and time of the day (day or night rhythmic).

Based on the results of previous studies of lynx in Europe, we predict that newly reintroduced lynx

1) do not avoid human settlements and select for areas closer to human disturbed areas at night than during the day.

2) at night use areas closer to main forestry roads and public roads than during the day.

3) choose higher terrain ruggedness (steeper areas with higher elevation) when resting (daytime GPS locations), whereas lower elevations and flatter terrain are selected during night.

4) select areas in proximity to grassland / meadows areas (human maintained) as hunting grounds during the night.

Material and methods

Study area

We conducted our study in the Palatinate Forest in the southwestern part of Germany, located in the temperate zone between Atlantic and continental climates (49°12'N, 7°45'N). With over 1,790 km² the Palatinate Forest is the largest contiguous forest area in Germany (**Fig. 1)** (Pfälzerwald-Nordvogesen 2021) and borders the northern part of the Vosges du Nord. The Palatinate Forest elevation ranges from 210 m to 609 m a.s.l.. Annual precipitation is about 700–800 mm and annual average temperature is 10–11.5 °C (2015–2020, Rheinland-Pfalz Kompetenzzentrum für Klimawandelfolgen (2021)). Geological processes created a variegated average mountain range with a dense and steep carved valley system and various hill formations (MUEEF RLP 2012). Intensive forestry is practiced in large parts of the state- and communally owned parts of the Palatinate Forest, which has led to a highly developed forestry road network and extensive forestry care. The Palatinate Forest contains only small settlements and little infrastructure. Increased recreational activities mainly takes place in the eastern and southern part. In addition to outdoor tourism like hiking and mountain biking, hunting is common in this region. The primary species of wild ungulates are roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*). In the northern part of the forest, mouflon (*Ovis musimon)* are found in small numbers. The annual harvest rate of red deer in the state-managed hunting areas in the center of the study area between 2007 and 2015 averaged 1.13 individuals / km², whereas roe deer and wild boar revealed 2.1 individuals / km² and 1.83 individuals / km², respectively (Hohmann et al. 2018).

Lynx Reintroduction and Location Data

In 2015, an EU-LIFE project supervised by the Foundation of Nature and Environment (SNU) Rhineland-Palatinate (SNU-RLP 2020) began reintroducing lynx in the Palatinate Forest. Over five years, from 2016 to 2020, 20 lynx originating from Slovakia (Carpathian Mountains) and Switzerland were released (SNU-RLP 2020; SNU-RLP 2018). The released lynx were mostly wild catches but also rescued orphans and differed in age (SNU-RLP 2020). GPS collars were fitted on all reintroduced lynx, with an approximately one/two year battery life. The temporal resolution of GPS positions differs slightly between individuals (SNU-RLP 2020). In spring 2020, 17 to 19 independent lynx were verified in the study area based on a systematic camera trapping survey and telemetry data from the reintroduction program (Port 2020; SNU-RLP 2020). The GPS locations of 14 lynx geographically located in the Palatinate Forest were used in this study (SNU-RLP 2020).

Explanatory variables

A total of nine explanatory variables were used in the habitat selection analysis of lynx in the Palatinate Forest (**Appendix 1 Tab. 1**). We applied a digital terrain model with 5 m resolution (LVermGeoRP 2020) to extract altitudes. Furthermore, we extracted slope and direction (aspect) for each single position. Three different road classifications were included in the analysis. Public roads are defined as paved roads. Forestry roads were differentiated between truck-drivable roads and not truck-drivable roads (only 4WD car, Landesforsten RLP Forest Taxation (2020)). The explanatory variables grassland and meadows (LVermGeoRP 2020) were used to determine the habitat selection of lynx. Grasslands are cultivated grassed areas which are not utilized as a farmland crop. The sizes ranged from a minimum of 0.01 km² to a maximum of 0.28 km². Meadows are defined as small grazing areas within the forest (wild meadows, glades), maintained by hunters bringing out seed mixtures on the meadows to attract ungulates and small mammals (hares). The sizes of meadows varied from a minimum of < 0.01 km² to a maximum of 0.026 km².

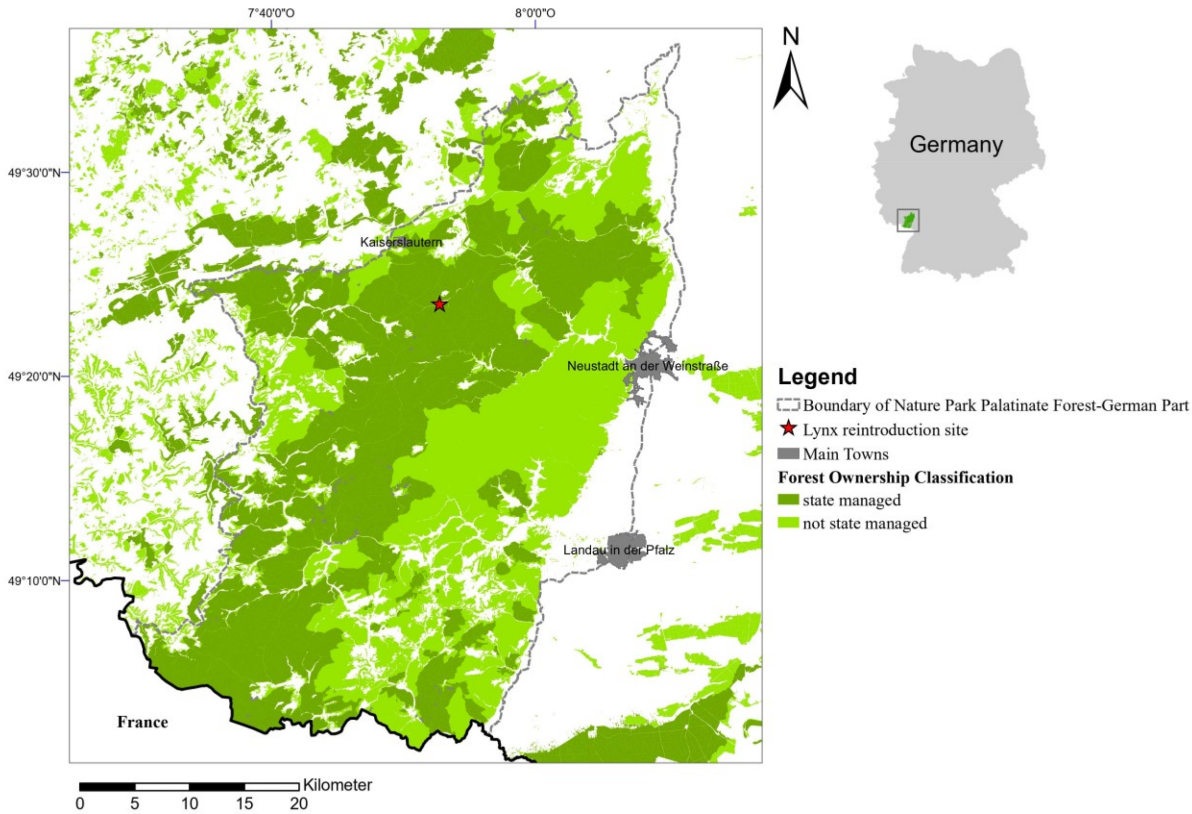

Fig. 1 Location of the Palatinate Forest within Germany (inset) with the Biosphere Reserve Boundary and the lynx reintroduction site. The area not colored comprises agricultural land, settlements and infrastructure.

Data was available from the forest taxation data base of Rhineland Palatinate (Landesforsten RLP Forest Taxation 2020; LVermGeoRP 2020) and the ATKIS data base (LVermGeoRP 2020). The distances from the above-mentioned variables to lynx locations and random locations were determined in R 3.5.3 (R Core Team 2020). Moreover, we calculated the distances to villages (human settlements) in order to determine if human disturbances affect the habitat selection of lynx.

Data structure and statistical analyses

The underlying dataset contained GPS locations of 14 lynx individuals from 11th August 2016 to 31st December 2019 within the boundary of the Palatinate Forest (98% of all registered lynx GPS positions, **Fig. 1**). There were between 404 and 4,648 GPS locations for each lynx individual. The first 14 days after reintroduction of lynx within the Palatinate Forest were removed from the data set to exclude behaviour patterns caused by the relocation. In order to compare the different activity phases of lynx, daytime locations were defined as locations after sunrise until nautical dawn (excluding), whereas night-time locations are locations including nautical dawn, nautical dusk and night-time. Calculations were carried out with the R package *suncalc* (Thieurmel and Elmarhraoui 2019).

Each lynx GPS location was buffered with 500 m (circle form; Bivand and Rundel (2020)) and within this circular buffer a corresponding random point was placed (Bivand et al. 2013; Pebesma and Bivand 2005). Habitat parameters (see environmental covariates) were calculated for each location (lynx and random locations) with the *raster* (Hijmans 2020) and *rgeos* packages (Bivand and Rundel 2020). We considered distances to forestry roads, which were greater than 1,000 m as outliers and excluded them from the data set ($n_{truck\ driv.} = 6$, $n_{not\ truck\ driv.} = 2$). For public roads we considered distances with 3,000 m as outliers ($n_{public} = 25$). Prior to the analysis, we checked multicollinearity with variance inflation factors using the *car* package (Fox and Weisberg 2011). We could not find any multicollinearity between the geographic habitat features.

We analysed the data with respect to the following aspects:

1) Comparison of random locations with lynx GPS locations (day- and night-time)

We applied a generalized linear model (GLM) when comparing lynx GPS locations with random locations. The response variable of the GLM was binomial (1 = GPS lynx locations day and night, 0 = random locations). The explanatory variables were the environmental covariables described above. The output of the model is connected to hypothesis 2, 3 and 4.

2) Comparison of random locations with night-time lynx GPS locations

We applied a generalized linear model (GLM) when comparing night-time lynx GPS locations with random locations. The response variable of the GLM was binomial (1 = GPS lynx locations night, 0 = random locations). The explanatory variables were the environmental covariables described above. The output of the model is connected to hypothesis 2, 3 and 4.

3) Comparison of daytime with night-time lynx GPS locations

We applied a generalized linear mixed-effect model (GLMM) when comparing daytime with night-time lynx GPS locations regarding their habitat selection. Lynx individual was used as a random effect to encounter for individual variation / preferences in lynx habitat selection (Gillies et al. 2006). The response variable of the GLMM was binomial (1 = GPS lynx locations night, 0 = GPS lynx locations day). The explanatory variables were the environmental covariables described above. The output of the model is connected to hypothesis 2, 3 and 4.

4) Comparison of daytime with night-time lynx GPS locations and additional random locations to lynx GPS locations regarding villages

For the comparison of random locations to lynx GPS locations (day- and night-time) regarding villages we used a generalized linear model (GLM). Again the response variable of the GLM was binomial (1 = GPS lynx locations day and night, 0 = random locations). The explanatory variable was the environmental covariable 'village'. The output of the model is connected to hypothesis 1.

We applied a generalized linear mixed-effect model (GLMM) when comparing daytime and night-time lynx GPS locations in relation to villages. Again, lynx identification was used as a random effect to account for individual variation in lynx habitat selection within this model. The response variable of the GLMM was binomial (1 = GPS lynx locations night, 0 = GPS lynx locations day). The explanatory variable was the environmental covariable 'village'.

To allow the models to converge, we scaled the variables (i.e. standardized by shifting the centre to their means, and scaling with the respective standard deviation). Model evaluation was done for all model set-ups by using the Akaike information criterion (AIC) for small sample size to select the most parsimonious model (Burnham and Anderson 2002). All analyses were done in R version 3.5.3 and 4.0.3 (R Core Team 2020).

Results

GPS data points of 14 reintroduced lynx in the Palatinate Forest provided us with 18,038 GPS locations. An equal sex ratio of seven individuals each was used in the data analysis (**Appendix 1 Tab. 2**). When analysing the data, we produced several models, which were similar to the best supported model (**Appendix 1 Tab. 3**).

Comparison of random locations with lynx GPS locations (day and night-time)

We found a strong selection for truck-drivable and not truck-drivable forestry roads for habitat selection of lynx if compared to random locations (truck-drivable: $p < 0.001$, not truck-drivable: $p = 0.045$, **Tab. 1, Fig. 2**). Lynx chose areas close to truck-drivable forestry roads, whereas the proximity to not truck-drivable forestry roads were less likely to be used (**Fig. 2**). Additionally lynx selected areas with higher slopes ($p < 0.001$, **Fig. 3**). Grassland areas and meadows were selected by lynx in comparison to random locations (grassland areas: $p = 0.007$; meadows: $p = 0.020$, **Fig. 3**).

Comparison of random locations with night-time lynx GPS locations

When examining the predicted probability of habitat selection of lynx at night in comparison to random locations, we found a strong selection of lynx for areas close to truck-drivable forestry roads and grassland (truck-drivable forest path: $p = 0.002$, grassland: $p = 0.02$, **Tab. 1**, **Fig. 4**). In addition, elevation, slope and direction had significant influence on night-time habitat selection of lynx (**Tab. 1**, **Fig. 4**). At night-time lynx selected lower elevations, higher slopes and south-orientated habitats in comparison to random locations (**Fig. 4**).

Comparison of daytime with night-time lynx GPS locations

We found a strong preference of lynx at night towards forestry roads and public roads (**Tab. 1**). Lynx at night-time selected habitats closer to public roads and to not truck-drivable forestry roads and preferred south-orientation habitats (**Fig. 5**). Furthermore, the best-supported model revealed high significance for the effects of elevation, slope and distance to grassland areas on the spatiotemporal habitat selection of lynx at night (**Fig. 6**). Lynx used habitats with lower elevation and lower slope at night-time in comparison to daytime (**Tab. 1**, **Fig. 6**).

At night, lynx utilized habitats closer to grassland areas than during daytime. Conversely, we found a marginally non-significant effect of distance to meadows on the spatiotemporal habitat selection of lynx (**Tab. 1, Fig. 6**); e.g. during daytime lynx utilized habitats closer to meadows than during night-time.

Comparison of daytime with night-time lynx GPS locations and random locations regarding villages

We found no evidence that lynx were avoiding villages when comparing lynx locations to random locations (distance to nearest village: $p = 0.467$). In examining the probability of habitat selection of lynx during different times of the day in relation to villages, we found a strong selection of lynx towards villages at night ($p < 0.001$, **Appendix 1 Fig. 1**).

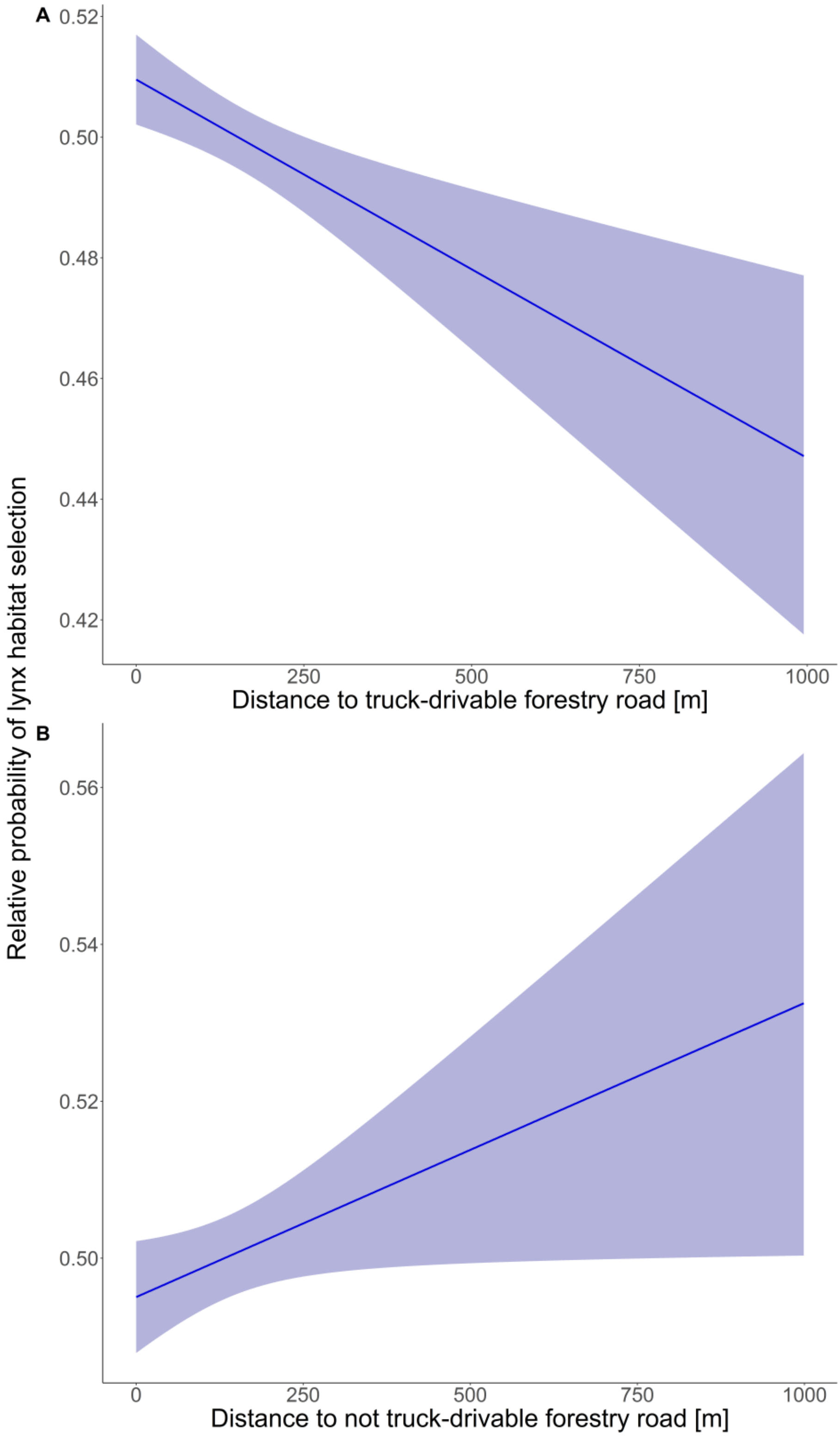

Fig. 2 Effect of truck-drivable and not truck-drivable forestry roads on the probability of lynx habitat selection compared to random locations in the Palatinate Forest.

Tab. 1 Parameter estimates for the GLM and GLMM models on the habitat selection of lynx comparing lynx GPS locations (day- and night-time) to random locations (**A**), night-time lynx GPS locations to random locations (**B**) and comparing between day- and night-time lynx GPS locations (**C**) of 14 lynx in the Palatinate Forest. Model C included the individual variation of lynx in a GLMM model. Coefficients at a 0.05 significance level are in bold.

A Comparison of random locations with lynx GPS locations (day- and night-time)			
Fixed effects	Estimate	Std. Error	P value
Road truck-drivable	-3.783e-02	1.079e-02	**<0.001**
Road not truck-drivable	2.327e-02	1.160e-02	**0.045**
Slope	2.885e-01	1.093e-02	**<0.001**
Grassland	-3.060e-02	1.134e-02	**0.007**
Meadow	-2.824e-02	1.217e-02	**0.020**
B Comparison of random locations with night-time lynx GPS locations			
Fixed effects	Estimate	Std. Error	P value
Road truck-drivable	-0.044	0.0144	**0.002**
Elevation	-0.037	0.015	**0.014**
Slope	0.124	0.015	**<0.001**
Direction	-0.043	0.020	**0.028**
Grassland	-0.033	0.014	**0.023**
C Comparison of daytime with night-time lynx GPS locations			
Fixed effects	Estimate	Std. Error	P value
Road Public Road	-0.091	0.017	**<0.001**
Road not truck-drivable	-0.075	0.017	**<0.001**
Elevation	0.146	0.017	**<0.001**
Slope	-0.445	0.017	**<0.001**
Direction	-0.095	0.016	**<0.001**
Grassland	-0.048	0.018	**0.01**
Meadow	0.044	0.025	0.078

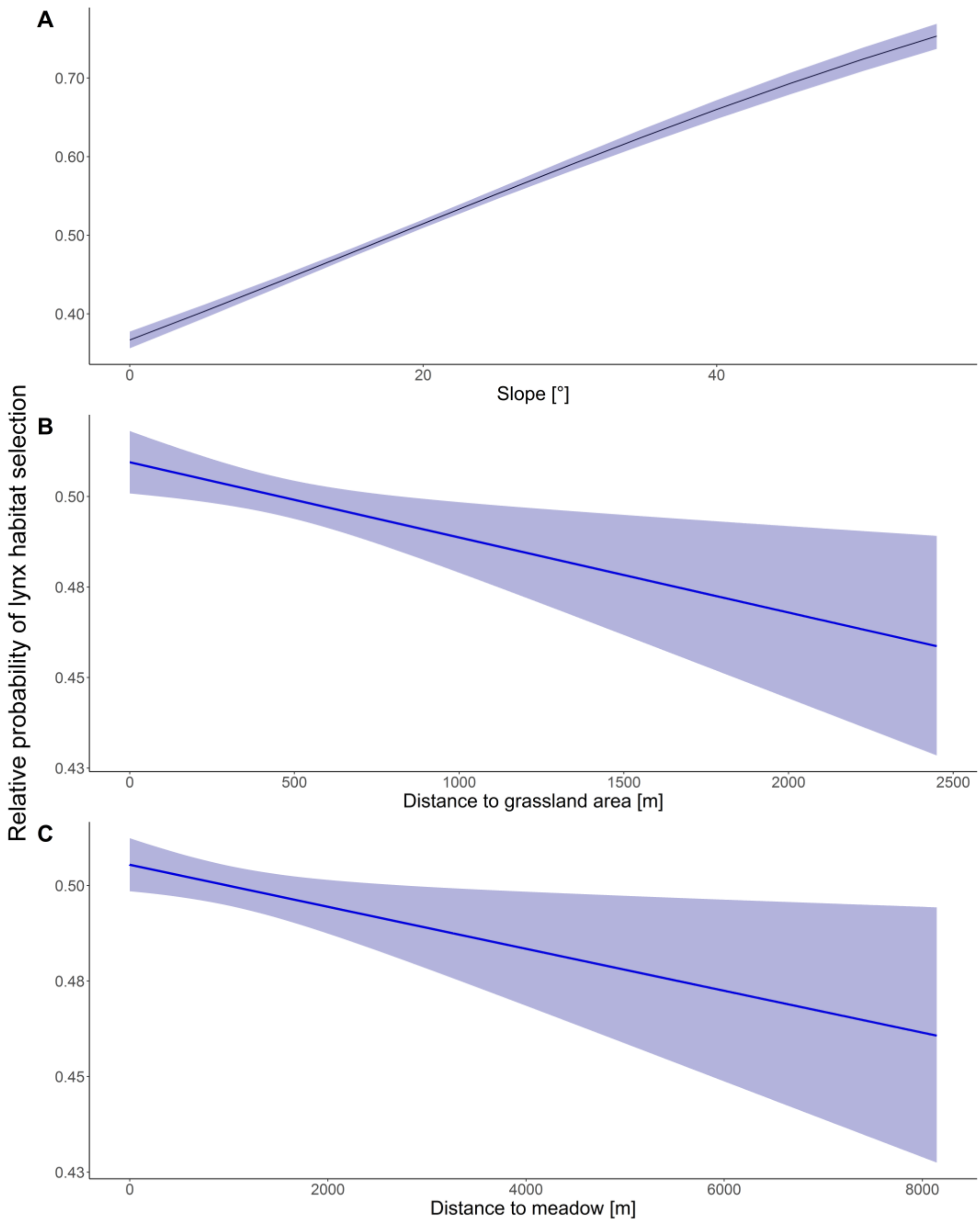

Fig. 3 Effect of slope, grassland areas and meadows on the probability of lynx habitat selection compared to random locations in the Palatinate Forest.

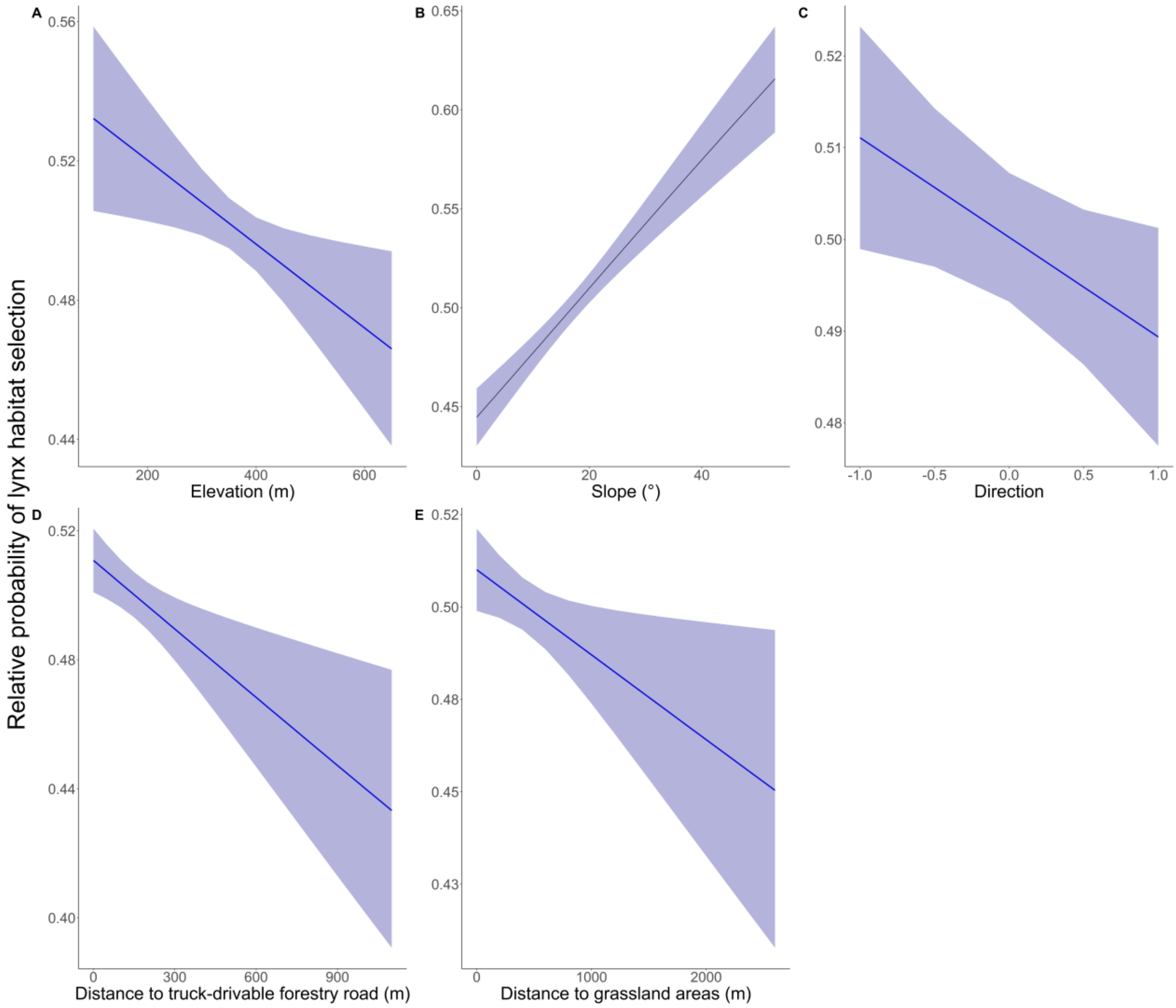

Fig. 4 Effect of truck-drivable roads, slope, grassland areas, direction and elevation on the probability of lynx habitat selection at night compared to random locations in the Palatinate Forest.

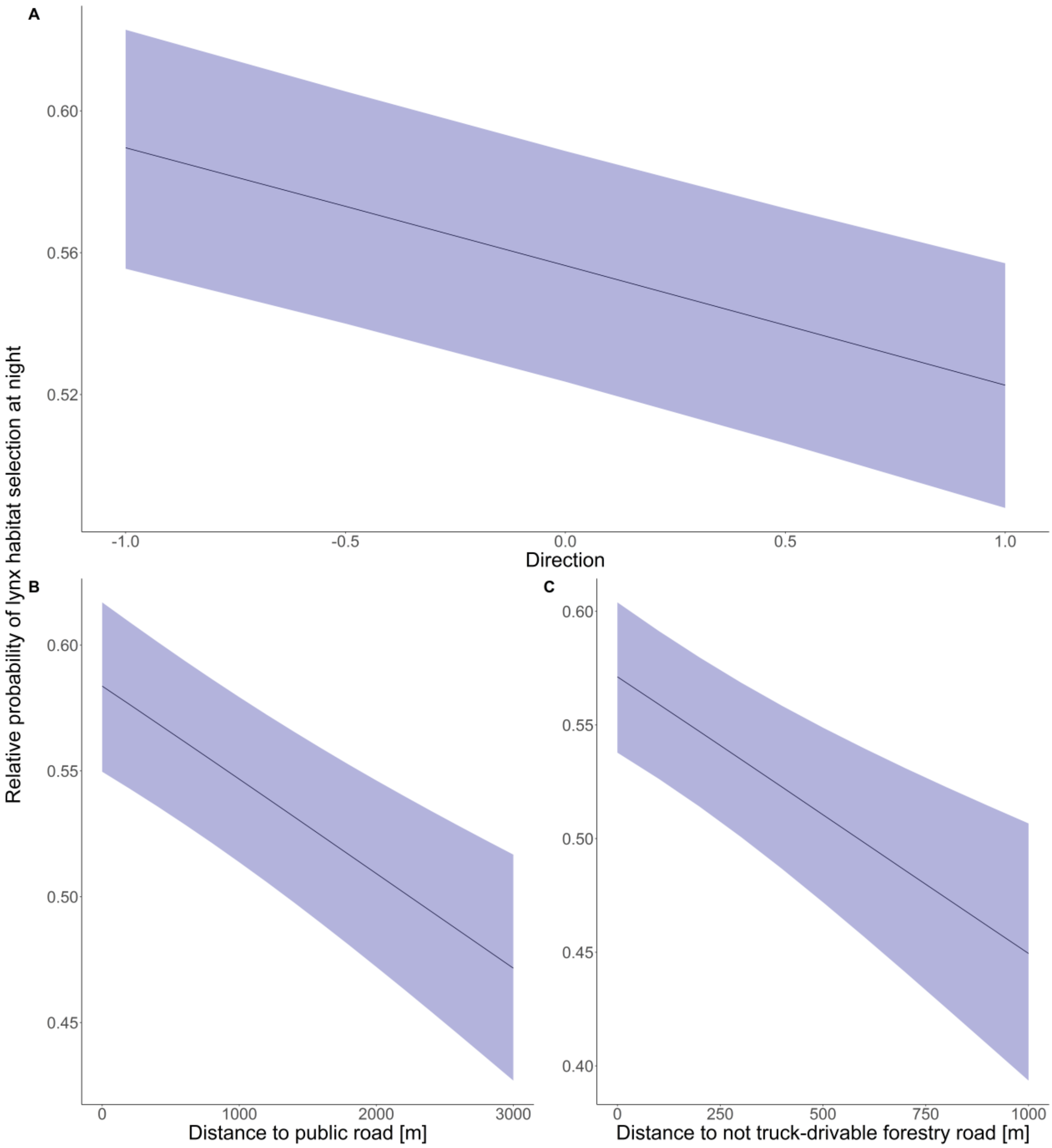

Fig. 5 Effect of public and not truck-drivable roads and direction on the probability of lynx habitat selection based on the comparison of daytime and night-time GPS locations of lynx in the Palatinate Forest. Lynx ID was used as random effect within the GLMM model.

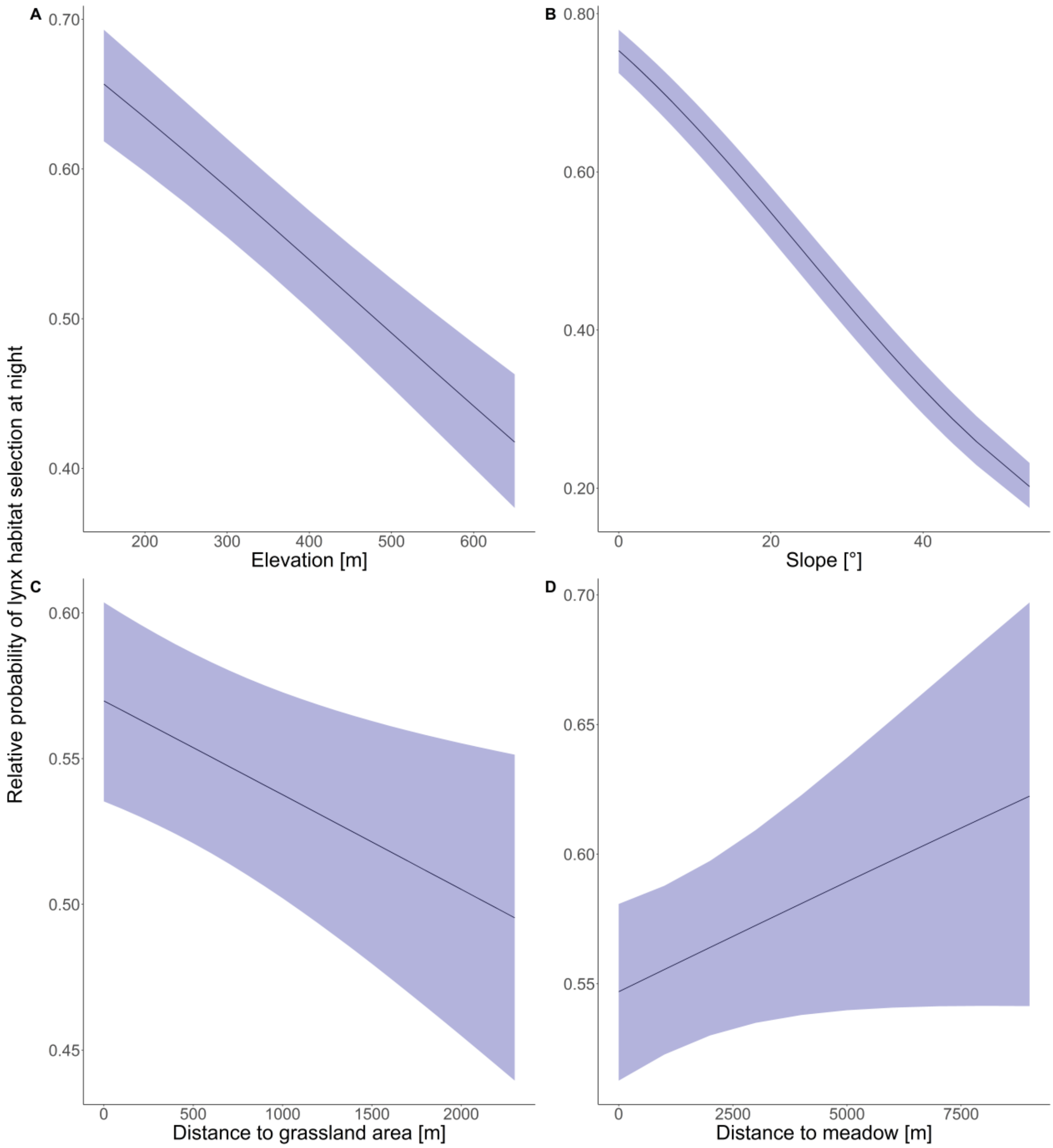

Fig. 6 Effect of elevation, slope, grassland areas and meadows on the probability of lynx habitat selection based on the comparison of daytime and night-time GPS locations of lynx in the Palatinate Forest. Lynx identification was used as random effect within the GLMM model.

Discussion

In accordance with the telemetry data of the newly reintroduced lynx in the Palatinate Forest Germany, we have obtained a first insight into lynx habitat selection in one of the largest continuous forested area in Germany.

In agreement with our prediction 1, our results reveal that lynx in general do not avoid the surroundings of villages in the Palatinate Forest (when comparing lynx to random locations) and even choose areas closer to them at night than during the day (when comparing lynx day to lynx night locations). Forestry roads and public roads play a crucial role in the habitat selection of lynx in our study area. When comparing lynx location data to a set of random locations, lynx actually choose areas close to truck-drivable forestry roads and even prefer areas closer to public roads and not truck-drivable roads at night compared to day. Our analysis shows that lynx prefer habitats on steep slopes and in close distances to grassland areas / meadows. In addition, habitat selection of lynx differs between day and night, with lynx at night selecting lower elevations, shallower terrain, closer distance to grassland and south-orientated areas.

Our results are in line with previous studies on habitat selection of lynx in Europe (Filla et al. 2017; Basille et al. 2009; Sunde et al. 1998). Human settlements do not seem to present a hurdle for lynx when certain habitat criteria are fulfilled. For instance, lynx in south-eastern Norway tolerate human disturbance when dense vegetation cover is present and mature stands are available (Sunde et al. 1998). Additionally, lynx prefer a medium level of modification (Bouyer, San Martin, et al. 2015), but seem to avoid very low and high modified areas as a trade-off between prey availability and avoidance of human activity (Bouyer, San Martin, et al. 2015; Basille et al. 2009).

Additionally we found clear differences in lynx habitat selection between day and night-time in relation to distances to villages, which also was found in the Bohemian Forest Ecosystem (Filla et al. 2017). Lynx in the Palatinate Forest used areas in proximity to human settlements more often during the night than during the day, supporting the results of Filla et al. (2017) that lynx during the day avoided settlements by up to one kilometre. Lynx select human-disturbed areas during times of low human encounter risk, i.e. during late evening and night (Filla et al. 2017; Gehr et al. 2017; Ordiz et al. 2011). The reason for this can be higher prey availability in proximity to human settlements (Basille et al. 2009). In our study area, villages present attractive grazing grounds for deer, offering ample prey and cover for lynx near these human settlements which may explain why lynx do not avoid these areas, especially during the night. Additionally, Sunde et al. (1998) found that lynx in Norway avoid human settlements and roads by 200 m while resting, which mostly happens during the day, supporting also the aforementioned results.

In contrast, lynx in Poland seem to avoid human settlements and transportation infrastructure on a large scale (Niedziałkowska et al. 2006). The authors found that lynx are sensitive to forest connectivity, which makes it difficult for lynx to disperse to the extensive woodlands in the west and north-west of Poland, and are mostly found in the east and south of the country (Niedziałkowska et al. 2006). To achieve such a dispersal, it would be necessary to cross the highly human-modified and heavily deforested central part of Poland (Niedziałkowska et al. 2006); thus the lynx avoid human settlements in connection to low forest cover density on a landscape scale. However, our study area is characterized by only minimal infrastructure and small villages within the forest. Furthermore, our results are based on a much smaller scale and we assume that human disturbance will be on a lower level than in other study areas, giving lynx the opportunity to choose areas close to human settlements in the Palatinate Forest at night-time.

Human settlements as well as infrastructure, represented by roads (public roads, forestry roads), might influence the habitat selection of large carnivores (Moen et al. 2010; Niedziałkowska et al. 2006). Lynx in the Palatinate Forest prefer to use areas close to forestry roads (truck-driveable and not truck-drivable forestry roads) regardless of the time of day, whereas at night-time, areas close to public roads and minor roads (not truck-drivable forestry roads) are selected over daytime. This supports our initial hypothesis 2. Again, lynx are selecting areas close to public roads at night-time, when the chance of human encounter is very low.

The forest road network within the Palatinate Forest is very dense with 50–90 m/ha forest (Simon and Kotremba 2016; Ministerium für Umwelt und Forsten RLP 2002). In comparison, the road networks of the Bavarian Forest National Park and Harz National Park are described as dense with 29 m/ha and 33 m/ha forest, respectively (Röhl 2013; Kellner 2012), giving the Palatinate Forest a special position with regard to the existing forestry road network. This network can be beneficial for lynx in terms of energetic perspectives (Moen et al. 2010). Lynx are known to use linear structures for long-distance movements, for dispersal, for shifting areas within their home range and for scent marking (Vogt et al. 2014; Donovan et al. 2011; Moen et al. 2010). Forestry roads in the Palatinate Forest may also be preferred by lynx due to possible higher detection rate of roe and red deer, the main prey of lynx in Europe (Breitenmoser and Breitenmoser-Würsten 2008). Thus, lynx selecting for areas close to roads might be also connected to prey availability and density. Forestry roads and public roads represent edge habitats that are characterized by a higher light regime and therefore often have more ground vegetation (Coffin 2007), which could be an attractive foraging ground for deer. Our results present a new insight into the habitat selection of lynx regarding different road and forestry road categories, which to our knowledge has not yet been published. We assume that different kind of road types (public roads and forestry roads) affect habitat selection of lynx in the Palatinate Forest and that lynx might benefit from the high availability of forestry roads.

In line with our third prediction, we found that lynx in the Palatinate Forest choose areas with lower terrain ruggedness (lower elevation and lower slopes) during the night than during the day. This is also known for lynx in the Bohemian Forest, where lynx choose rugged terrain during the day (Filla et al. 2017). Additionally, these results were also consistent with the research conclusions found in Norway by Bouyer, San Martin, et al. (2015) and partially by Sunde et al. (1998) (steep slopes). Also, Signer et al. (2019) found that lynx select their day resting sites in proximity to rock formations. Rugged terrain and steepness of relief correlate with a lower probability of being disturbed by or encountering humans (Bouyer, San Martin, et al. 2015; Basille et al. 2009) and possibly offer higher availability for shelter, resting sites or dens. On the other hand, habitat preferences of lower elevation and lower steepness at night suggests that lynx in the Palatinate Forest choose areas with higher prey density. Gehr et al. (2017) found that lynx in the Swiss Alps, use areas of high prey availability during the night when human activity is low, supporting our hypothesis. Higher prey density can presumably be found close to grasslands areas and also in valleys in the Palatinate Forest.

Our results show that lynx in the Palatinate Forest chose areas close to grassland areas, especially during the night, supporting our fourth hypothesis, that grassland areas are attractive hunting grounds for lynx at night. This is also in line with previous studies of Eurasian Lynx (Filla et al. 2017; Poole et al. 1996). In the Bohemian Forest Ecosystem for instance, lynx selected meadows (cultivated, natural and wetland pooled together) over mature stands during the nights. Filla et al. (2017) assume that lynx choose this habitat due to sufficient vegetation cover of high grasses to stalk prey. This habitat selection was also described for bobcats (*Lynx rufus*) and Canadian lynx (*Lynx canadensis*) (Poole et al. 1996; Rolley and Warde 1985). We agree with Filla et al. (2017) and additionally assume that lynx in the Palatinate Forest select areas close to grassland (open areas) due to a higher prey population (higher prey encounter rate). On the other hand, lynx seem to choose habitats near meadows during day. Here, we would assume that human disturbance at meadows within the forest during day is less than near the grassland areas, hence lynx might select their day resting sites in proximity to meadows.

Our study reveals details on habitat selection of lynx, especially shortly after reintroduction into a closed forest ecosystem. We conclude that the habitat selection of lynx in the Palatinate Forest during the night is driven by prey availability and decreased human disturbance. During the night, areas close to grasslands with low elevation and lower slopes are selected, which are represents habitats with high prey density. Habitat selection for public roads and proximity to villages during the night reveal that lynx make use of the human-modified landscape, however at times when human disturbance is low.

We investigated the habitat selection of recently-reintroduced lynx within the largest closed forest ecosystem of Germany, which is characterized by a very high density of forestry roads. Our study highlights the strong preference of lynx to forestry roads as linear structures. Lynx might not only use the forestry roads for movement and territorial delimitation, but also for hunting purpose due to the extensive coverage of forestry roads. This hypothesis must be further investigated. Nevertheless, our results suggest also that lynx show a preference to the proximity of public roads at night compared to day. Reasons for this could be the lower traffic volume at night and thus the lower encounter rate with humans. This could lead to a reduction in the mortality risk for lynx along public roads. On the other hand, roads with little traffic but high speed limit embedded high risk of accidents (Seiler 2003), perhaps because animals often do not perceive these roads as a danger, which in turn can lead to an increased risk of mortality.

An additional unnatural lynx mortality risk within such a young vulnerable population where each individual is a valuable contribution to the population establishment within the Palatinate Forest, should be avoided. Traffic collisions make up around 20–42% of lynx mortality cases (Herdtfelder 2012, Heurich et al. 2018). So far, only two fatal accidents involving traffic collisions (train and car collision) have been recorded for lynx in the Palatinate Forest. Road risk maps could help in identifying collision hotspot (Herdtfelder 2012, Heurich et al. 2018), also referred to road-kill black spots (Garrote et al. 2018) and lead to direct management implications by deploying for example warning signs, speed limitations and crossing aids (bridges, tunnels). Conservation managers often have to make decisions lacking scientifically evaluated research, which justifies further detailed research on the spatial requirements of large carnivores in fragmented landscape (Schadt, Knauer, et al. 2002). Our findings complement current knowledge about the habitat requirements of large carnivores and could improve management and conservation plans in the heavily fragmented European landscapes.

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References

Basille M, Herfindal I, Santin-Janin H, Linnell JD, Odden J, Andersen R, Arild Høgda K, Gaillard J-M (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography 32:683-691

Basille M, Van Moorter B, Herfindal I, Martin J, Linnell JD, Odden J, Andersen R, Gaillard J-M (2013) Selecting habitat to survive: the impact of road density on survival in a large carnivore. PloS one 8:e65493

Belotti E, Červený J, Šustr P, Kreisinger J, Gaibani G, Bufka L (2013) Foraging sites of Eurasian lynx *Lynx lynx*: relative importance of microhabitat and prey occurrence. Wildlife Biol 19:188-201

Bivand R, Rundel C (2020) rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.5-5 2020

Bivand RS, Pebesma EJ, Gómez-Rubio V (2013) Applied Spatial Data Analysis with R. Springer Science, New York

Bouyer Y, San Martin G, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. Biological Conservation 191:291-299

Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs. Salm Verlag, Wohlen/Bern, Switzerland: 1-537

Breitenmoser U, Breitenmoser-Würsten C, Okarma H, Kaphegyi T, Kaphegyi U, Wallmann U, Müller M (2000) Action plan for the conservation of the Eurasian lynx in Europe. Council of Europe, Nature and Environment, 112: 1-69

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach (2nd edition). Springer-Verlag, New York

Červený J, Koubek P, Bufka L (2002) Eurasian lynx (*Lynx lynx*) and its chance for survival in central Europe: the case of the Czech Republic. Acta Zoologica Lituanica 12:428-432

Chapron G, Kaczensky P, Linnell JD, von Arx M, Huber D, Andrén H, López-Bao JV, Adamec M, Álvares F, Anders O (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517-1519

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transport Geography 15:396-406

Donovan TM, Freeman M, Abouelezz H, Royar K, Howard A, Mickey R (2011) Quantifying home range habitat requirements for bobcats (*Lynx rufus*) in Vermont, USA. Biological Conservation 144:2799-2809

Filla M, Premier J, Magg N, Dupke C, Khorozyan I, Waltert M, Bufka L, Heurich M (2017) Habitat selection by Eurasian lynx *(Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. Ecology and Evolution 7:6367-6381

Fox J, Weisberg S (2011) An R companion to applied regression. Sage Publications, Los Angeles

Gehr B (2016) Predator-prey Interactions in a Human-dominated Landscape. Doctoral dissertation. University of Zurich, Switzerland

Gehr B, Hofer EJ, Muff S, Ryser A, Vimercati E, Vogt K, Keller LF (2017) A landscape of coexistence for a large predator in a human dominated landscape. Oikos 126:1389-1399

Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL (2006) Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887-898

Herrero A, Heikkinen J, Holmala K (2020) Movement patterns and habitat selection during dispersal in Eurasian lynx. Mammal Research 65:523-533 doi:10.1007/s13364-020-00499-7

Heurich M, Möst L, Schauberger G, Reulen H, Sustr P, Hothorn T (2012) Survival and causes of death of European roe deer before and after Eurasian lynx reintroduction in the Bavarian Forest National Park. European Journal of Wildlife Research 58:567-578

Hijmans RJ (2020) Introduction to the'raster'package (version 3.0-12).

Hohmann U, Hettich U, Ebert C, Huckschlag D (2018) Evaluierungsbericht zu den Auswirkungen einer dreijährigen Jagdruhe in der Kernzone „Quellgebiet der Wieslauter“ im Wildforschungsgebiet „Pfälzerwald“ (Langfassung). vol Nr. 84/18. Forschungsanstalt für Waldökologie und Forstwirtschaft FAWF, Mitteilungen aus der Forschungsanstalt für Waldökologie und Forstwirtschaft FAWF

Hutto RL (1985) Habitat selection by nonbreeding, migratory land. In: Cody ML (ed) Habitat selection in birds, vol 455. Academic Press, Orlando, Fla., pp 455-476

Kellner C (2012) Komitee-Bericht zur Evaluierung des Nationalparks Harz. Ingenieurbüro für Planung und Umwelt - IPU

Koehler GM, Brittell JD (1990) Managing spruce-fir habitat for lynx and snowshoe hare. Journal of Forestry 88:10-14

Kramer-Schadt S, Revilla E, Wiegand T (2005) Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biol Conserv 125:169-182

Landesforsten RLP Forest Taxation (2020).

Linnell JD, Swenson JE, Anderson R (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation 4:345-349

Lüchtrath A, Schraml U (2015) The missing lynx - understanding hunters' opposition to large carnivores. Wildlife Biology 21:110-119

LVermGeoRP, GeoBasis-DE (2020) dl-de/by-2-0. lvermgeo.rlp.de.

Ministerium für Umwelt und Forsten RLP (2002) Wildkatzen in RLP.

Moen R, Terwilliger L, Dohmen AR, Catton SC (2010) Habitat and road use by Canada lynx making long-distance movements. Center for Water and Environment, Natural Resources Research Institute, Duluth

MUEEF RLP (2012) Klimawandel-Informationssystem RLP: Regionale Informationen - Pfälzerwald. Ministry of Environment, Energy, Food and Forestry Rhineland-Palatinate. kwis-rlp.de/de/anpassungsportal/regionale-informationen/pfaelzerwald/. Accessed 15.01.2018

Niedziałkowska M, Jędrzejewski W, Mysłajek RW, Nowak S, Jędrzejewska B, Schmidt K (2006) Environmental correlates of Eurasian lynx occurrence in Poland – Large scale census and GIS mapping. Biological Conservation 133:63-69

Ordiz A, Støen O-G, Delibes M, Swenson JE (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166:59-67

Pebesma E, Bivand RS (2005) S classes and methods for spatial data: the sp package. R news 5:9-13

Pfälzerwald-Nordvogesen B (2021) Biosphärenreservat Pfälzerwald-Nordvogesen. www.pfaelzerwald.de. Accessed 01.10. 2020

Podgórski T, Schmidt K, Kowalczyk R, Gulczyńska A (2008) Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica 53:97-110

Poole KG, Wakelyn LA, Nicklen PN (1996) Habitat selection by lynx in the Northwest Territories. Canadian Journal of Zoology 74:845-850

Port M (2020) Systematisches Fotofallenmonitoring des Luchses im Pfälzerwald. FAWF Mitteilungen. Institute for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Trippstadt

R Core Team (2020) R: A language and environment for statistical computing.R Foundation for Statistical Computing.Vienna.

Rheinland-Pfalz Kompetenzzentrum für Klimawandelfolgen (2021). www.kwis-rlp.de. Accessed 01.04 2021

Röhl U (2013) Komitee-Bericht zur Evaluierung des Nationalparks Bayerischer Wald. Ingenieurbüro für Planung und Umwelt - IPU

Rolley RE, Warde WD (1985) Bobcat habitat use in southeastern Oklahoma. The Journal of Wildlife Management 49:913-920

Sandrini J (2010) Eignungsanalyse von Fotofallen-Standorten für das Monitoring von Luchsen (*Lynx lynx L.*) im Bayerischen Wald. Diplomarbeit, Universität Freiburg

Schadt S, Knauer F, Kaczensky P, Revilla E, Wiegand T, Trepl L (2002) Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. Ecological Applications 12:1469-1483

Schadt S, Revilla E, Wiegand T, Knauer F, Kaczensky P, Breitenmoser U, Bufka L, Červený J, Koubek P, Huber T (2002) Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecology 39:189-203

Seiler A (2003) The toll of the automobile: Wildlife and roads in Sweden. Doctoral thesis, Departmen of Conversation Biology, Swedish University of Agricultural Science, Uppsala, Sweden

Signer J, Filla M, Schoneberg S, Kneib T, Bufka L, Belotti E, Heurich M (2019) Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. Wildlife Biology 2019 (1):1-5

Simon O, Kotremba C (2016) Lebensraumgutachten Rotwild in der Hegegemeinschaft Pfälzerwald-Süd KdöR - Lebensraumanalyse und Maßnahmenempfehlungen 2014/2015. Unveröffentlichtes Gutachten. Auftraggeber Rotwildhegegemeinschaft "Pfälzerwald-Süd", 1-70, Institut für Tierökologie und Naturbildung.

SNU-RLP (2018) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed Januar 18, 2018

SNU-RLP (2020) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed 15.11.2020

Sunde P, Stener SØ, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. Wildlife Biol 4:177-183

Thieurmel B, Elmarhraoui A (2019) Suncalc: Compute sun position, sunlight phases, moon position and lunar phase. R Package Version 50

Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324-336

Vogt K, Zimmermann F, Kölliker M, Breitenmoser U (2014) Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behav Processes 106:98-106

Weingarth K, Heibl C, Knauer F, Zimmermann F, Bufka L, Heurich M (2012) First estimation of Eurasian lynx (*Lynx lynx*) abundance and density using digital cameras and capture–recapture techniques in a German national park. Anim Biodivers Conserv 35:197-207

Weingarth K, Zeppenfeld T, Heibl C, Heurich M, Bufka L, Daniszová K, Müller J (2015) Hide and seek: extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. Biodiversity and Conservation 24:2935-2952

White S, Briers RA, Bouyer Y, Odden J, Linnell JDC (2015) Eurasian lynx natal den site and maternal home-range selection in multi-use landscapes of Norway. Journal of Zoology 297:87-98

Zimmermann F, Breitenmoser-Würsten C, Breitenmoser U (2005) Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. Journal of Zoology 267:381-395

Zimmermann F, Breitenmoser U (2007) Potential distribution and population size of the Eurasian lynx *Lynx lynx* in the Jura Mountains and possible corridors to adjacent ranges. Wildlife Biology 13:406-416

Supporting Information Appendix 1

Appendix 1 Tab. 1 Description of nine explanatory variables included as predictors in the habitat selection analysis of lynx in the Palatinate Forest.

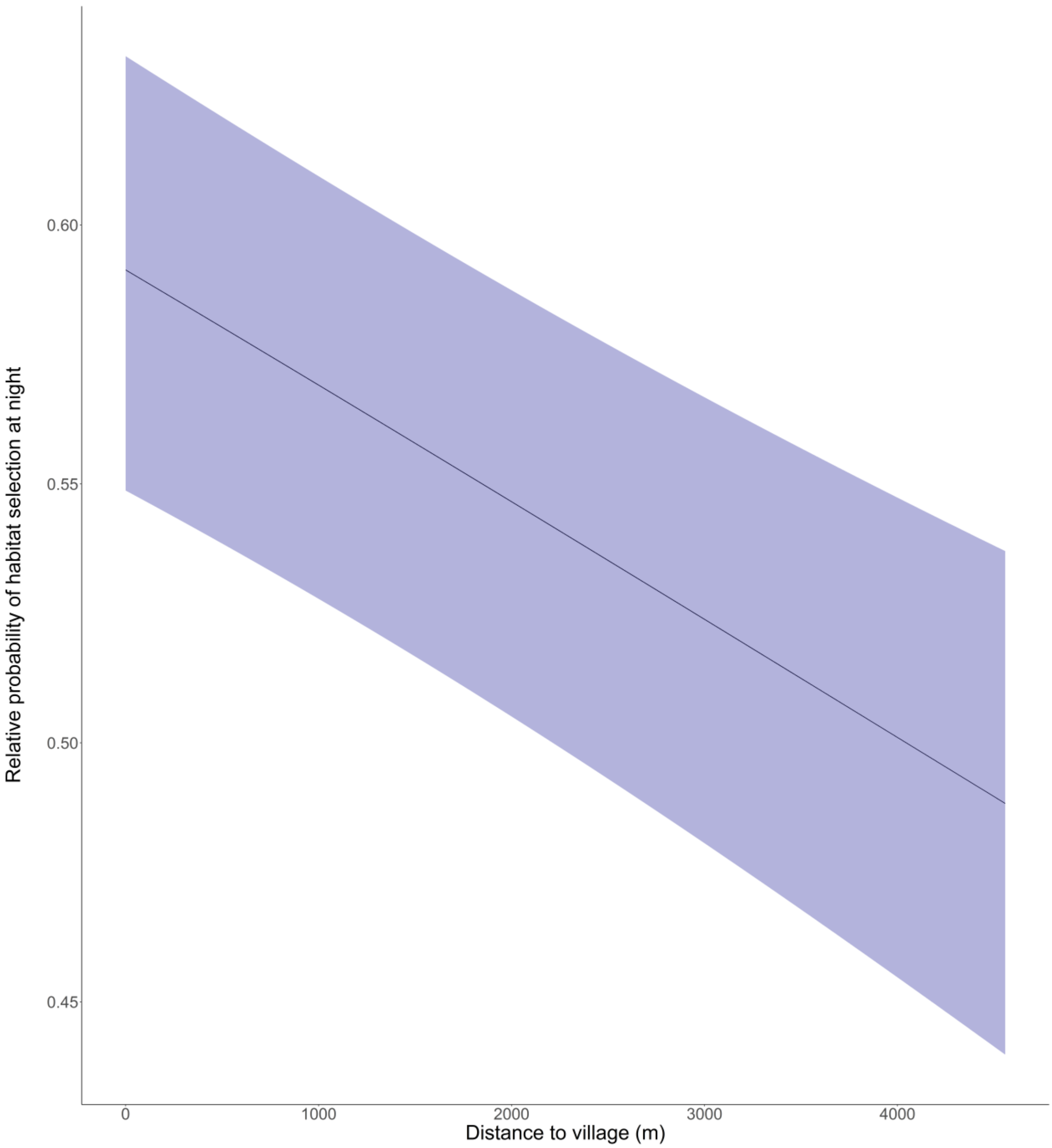
Anthropogenic-related variables	
Truck-drivable forestry road	Main forestry roads, passable by truck for wood transportation, by car and rescue vehicles with a minimum width of 3.0 m
Not truck-drivable forestry road	Smaller forestry roads, not passable by trucks, under certain weather conditions only passably by 4WD car
Public road	Paved public roads
Grassland	Cultivated grassed areas, not utilized as farmland crop, size range from 0.01 km² and 0.28 km²
Meadow	Small grazing areas within the forest with attractive grazing plants for ungulates and hares, maintained by hunters, usually presence of a hunting tower
Village	Human settlements
Geographic-related variables	
Elevation	
Slope	Based on a digital terrain model with 5m resolution
Direction	

Appendix 1 Tab. 2 Overview of lynx individuals whose GPS data was included in the data analysis. The first two weeks after release in the Palatinate Forest were excluded from the data set in order to remove possible behavioural actions due to relocation procedure. Lynx IDs of the Federal Agency for Nature Conservation (BfN) are also presented. Lynx GPS data were provided by the Foundation of Nature and Environment (SNU) Rhineland-Palatinate.

Lynx ID (BfN ID)	Sex	Period of time	Total no of GPS positions
Alfi (B2014)	Male	25.09.2018 – 27.02.2019	404
Brano (B2015)	Male	20.06.2019 – 09.10.2019	708
Cyril (B2004)	Male	20.06.2017 – 10.02.2018	1266
Gaupa (B354)	Female	27.03.2019 – 31.12.2019	1384
Jara (B315)	Female	03.05.2018 – 22.11.2018	986
Juri (B623)	Male	31.03.2018 – 25.11.2018	981
Kaja (B2002)	Female	12.08.2016 – 28.07.2017	1455
Labka (B2007)	Female	29.12.2017 – 25.02.2018	414
Libre (B628)	Male	21.03.2019 – 21.09.2019	1725
Lucky (B2000)	Male	12.08.2016 – 13.05.2019	6249
Luna (B2001)	Female	12.08.2016 – 03.12.2016	697
Mala (B264)	Female	27.02.2019 – 03.10.2019	1228
Rosa (B314)	Female	27.04.2017 – 11.06.2018	1404
Wrano (B2013)	Male	25.09.2018 – 23.06.2019	738

Appendix 1 Tab. 3 Results of model fitting for the habitat selection of lynx in the Palatinate Forest. Group of models were fitted separately for the lynx GPS locations (day and night-time) compared to random locations (**A**), night lynx locations compared to random locations (**B**) and lynx locations compared between day and night (**C**). Models were compared on the number of parameters and Akaike´s Information Criterion. All model parameters were scaled in order to converge. Path_cat_0 = truck drivable-paths, Path_cat_2 = public roads, Path_cat_3 = not truck-drivable paths (only 4WD car).

Data set	Model	AICc	Δ AICc	w
1) Comparison random locations with lynx GPS locations (day and night-time)	Path_cat_0 + Path_cat_3 + Slope + Grassland + Meadow	49190.1	0.00	0.289
	Path_cat_0 + Path_cat_3 + Elevation +Slope + Grassland + Meadow	49190.7	0.63	0.210
	Path_cat_0 + Path_cat_3 + Direction +Slope + Grassland + Meadow	49191.2	1.13	0.164
	Path_cat_0 + Path_cat_3 + Direction + Elevation +Slope + Grassland + Meadow	49191.9	1.80	0.117
	Path_cat_0 + Path_cat_2 + Path_cat_3 + Slope + Grassland + Meadow	49192.0	1.88	0.113
	Path_cat_0 + Path_cat_3 + Slope + Grassland + Meadow + Villages	49192.1	2.00	0.106
2) Comparison of random locations with night-time lynx GPS locations	Elevation + Slope + Direction + Path_cat_0 + Grassland+ Villages	27124.8	0.00	0.244
	Elevation + Slope + Direction + Path_cat_0 + Grassland	27125.1	0.29	0.210
	Elevation +Slope +Direction + Path_cat_0 +Path_cat_3 +Grassland +Villages	27125.8	0.98	0.149
3) Comparison of daytime with night-time lynx GPS locations	Elevation + Slope + Direction + Path_cat_2 +Path_cat_3 + Grassland + Meadow	23761.3	0.00	0.227
	Elevation + Slope + Direction + Path_cat_0 + Path_cat_2 +Path_cat_3 + Grassland + Meadow	23761.6	0.36	0.19
	Elevation + Slope + Direction + Path_cat_2 +Path_cat_3 + Grassland	23762.3	1.07	0.133



Appendix 1 Fig. 1 Effect of human settlements (villages) on the probability of lynx habitat selection based on the comparison of daytime and night-time lynx GPS locations in the Palatinate Forest. Lynx identification was used as random effect within the GLMM model.

General Discussion

General Discussion

The analyses and results of this PhD thesis provide new insights into the interaction of Eurasian lynx (*Lynx lynx*) with its main prey, European roe deer (*Capreolus capreolus*), as well as the habitat selection of this predator in the Palatinate Forest after the first four years of its reintroduction. The conclusions of my results provide substantial information for management actions regarding large carnivores and additionally present a corner-stone of a rare situation in animal conservation ecology in Europe. The data presented here also offer a first insight into a long-term interaction process between a large carnivore and its prey in the Palatinate Forest in southwestern Germany.

In the first manuscript of my thesis, I investigate the potential influence of this newly established predator on its main prey population dynamics. I estimated the prey population density before and under the presence of lynx in the Palatinate Forest. Additionally, I evaluated hunting bag data from 2012 to 2019. I found fluctuations within the roe deer population density in the Palatinate Forest, which included a slight decrease in the estimated prey population in 2018 and 2019, after a two-year presence of lynx. I also found fluctuations in roe deer hunting bag, particularly in 2013 to 2014 and 2018 to 2019, suggesting a possible fluctuation in population density in the years prior to the predator's return to the area. No significant difference was found between roe deer population index and roe deer hunting bag in relation to lynx reintroduction.
Based on the results, I conclude that lynx had no measurable influence on the roe deer population in the Palatinate Forest in the first years of its return. However, it must be taken into account here that the population density of lynx in the Palatinate Forest was still low at that time. Long-term data are needed to assess the interaction between the two species and in particular the impact on population dynamics.

In the first four years of lynx reintroduction, we experienced a still low lynx population in the Palatinate Forest over an area of 1,790 km². In the first half of 2019, about twelve independent lynx were documented in the area (SNU-RLP 2020), corresponding to around 0.67 lynx per 100 km². In winter 2019 to 2020, lynx density was estimated at 0.65 individuals per 100 km² (Port 2021; Port 2020). The roe deer population estimate was monitored from 2016 to 2019, with lynx density during this time ranging from approximately 0.17 lynx per 100 km² in 2016 to 0.67 lynx per 100 km² in 2019. Calculating the predation rate of lynx for 2020, we estimated kill rates based on Belotti et al. (2015) with around 0.46–0.75 roe deer per km² per year in the

Palatinate Forest. Consequently, the predation rate must have been much lower in 2016 to 2019 than in 2020, making it difficult for the distance sampling method to detect such small differences given a confidence interval of about ± 2.5 roe deer per km² in density estimates. Thus, human hunters in the Palatinate Forest currently harvest two to four times as many roe deer per km² per year as lynx.

Of course, the impact of such a predator on its prey can shift at any time. Breitenmoser et al. (2010) describe that the predation impact of lynx on prey can be considerable on a local scale and even lead to the local extinction of roe deer (Haller 1992). Naïve prey that were vulnerable to predation had to readapt to a natural predator and stabilised the predator-prey system after a short period (Breitenmoser and Haller 1993). Breitenmoser et al. (2010) described three different scenarios observed to date, ranging from changing impact during lynx recolonisation with naïve prey, to low to moderate impact after readaptation and a very high impact on prey population after many years of stability. There is no precise description of when a roe deer population is still considered naïve and when it has readapted to its natural predator. I will attempt to consider certain parameters here, although the majority of the values of each parameter used in this equation have not been proven for our study area. Nineteen lynx were detected in the monitoring year 2019 (Mai 2019 to April 2020) within the study area. Assuming a predation rate of 60 roe deer per year and lynx (46–74, Belotti et al. (2015)), this results in a total of approximately 1,140 roe deer per year that are preyed upon in the Palatinate Forest. Assuming an average summer roe deer density of 10 roe deer km^{-2}, this would be approximately 6.3% of the total roe deer population taken by the lynx per year. The hunting success rate of the lynx has only been studied in a few cases. In Scandinavian areas, a hunting success rate of about 65% was found (Pedersen et al. 1999 in Breitenmoser and Breitenmoser-Würsten 2008; Haglund 1966 in Breitenmoser and Breitenmoser-Würsten 2008), while in Poland a success rate of about 25–50% was described (Matjuschkin 1978 in Breitenmoser and Breitenmoser-Würsten 2008). Taking the latter lynx success rate for further calculations, I assume that at least about 12–25% of the roe deer population has already experienced a lynx attack within the 2019 monitoring year. Thus, the roe deer population in the Palatinate Forest is most likely in the preadaptation phase, where prey are still naïve and need to learn about the natural predator. Further research on this particular topic needs to be conducted to draw firm conclusions.

In fact, it was planned to continue the monitoring of the roe deer population in 2020 and 2021 to observe the population dynamics in the Palatinate Forest in the long term. Unfortunately, this was not possible due to the occurrence of the Covid-19 pandemic in the spring of 2020. Breitenmoser and Breitenmoser-Würsten (2008) argue that many scientific studies only last for about three to four years (average time span of a PhD or project funding time span), which complicates the interpretation of ecological data and even leads to misinterpretation since only a section of the overall process is analysed. I have taken this aspect into account in the interpretation of my results and advice to continue the monitoring of both species in the coming years, because only long-term data can help to understand the top-down and/or bottom-up processes in such an ecosystem.

Imperio et al. (2010) postulated that hunting bag data can provide valuable information on prey population trends and can be used as proxies for population density. In our investigation we were able to examine hunting bag data of a large part of our study area over an eight-year period (2012-2019). Imperio et al. (2010) argue that hunting bag data that are not corrected for hunting effort and are not validated could lead to incorrect abundance estimation indices. As an index, I used the hunting bag of the Palatinate Forest over the years, assuming no remarkable changes in hunting effort, based on previous studies of hunting licenses and effort monitoring in the same research area (Hohmann et al. 2016). The analysed hunting bag revealed a decrease of hunted deer in the hunting years 2018 and 2019. Based on previous fluctuations in hunting years (2013 and 2014), it might also be possible that other factors such as abiotic or density-dependent factors (Breitenmoser et al. 2010) influence roe deer population dynamics and thus human hunting success.

One potential criticism is that our methodological approach to estimate the roe deer population in the Palatinate Forest has certain dependencies. Our estimation based on distance sampling is dependent on forestry roads, which may not provide valid information on the ungulate population throughout the study area, but rather density estimates in the immediate vicinity of forestry roads (Buckland et al. 2001). In addition, responsive movement – the reaction of the animal to the observer car – influences the detection probability in the vicinity of the transect, leading to an underestimation of the population (Buckland et al. 2001). Hunting bag data pooled at the spatial scale of forestry departments and districts do not provide evidence of changes in population dynamics at a smaller landscape scale (< 1,300 ha).

The hunting tactic of lynx is to move from one area of its home range to another after successful prey capture (Breitenmoser and Breitenmoser-Würsten 2008), using the so-called surprise effect. This is not possible for a female lynx with kittens, at least for a short period of the year, so prey must be killed in the closer vicinity of the den (Breitenmoser and Breitenmoser-Würsten 2008; Schmidt 1998), possibly leading to a stronger local influence on the prey population. The use of only 4% of their own territory shows the reduction of the spatial activity pattern of female lynx with cubs in the period from May to July, whereas female lynx without cubs used about 40% of their territory (Breitenmoser and Breitenmoser-Würsten 2008). The population dynamics and behaviour on such a small spatial and temporal scale is not detectable with the methods applied within this study. Another criticism within my analysis is the comparison of roe deer hunting bag and roe deer count index of lynx-free areas with lynx-rich areas. Here, the sample size is so small that this should be taken into account in the interpretation.

In the second manuscript, I investigated the direct interaction between lynx and roe deer on a small spatial scale. Habitats in which a predator successfully hunts its prey provide important information about lynx hunting pattern at the microhabitat scale. Here, I addressed the question in which habitat roe deer have a higher predation risk, or in which habitat lynx successfully hunt prey that has not experienced a natural predator in the Palatinate Forest for a long time. The kill sites indicated that prey were found in structure-rich and complex habitats, which might present an increased encounter probability and plenty of cover to stalk up on the prey. Seasonal differences in habitat criteria of the kill sites are very likely, even though we only found differences in canopy cover. Low elevations and slopes showed a higher risk of predation on prey, which has also been found to be important in other research areas (Krofel et al. 2007). Signer et al. (2019) found that lynx use rock formations as resting sites, possibly explaining our significant difference in day and night slope levels. Rock formations provide cover, shelter from changing weather conditions and are difficult to access for humans (Signer et al. 2019), hence they are perfect for a carnivore to rest during the day. Additionally, the data revealed a higher predation risk for roe deer near grasslands and roads (forest and public). The aspect that roads might pose a higher predation risk to roe deer may be biased by the density of forestry roads in the Palatinate Forest and may not apply to other study areas with lower forestry road densities. The large road network might strongly influence lynx habitat selection. It is known that lynx use forestry roads to move quickly through their home range, hereby saving energy and at the same time using them to scent-mark their territory (Weingarth et al. 2015; Vogt et al. 2014; Weingarth et al. 2012; Sandrini 2010; Breitenmoser and Breitenmoser-Würsten 2008; Zimmermann and Breitenmoser 2007; Koehler and Brittell 1990). We assume that lynx in the Palatinate Forest also use the widespread forestry road network for hunting. This might be active use or a side effect of moving within the territory. Further research on this specific aspects

is required and in prospect.
Kill sites were found to be less likely in close distances to villages. Kill sites were investigated at times when lynx did not yet occupy the entire area of the Palatinate Forest and were probably still searching for optimal home ranges. In addition, the kill site data were not collected systematically. This may have led to the habitat use of areas with low human disturbance for the time being, especially because the reintroduction site was chosen according to these criteria. Several studies have shown that both roe deer and lynx can cope with human disturbance at different levels (Gehr et al. 2017; Gehr 2016; Bouyer, Gervasi, et al. 2015; Bouyer, San Martin, et al. 2015; Basille et al. 2009; Sunde et al. 1998).

In the final manuscript of my thesis, I was able to show how recently-reintroduced lynx utilise their habitat on a medium landscape scale. Forestry roads and public roads seem to play a crucial role in the habitat selection and movement patterns of lynx within the study area. Due to a different light regime and a different assortment of plant groups compared to their surroundings, forestry roads represent marginal habitats (Coffin 2007). Thus, ungulates find a different grazing supply on and near roads (forest and public roads). As mentioned above, lynx are also known to use forestry roads (Weingarth et al. 2015; Weingarth et al. 2012; Sandrini 2010; Breitenmoser and Breitenmoser-Würsten 2008; Zimmermann and Breitenmoser 2007; Koehler and Brittell 1990), probably explaining the higher predation risk within these habitats. Besides this, lynx can also use forestry roads to gain a good view and easily spot prey in the surrounding. Consequently, the potentially higher encounter rate of prey in close proximity to roads may be an additional reason for lynx to intensively use forestry roads in addition to movement patterns and territory marking. I found that lynx do not avoid human settlements within the Palatinate Forest and that they especially utilise areas closer to villages at night. These results are in line with other European research studies (Bouyer, Gervasi, et al. 2015; Basille et al. 2009; Sunde et al. 1998). I must highlight that I only considered lynx GPS positions within the boundaries of the Biosphere Reserve of the Palatinate Forest. The surrounding of the study area considerably differs from the Palatinate Forest. Here, it would be very interesting to observe how lynx use habitats in the near future that are increasingly disturbed by humans, and have a lower proportion of forest cover, but offer a higher prey abundance than the closed forest ecosystem of the Palatinate Forest. The lynx GPS locations surveyed so far outside of the boundaries of the Palatinate Forest could possibly already provide initial answers to this very important question for conservation management.

Geographic relief criteria also play an important role for lynx in selecting their habitat. Lynx seem to prefer lower elevations and less steep areas during the night, whereas during the day the opposite is the case. This indicates that lynx in the Palatinate Forest select areas with higher prey density, such as valleys or grassland areas (lower elevation, less steep) at night. Overall, our results in manuscript 3 support the observed patterns in the kill site analysis of manuscript 2, except for the human settlements.

Further research aspects

My research on the influence of lynx on the prey population over a period of four years in the Palatinate Forest gave me the opportunity to observe the first years of a long-term interaction process. Like Breitenmoser and Breitenmoser-Würsten (2008) argue, many research projects are conducted on an insufficient temporal scale, and thus I would suggest to continue the monitoring and the research on the predator-prey interaction within the Palatinate Forest. Over a time scale of 10 to 15 years, the dynamics of both populations can be displayed based on a reliable data set. In the first years, we could not detect any influence of the predator on the prey population, but here the still low predator density in the first years should be taken into account. The approach to estimate prey population density on such a large scale (1,790 km² study area) with the help of distance sampling still seems applicable given the costs and benefits, although it has its drawbacks (dependency on roads, roads as special habitat, underestimation of the population). For the future, it would be very helpful to validate the method used here with an additional census method, such as non-invasive genetic capture-mark-recapture (Ebert, Sandrini, et al. 2012; Pollock et al. 1990), pellet counts (Putman 1984), spotlight counts (Anderson 1959), or camera trapping (Silver et al. 2004; Karanth 1995).

In examining the characteristics of kill sites and the impact of a predator on its prey population, it became apparent that determining lynx prey spectrum, preference for certain prey species, age class and/ or sex, and consumption rate of the predator could be an additional way to understand how predators may affect prey populations, especially in the early years of return. The SNU-RLP (2020) has already started to track two lynx individuals more closely and analysed kill series over a period of three to four weeks. This data acquisition could be extended to more individuals over a longer period of time to obtain an average consumption rate and prey preference of different lynx individuals. More than 600 kills were examined in the Swiss Jura Mountains to assess consumption rates, prey spectrum and preferences of lynx (Jobin et al. 2000). It was found that the prey spectrum varied from roe deer, chamois, red fox (*Vulpes*

vulpes), brown hare (*Lepus europaeus*), marmot (*Marmota marmot*) and badger (*Meles meles*, Jobin et al. (2000)). Moreover, the consumption rate also depended on the sex and reproductive status of lynx (Jobin et al. 2000), and it also varied over the course of the year (Nilsen et al. 2009). External abiotic factors (such as weather) have been shown to influence the lynx consumption rate, illustrating how climatic variability can affect the dynamics of a predator-prey system (Stenseth et al. 2004). Understanding lynx prey preferences in the Palatinate Forest can help us to gain further insights into the impact of lynx on ungulate communities (Nilsen et al. 2009; Jobin et al. 2000), including climate change impacts.
Due to the limited financial and staff capacity of this project, it was not possible to more closely monitor the prey population behaviour patterns with and without predator presence in the area. In addition, the observation of direct interactions would be an interesting research question to follow up in the future. One way to address this issue would be to attach GPS collars on roe deer within the home range of independent adult lynx that are also fitted with GPS collars. Scientific studies to determine direct interspecific spatial behaviour between predator and its prey have already been successfully conducted with wolf and red deer (Michler et al. 2018). Depending on the number of tagged roe deer, the probability of prey encountering a collared lynx will be low to observe direct interactions, so the costs and benefits of this study design must be carefully weighed. One possibility would be to observe a female lynx with cubs during the first months after the birth of the cubs, since then only a small part of the territory is used, thus increasing the encounter rate with the prey. The use of proximity sensors in these collars provides the ability to automatically change the frequency of GPS measurements as the prey and predator approach each other (Michler et al. 2018), allowing observing direct interaction between the two species. At the same time, GPS data of roe deer individuals can provide further insights into the spatial and temporal use of forest roads by roe deer in the presence and absence of predators in the Palatinate Forest.

As part of my research project, I have already begun to investigate the diurnal habitat use of roe deer in relation to small meadows (hunting meadows) using camera traps. I tried to relate this to the presence of lynx in the study area. The aim of this study is to investigate the impact of lynx presence on the daily activity of roe deer in small meadows in the Palatinate Forest. Day activity was described by the exit time, dwell time and vigilance behaviour of roe deer in the meadows. Lynx presence was assessed according to GPS locations of reintroduced lynx and opportunistic and systematic lynx indications (SCALP criteria) within the study area. Eccard et al. (2015) found that roe deer respond to lynx urine despite the long absence (160 years ago) of the predator within the Bavarian Forest National Park, and the authors' results support the risk allocation hypothesis, which states that roe deer respond to pulses of high predation risk but not to continuous predation risk. In this study, the main focus is on comparing lynx-free and lynx-occupied areas rather than finding differences in acute and continuous predation risk for prey species. The evaluation of the data has not yet been completed (Kopaniak 2021). The data acquisition was limited to day time due to the plot function of the camera trap to observe more than only a 10 m range of the meadow. This plot function provided us with images of the meadow every 5 minutes during the day (sunrise to sunset). Because roe deer increase their activity between dusk and dawn, the recorded data represent the lowest activity segments of a 24-hour cycle. Here, it would be very important to rethink the methodical setup to obtain more scientifically valuable data. Hunters in the Palatinate Forest and other areas with a lynx presence (Heurich 2018) complain about an increased effort to hunt ungulates, combined with allegations of altered ungulate behaviour and reduced population due to predator presence in the area. To assist local hunters and game keepers in their management goals, an insightful and applied approach would be to understand the potential changes for human hunters, as well as the anti-predator behaviour of a still naïve prey population within a closed forest system.

Conservation and management implications

The return of large carnivores to Western Europe is a huge success for wildlife management and conservation. By reintroducing lynx to the Palatinate Forest in southwestern Germany, SNU-RLP (2020) has established a sub-population that has the potential to spread into the Northern Vosges, and in the long term create genetic exchange between the populations in the Central and Southern Vosges and even with the populations in the Jura and Alps, which would then constitute a metapopulation (SNU-RLP 2020). The instructions of lynx management in Rhineland-Palatinate are formulated in the management plan of 2016 (MUEEF RLP 2016), which also describes in detail the objectives of management in Rhineland-Palatinate. It is too early to make any statements about the long-term impact (ten-year time scale) of lynx on the roe deer population in the Palatinate Forest, and therefore I cannot derive any management implications regarding the prey population for hunters, nature conservation and hunting authorities.

As my results suggest (manuscript 2 and 3), lynx use the vicinity of forestry and public roads primarily during twilight and night times. Minimising unnatural lynx mortality within such a young vulnerable population where each individual is a valuable contribution to the population establishment within the Palatinate Forest should potentially be considered as part of the management implications for lynx. Traffic-related mortality of lynx is an important cause of mortality in Scandinavia (Andrén et al. 2006) and Switzerland (Schmidt-Posthaus et al. 2002), where 34% of non-infectious causes of death are human-related, mostly from vehicle collisions. In the Bohemian Forest Ecosystem, illegal hunting is the most prominent cause of death, followed by 20% of fatalities caused by traffic collisions (Heurich et al. 2018). A high mortality rate among adult lynx increases the threat for the long-term population survival (Schmidt-Posthaus et al. 2002). In France, lynx mortality is more likely to be due to humans within adults than in juveniles (Stahl and Vandel 1999). The creation of a road mortality risk map (Heurich et al. 2018) in the Palatinate Forest could help to identify spots of high mortality risk and thus reduce the risk of additional mortality to a newly established carnivore population. Even though only two lynx individuals have been killed by traffic thus far (vehicle collision and train collision), the creation of such a map could prevent further fatalities in the Palatinate Forest. Poaching of lynx within this study area has not been recorded to date due to intensive environmental education and communication with all directly affected parties prior to the lynx reintroduction.

Concluding remarks

The reintroduction of a large carnivore into a human-dominated landscape in Europe plays an important role in management and conservation efforts of endangered and rare species. This work shows that after the first four years of lynx reintroduction in the Palatinate Forest, there were no changes in estimated roe deer population density associated with lynx presence. Long-term studies on the establishment of the large carnivore and the dynamics of the prey population in the study area are necessary to evaluate the potential impact on its prey, as well as the success of the reintroduction program. This thesis thus contributes to a better understanding of where lynx establish their home ranges and hunt successfully after their reintroduction to the Palatinate Forest. It also gives insights to the habitat selection of newly reintroduced lynx within Germany's largest contiguous forest ecosystem. Furthermore, our results raise new questions for additional research on lynx habitat selection in relation to roads, predator-prey dynamics, predation rates and anti-predator behaviour of prey in the Palatinate Forest. Increasing knowledge of large carnivores' habitat selection in our human-modified landscape and its influence on other species will improve conservation and management decisions.

References

Anderson CF (1959) Nocturnal activities of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* Richardson, affecting spotlight census results in the Oregon Coast Range. Thesis, Oregon State University, Corvallis, Oregon, USA

Andrén H, Linnell JD, Liberg O, Andersen R, Danell A, Karlsson J, Odden J, Moa PF, Ahlqvist P, Kvam T (2006) Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23-32

Basille M, Herfindal I, Santin-Janin H, Linnell JD, Odden J, Andersen R, Arild Høgda K, Gaillard J-M (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography 32:683-691

Belotti E, Weder N, Bufka L, Kaldhusdal A, Küchenhoff H, Seibold H, Woelfing B, Heurich M (2015) Patterns of Lynx predation at the interface between protected areas and multi-use landscapes in Central Europe. Plos One 10: e0138139

Bouyer Y, Gervasi V, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. Animal Conservation 18:271-278

Bouyer Y, San Martin G, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. Biological Conservation 191:291-299

Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs. Salm Verlag, Wohlen/Bern, Switzerland: 1-537

Breitenmoser U, Haller H (1993) Patterns of predation by reintroduced European lynx in the Swiss Alps. Journal of Wildlife Management 57:135-144

Breitenmoser U, Ryser A, Molinari-Jobin A, Zimmermann F, Haller H, Molinari P, Breitenmoser-Würsten C (2010) The changing impact of predation as a source of conflict between hunters and reintroduced lynx in Switzerland. In: Macdonald, D.W.& Loveridge, A.J. (Eds.), Biology and Conservation of Wild Felids (pp. 493-506). Oxford: Oxford University Press.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling. Estimating Abundance of Biological Populations. Oxford University Press, Oxford

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transport Geography 15:396-406

Ebert C, Sandrini J, Spielberger B, Thiele B, Hohmann U (2012) Non-invasive genetic approaches for estimation of ungulate population size: a study on roe deer (*Capreolus capreolus*) based on faeces. Animal Biodiversity and Conservation 35:267-275

Eccard JA, Meißner JK, Heurich M (2015) European roe deer increase vigilance when faced with immediate predation risk by Eurasian lynx. Ethology 123(1):30-40

Gehr B (2016) Predator-prey Interactions in a Human-dominated Landscape. Doctoral dissertation. University of Zurich, Switzerland

Gehr B, Hofer EJ, Muff S, Ryser A, Vimercati E, Vogt K, Keller LF (2017) A landscape of coexistence for a large predator in a human dominated landscape. Oikos 126:1389-1399

Haglund B (1966) Winter habits of the lynx (*Lynx lynx L.*) and wolverine (*Gulo gulo L.*) as revealed by tracking in the snow. Viltrevy 4:81-229

Haller H (1992) Zur Ökologie des Luchses *Lynx lynx* im Verlauf seiner Wiederansiedlung in den Walliser Alpen.Mammalia depicta. Paul Parey, Hamburg, Berlin.

Heurich M (2018) Naturschutzökologische Grundlagen der Luchspopulation im Böhmerwald-Ökosystem. Naturschutz und Landschaftsplanung 50 (04):101-109

Heurich M, Schultze-Naumburg J, Piacenza N, Magg N, Červený J, Engleder T, Herdtfelder M, Sladova M, Kramer-Schadt S (2018) Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. Biological Conservation 224:355-365

Hohmann U, Ebert C, Huckschlag D, Hettich U, Sandrini J (2016) Jagd als Regulierungsinstrument? Untersuchungsbefunde am Beispiel zweier Schwarzwildpopulationen (*Sus scrofa*) in Südwestdeutschland. Institue for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Landesforsten RLP, Trippstadt

Imperio S, Ferrante M, Grignetti A, Santini G, Focardi S (2010) Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? Wildlife Biology 16:205-214

Jobin A, Molinari P, Breitenmoser U (2000) Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. Acta Theriologica 45:243-252

Karanth KU (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture - recapture models. Biological Conservation 71:333-338

Koehler GM, Brittell JD (1990) Managing spruce-fir habitat for lynx and snowshoe hare. Journal of Forestry 88:10-14

Kopaniak L (2021) Nutzung von Wildwiesen durch Rehwild vor und nach der Wiederansiedlung des Luchses im Pfälzerwald. Masterthesis, Albert-Ludwigs-Universität Freiburg

Krofel M, Potočnik H, Kos I (2007) Topographical and vegetational characteristics of lynx kill sites in Slovenian Dinaric Mountains. Natura Sloveniae 9:25-36

Matjuschkin E (1978) Der Luchs: *lynx lynx.* A. Ziemsen Verlag, Wittenberg-Lutherstadt

Michler F-U, Gilllich B, Michler A, Rieger S (2018) Interspezifisches Interatkionsverhalten von Wölfen und Rotwild in Sachsen-Anhalt - eine Projektvorstellung. Paper presented at the Conference "Wald-Wild-Wolf, was Forstleute bewegt" Freising, Germany, 2018

MUEEF RLP (2016) Managementplan für den Umgang mit Luchsen in Rheinland-Pfalz. Stiftung Natur und Umwelt Rheinland-Pfalz, Mainz

Nilsen EB, Linnell JD, Odden J, Andersen R (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. Journal of Animal Ecology 78:741-751

Pedersen VA, Linnell JD, Andersen R, Andrén H, Lindén M, Segerström P (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. Wildlife Biology 5:203-211

Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture-recapture experiments. Wildlife Monographs 107:3-97

Port M (2020) Systematisches Fotofallenmonitoring des Luchses im Pfälzerwald. FAWF Mitteilungen. Institute for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Trippstadt

Port M (2021) Systematisches Fotofallenmonitoring des Luchses im Pfälzerwald 2019/20 und 2020/21, unpublished report. Institute for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Trippstadt

Putman RJ (1984) Facts from faeces. Mammal Review 14:79-97

Sandrini J (2010) Eignungsanalyse von Fotofallen-Standorten für das Monitoring von Luchsen (*Lynx lynx L.*) im Bayerischen Wald. Diplomarbeit, Universität Freiburg

Schmidt-Posthaus H, Breitenmoser-Wörsten C, Posthaus H, Bacciarini L, Breitenmoser U (2002) Causes of mortality in reintroduced Eurasian lynx in Switzerland. Journal of Wildlife Diseases 38:84-92

Schmidt K (1998) Maternal behaviour and juvenile dispersal in the Eurasian lynx. Acta Theriologica 43:391-408

Signer J, Filla M, Schoneberg S, Kneib T, Bufka L, Belotti E, Heurich M (2019) Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. Wildlife Biology 2019 (1):1-5

Silver SC, Ostro LE, Marsh LK, Maffei L, Noss AJ, Kelly MJ, Wallace RB, Gómez H, Ayala G (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38:148-154

SNU-RLP (2020) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed 15.11.2020

Stahl P, Vandel J-M (1999) Mortalité et captures de lynx (*Lynx lynx*) en France (1974-1998). Mammalia 63:49-60

Stenseth NC, Shabbar A, Chan K-S, Boutin S, Rueness EK, Ehrich D, Hurrell JW, Lingjærde OC, Jakobsen KS (2004) Snow conditions may create an invisible barrier for lynx. Proceedings of the National Academy of Sciences 101:10632-10634

Sunde P, Stener SØ, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. Wildlife Biol 4:177-183

Vogt K, Zimmermann F, Kölliker M, Breitenmoser U (2014) Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behav Processes 106:98-106

Weingarth K, Heibl C, Knauer F, Zimmermann F, Bufka L, Heurich M (2012) First estimation of Eurasian lynx (*Lynx lynx*) abundance and density using digital cameras and capture–recapture techniques in a German national park. Anim Biodivers Conserv 35:197-207

Weingarth K, Zeppenfeld T, Heibl C, Heurich M, Bufka L, Daniszová K, Müller J (2015) Hide and seek: extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. Biodiversity and Conservation 24:2935-2952

Zimmermann F, Breitenmoser U (2007) Potential distribution and population size of the Eurasian lynx *Lynx lynx* in the Jura Mountains and possible corridors to adjacent ranges. Wildlife Biology 13:406-416

Summary

Understanding the influence of a predator on its prey and the resulting changes in prey behaviour and/or abundance is a widely-discussed subject in wildlife ecology, yet large gaps in knowledge remain. In addition, the return of a long absent predator in our human-altered environment prompts conflicts of human interests, especially among hunters and livestock breeders. Hence, understanding the predator-prey dynamics is a highly interesting topic scientifically as well as from an applied management perspective regarding the forest-game conflict. At the same time, studying habitat selection of large carnivores in our human-dominated landscape provides valuable information about their habitat requirements and adaptation to human disturbance. This supports management implications to establish and maintain viable metapopulations connected through corridors and thus can ensure genetic exchange. This thesis contributes in addressing this topic, aiming to investigate the establishment of newly reintroduced lynx (*Lynx lynx*) and its effect on the main prey species in a forest-dominated low mountain range in Germany.

In the first manuscript, I examined how the roe deer (*Capreolus capreolus*) population trend in the Palatinate Forest developed under the newly established presence of a large carnivore, the lynx (*Lynx lynx*). In particular, I started to monitor the roe deer populations before lynx reintroduction (2016) and continued this under the presence of the predator (2017–2019). The estimation of roe deer population density was based on a distance sampling approach with ten fixed transects with an average transect length of 48 km within the study area. Data acquisition was undertaken at night with the use of thermal imaging cameras. Roe deer hunting bag were queried from forestry departments for state-managed hunting areas. The average roe deer population density was estimated at around 6.54 ± 1.28 roe deer km^{-2} (2016–2019), whereas the average roe deer hunting bag within state-managed forests was around three individuals km^{-2}, leading to the assumption that the models underestimate the roe deer density within the Palatinate Forest. Lynx home range calculations based on kernel density estimations were used to define lynx presence and absence areas over the whole investigation period. Roe deer hunting bag, roe deer count index and lynx spatial habitat use were linked to investigate short-term effects of lynx on the roe deer population in the first years after reintroduction in the Palatinate Forest by comparing areas of lynx presence and absence. I did not find negative effects of the lynx on the roe deer population in the Palatinate Forest. Here, it has to be considered that the

time span of four years and the still-low lynx population density – especially in the first two years – most probably influenced the results. Monitoring based on 10 to 15 years is suitable to reveal long-term dynamics in both predator and prey populations.

Investigating the impact of the predator on the prey individual, I was observing the habitat structure, where direct and lethal encounters of the predator with its prey occurred. In manuscript two, 123 roe deer kill sites caused by thirteen radio-tracked lynx (6 females and 7 males) between 2016 and 2019 were investigated on a microhabitat scale. The investigation of these microhabitats should identify habitats in which lynx successfully hunt roe deer and where roe deer are at increased risk of predation. Kill sites were compared with habitat availability – represented by random locations – and with the habitat use of the corresponding lynx by using their GPS locations. In total, 95% of the kill sites were related to ground cover, and summer kill sites displayed a significant lower canopy cover than winter kill sites. The results also indicate that there is a higher kill probability of roe deer in proximity to forestry roads, paved public roads, grassland areas and at low elevations. By contrast, lower predation risk for roe deer was found at closer distances to human settlements. This leads to the assumption that the predator or the prey might avoid human-disturbed areas. However, roe deer and lynx are known to cope with human disturbance near settlements.

After all, the establishment of lynx in the Palatinate Forest is still at its beginning, leaving still free home ranges within the area to be occupied by lynx, and hence possibly creating bias in our kill site analyses regarding human settlements, which are sparsely distributed in the Palatinate Forest. The analyses also revealed that structure-rich and complex habitats that might present an increased encounter probability and high amounts of cover for stalking up on the prey are important for lynx to kill its prey. In addition, low elevations and slopes revealed higher predation risk for the prey. This could possibly be related to a higher prey density near grassland areas, which are often located in valleys or on plateaus and therefore presenting lower elevation and/or slopes. Increased predation risk for deer in short distances to linear infrastructures reveals the intensive use of forestry roads by lynx in the Palatinate Forest, possibly due to a very high density of forestry roads and the increased use of the wayside areas by the prey animals. Future investigations on this specific subject will possibly offer more insights into how lynx utilise their territory for hunting, especially when it comes to the proximity of human settlements.

In manuscript three, I investigated the habitat selection of fourteen newly reintroduced lynx between 2016 and 2019 in the Palatinate Forest in relation to anthropogenic structures. I compared lynx locations versus random locations and time of the day (day time with night time) in relation to anthropogenic and environmental variables. Our study highlights the strong preference of lynx to forestry roads as linear structures. Lynx might not only use the forestry roads for movement and territorial delimitation, but also for hunting purpose due to the extensive coverage of forestry roads. This hypothesis should be further investigated. Nevertheless, our results suggest also that lynx show a preference to the proximity of public roads at night compared to day. Reasons for this could be the lower traffic volume at night and thus the lower encounter rate with humans. Along with this, our results reveal that lynx did not avoid human settlements and even chose to remain in areas near them at night, when the human encounter rate is low. These results do not agree with the results from the kill site analyses (manuscript 2), thus concluded an avoidance of human settlements. This can be refuted by the results of manuscript 3. The kill sites were investigated when the lynx were still establishing in the central part of the Palatinate Forest, which is characterised by low human settlement density. Geographic relief criteria also play an important role for lynx in selecting their habitat. At night, lynx choose lower terrain ruggedness (lower elevation and lower slopes) and closer distances to grassland areas than during the day, supporting the results of manuscript 2.

Overall, in my thesis I focus on the interaction between a recently-returned predator and its main prey, considering the influence on population dynamics of still naïve prey in the first four years of predator presence. In addition, I conducted a microhabitat analyses of roe deer kill sites, characterising habitats in which lynx successfully hunt roe deer and roe deer experience increased predation risk. Furthermore, I examined the habitat selection of recently-established lynx within the study area, focussing on the spatial and temporal changes towards prey availability and human-dominated habitats. The results illustrate that predator-prey dynamics are working on larger temporal scales than four years and that habitat selection of lynx in our study area depends on prey availability and minimising human disturbance by using attractive hunting habitats at times of low human activity. Finally, my work serves as a corner-stone for long-term research on the predator-prey dynamics of lynx and roe deer in the Palatinate Forest, and contributes to a better understanding of lynx establishment in our patchy landscape. It may also help to improve wildlife management plans to create viable metapopulations of lynx within Europe to make the return of large carnivores feasible.

Zusammenfassung

Den Einfluss eines Prädators auf seine Beute und die daraus resultierenden Veränderungen in Verhalten und/oder der Abundanz der Beute ist ein faszinierendes und viel diskutiertes Thema im Bereich der Wildtierökologie und weist weiterhin noch große Wissenslücken auf. Darüber hinaus führt die Rückkehr eines lange abwesenden Räubers in unsere vom Menschen dominierte Landschaft zu Konflikten, insbesondere unter Jägern und Viehzüchtern. Daher ist die Beobachtung und das Verstehen der Räuber-Beute-Dynamik ein grundlegendes Anliegen, sowohl aus wissenschaftlicher als auch aus der Perspektive des angewandten Wildtiermanagements, speziell im Hinblick auf den Wald-Wild-Konflikt. Gleichzeitig liefert die Habitatselektion von Großraubtieren in unserer vom Menschen geprägten Landschaft wertvolle Informationen über ihre Lebensraumansprüche und ihre Anpassung an menschliche Störungen. Diese Erkenntnisse unterstützen Managementmaßnahmen für die Etablierung und Erhaltung von lebensfähigen Metapopulationen, die durch Korridore miteinander verbunden sind und somit den genetischen Austausch der Populationen ermöglichen.

Im ersten Kapitel habe ich die Entwicklung der Rehpopulation (*Capreolus capreolus*) im Pfälzerwald unter der neu etablierten Anwesenheit des Luchses (*Lynx lynx*) untersucht. In erster Linie wurde hier die Rehwildpopulation vor der Wiederansiedlung (2016) und unter Anwesenheit des Prädators (2017 - 2019) beobachtet. Die Schätzung des Rehwildbestandes basierte auf der Distance Sampling-Methode, welche auf 10 festgelegten Transekten mit einer durchschnittlichen Transektlänge von 48 km im Untersuchungsgebiet angewandt wurde. Die Datenerfassung erfolgte nachts mit Hilfe von Wärmebildkameras. Die jährlichen Rehwildjagdstrecken wurden bei den zuständigen Forstämtern für die der Regiejagd unterliegenden Reviere abgefragt. Die durchschnittliche Rehwildpopulationsdichte wurde auf ca. 6.54 ± 1.28 Rehwild km^{-2} (2016–2019) geschätzt, während die durchschnittliche Rehwildstrecke innerhalb der staatlich bewirtschafteten Reviere bei ca. 3 Individuen km^{-2} lagen. Dies lässt vermuten, dass die Populationsschätzungsmodelle für Rehwild innerhalb des Pfälzerwaldes den tatsächlichen Bestand unterschätzen. Luchs-Aktionsräume („home range“) wurden mit Hilfe von kernel density-Schätzungen berechnet, um Gebiete mit Luchs Anwesenheit und Abwesenheit über den gesamten Untersuchungszeitraum zu definieren. Die Rehwildstrecke, der Rehwilderfassungsindex und die Aktionsräume der Luchse wurden miteinander verschnitten, um kurzfristige Auswirkungen des Luchses auf die

Rehwildpopulation in den ersten Jahren nach der Wiederansiedlung im Pfälzerwald zu untersuchen. Ich konnte keine negativen Auswirkungen der Luchsanwesenheit auf die Rehwildpopulation im Pfälzerwald feststellen. Dabei ist zu berücksichtigen, dass die Zeitspanne von vier Jahren und die noch geringe Luchspopulationsdichte, vor allem in den ersten beiden Jahren, die Ergebnisse maßgeblich beeinflusst haben. Ein auf 10 bis 15 Jahre angelegtes Monitoring wäre in der Lage, langfristige Dynamiken, sowohl in der Räuber- als auch in der Beutepopulation, aufzuzeigen.

Um den Einfluss des Prädators auf sein Beutetier bewerten zu können, untersuchte ich die Habitatstrukturen, in denen es zur direkten und tödlichen Begegnung des Prädators mit seinem Beutetier kam. Im zweiten Kapitel wird auf die Mikrohabitatuntersuchung von 123 Rehwildrissen, die auf 13 telemetrierte Luchse (6 Weibchen und 7 Männchen) zwischen 2016 und 2019 zurückzuführen sind, eingegangen. Die Untersuchung dieser Mikrohabitate sollte Aufschluss geben, in welchem Habitat Luchse erfolgreich Rehwild erbeuten und in welchem Habitat Rehwild erhöhtem Prädationsrisiko ausgesetzt ist. Das Habitat der Rissplätze wurde mit dem verfügbaren Habitat (Angebot), repräsentiert durch Zufallsstandorte, und mit dem Habitatnutzungsmuster der hier in der Analyse einbezogenen Luchse (GPS-Positionen) verglichen. Insgesamt 95% der Rissplätze wiesen Bodenbedeckung auf. Zusätzlich konnte im Sommer ein signifikant geringerer Überschirmungsgrad als im Winter festgestellt werden. Die Ergebnisse zeigen auch, dass sich ein erhöhtes Prädationsrisiko für Rehe in der Nähe von Forststraßen, befestigten öffentlichen Straßen, Grünlandflächen und in niedrigen Höhenlagen abbildet. Im Gegensatz dazu wurde ein geringeres Prädationsrisiko für Rehwild in der Nähe von menschlichen Siedlungen nachgewiesen. Strukturreiche und komplexe Habitate scheinen für eine erfolgreiche Jagd durch den Luchs von Bedeutung zu sein, da diese möglicherweise eine erhöhte Begegnungswahrscheinlichkeit und gleichzeitig ein erhöhtes Deckungspotenzial zum Anschleichen an die Beute bieten. Darüber hinaus zeigten niedrige Höhenlagen und Gefälle (Neigungen) ein höheres Prädationsrisiko für die Beute. Dies könnte möglicherweise mit einer höheren Beutedichte in der Nähe von Grünlandflächen zusammenhängen, welche sich oft in Tälern oder auf Hochplateaus befinden und daher geringere Gefälle aufweisen. Die intensive Nutzung von Forstwegen durch den Luchs im Pfälzerwald, welche möglicherweise auf die sehr hohe Wegedichte und die verstärkte Nutzung der Wegrandbereiche durch die Beutetiere zurückzuführen ist, resultiert in einem erhöhten Prädationsrisiko für Rehe in näherer Umgebung zu diesen linearen Infrastrukturen.

Kapitel drei beschreibt die Habitatselektion von 14 wiederangesiedelten Luchsen im Pfälzerwald im Zeitraum von 2016 bis 2019 in Abhängigkeit anthropogener Strukturen dar. Dazu habe ich die Luchsstandorte mit den Zufallsstandorten und der Tageszeit (Tag gegen Nacht), in Abhängigkeit von anthropogenen und umweltbezogenen Variablen, untersucht. Forstwege und öffentliche Straßen spielen eine wichtige Rolle bei der Habitatselektion von Luchsen im Pfälzerwald, da Luchse vor allem nachts Gebiete in deren Nähe aufsuchen. Forstwege stellen, aufgrund ihrer Struktur bezüglich des Lichtregimes, der Vielzahl der Pflanzenarten, des Wasserhaushaltes und der Bodennährstoffe im Vergleich zu ihrer Umgebung, eine Besonderheit dar, die einerseits für Beutetiere und andererseits für Prädatoren von Vorteil sind. Darüber hinaus zeigen meine Ergebnisse, dass Luchse menschliche Siedlungen nicht meiden und sich vor allem nachts in deren Nähe aufhalten, da nachts mit einer geringeren Begegnungsrate mit Menschen zu rechnen ist. Diese Schlussfolgerungen stimmen nicht mit den Ergebnissen aus den Rissplätzen (Kapitel 2) überein, da dort die Analysen durch das Verteilungsmuster der Rissplätze beeinflusst wurden und somit auf eine Meidung von menschlichen Siedlungen hindeuteten. Dies kann durch die Ergebnisse aus Kapitel 3 widerlegt werden. Die Rissplätze wurden untersucht, als die Luchse sich noch im zentralen Teil des Pfälzerwaldes ansiedelten, der sich durch eine geringe menschliche Siedlungsdichte auszeichnet. Die geografischen Reliefkriterien spielen für den Luchs bei der Auswahl seines Habitats ebenfalls eine wichtige Rolle. Nachts wählen Luchse eine geringere Geländerauhigkeit (geringere Höhenlage und Hangneigung) und geringere Abstände zu Grünlandflächen als tagsüber, was die Ergebnisse aus Kapitel zwei unterstützt.

Zusammenfassend konzentrierte ich mich in meiner Dissertation auf die Interaktion zwischen einem kürzlich zurückgekehrten Prädator und seiner Hauptbeute unter Berücksichtigung des Einflusses auf die Populationsdynamik der noch naiven Beutetiere in den ersten vier Jahren der Prädatorpräsenz. Darüber hinaus führte ich eine Mikrohabitat-Analyse von Rehwildrissplätzen durch, um Habitate, in denen der Luchs erfolgreich jagt und in denen Rehe einem erhöhten Prädationsrisiko ausgesetzt ist, zu bestimmen. Außerdem untersuchte ich die Habitatselektion von den im Untersuchungsgebiet wiederangesiedelten Luchsen in Bezug auf Tag- und Nachtrhythmus zu den angebotenen Habitaten. Die Ergebnisse zeigen, dass die Räuber-Beute-Dynamik auf einer größeren zeitlichen Skala als vier Jahren stattfindet und dass die Habitatselektion der Luchse im Untersuchungsgebiet von der Verfügbarkeit der Beutetiere und von der Vermeidung menschlicher Störungen abhängt, indem sie attraktive Jagdhabitate während geringer menschlicher Aktivität nutzen. Am Ende stellt meine Arbeit einen Teil der Basis für eine langfristige Erforschung der Räuber-Beute-Dynamik von Luchs und Rehwild im Pfälzerwald dar und trägt zu einem besseren Verständnis der Luchsetablierung in unserer fragmentierten Landschaft bei. Ebenso können die hier dargelegten Ergebnisse zur Verbesserung der Wildtiermanagementpläne beitragen, um somit lebensfähige Luchsmetapopulationen innerhalb Europas zu erschaffen und damit die Rückkehr dieses Räubers zu ermöglichen.

General Reference List

Andersen R, Karlsen J, Austmo LB, Odden J, Linnell JD, Gaillard J-M (2007) Selectivity of Eurasian lynx *Lynx lynx* and recreational hunters for age, sex and body condition in roe deer *Capreolus capreolus*. Wildlife Biology 13:467-474

Anderson CF (1959) Nocturnal activities of the Columbian black-tailed deer, *Odocoileus hemionus columbianus* Richardson, affecting spotlight census results in the Oregon Coast Range. Thesis, Oregon State University, Corvallis, Oregon, USA

Andrén H, Liberg O (2015) Large impact of Eurasian lynx predation on roe deer population dynamics. PloS One 10:e0120570

Andrén H, Linnell JD, Liberg O, Andersen R, Danell A, Karlsson J, Odden J, Moa PF, Ahlqvist P, Kvam T (2006) Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. Biological Conservation 131:23-32

Apollonio M, Andersen R, Putman R (2010) European ungulates and their management in the 21st century. Cambridge University Press

Basille M, Calenge C, Marboutin É, Andersen R, Gaillard J-M (2008) Assessing habitat selection using multivariate statistics: Some refinements of the ecological-niche factor analysis. Ecol Modelling 211:233-240

Basille M, Herfindal I, Santin-Janin H, Linnell JD, Odden J, Andersen R, Arild Høgda K, Gaillard J-M (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography 32:683-691

Basille M, Van Moorter B, Herfindal I, Martin J, Linnell JD, Odden J, Andersen R, Gaillard J-M (2013) Selecting habitat to survive: the impact of road density on survival in a large carnivore. PloS one 8:e65493

Begon M, Harper J, Townsend C (2006) Ecology: from Individuals to Ecosystems. p 471–472 Blackwell. United Kingdom, Oxford

Belotti E, Červený J, Šustr P, Kreisinger J, Gaibani G, Bufka L (2013) Foraging sites of Eurasian lynx *Lynx lynx*: relative importance of microhabitat and prey occurrence. Wildlife Biol 19:188-201

Belotti E, Heurich M, Kreisinger J, Sustr P, Bufka L (2012) Influence of tourism and traffic on the Eurasian lynx hunting activity and daily movements. Animal Biodiversity Conservation 35:235-246

Belotti E, Mayer K, Kreisinger J, Heurich M, Bufka L (2018) Recreational activities affect resting site selection and foraging time of Eurasian lynx (*Lynx lynx*). Hystrix 29:181-189

Belotti E, Weder N, Bufka L, Kaldhusdal A, Küchenhoff H, Seibold H, Woelfing B, Heurich M (2015) Patterns of Lynx predation at the interface between protected areas and multi-use landscapes in Central Europe. Plos One 10: e0138139

Bivand R, Rundel C (2020) rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.5-5 2020

Bivand RS, Pebesma EJ, Gómez-Rubio V (2013) Applied Spatial Data Analysis with R. Springer Science, New York

Borchers DL, Buckland ST, Zucchini W (2002) Estimating animal abundance: closed populations. Vol. 13. Springer Science & Business Media

Bouyer Y, Gervasi V, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. Animal Conservation 18:271-278

Bouyer Y, San Martin G, Poncin P, Beudels-Jamar RC, Odden J, Linnell JDC (2015) Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. Biological Conservation 191:291-299

Breitenmoser-Würsten C, Zimmermann F, Molinari-Jobin A, Molinari P, Capt S, Vandel J-M, Stahl P, Breitenmoser U (2007) Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. Wildlife Biology 13:365-380

Breitenmoser C, Zimmermann F, Ryser A, Capt S, Laass J, Siegenthaler A, Breitenmoser U (2001) Untersuchungen zur Luchspopulation in den Nordwestalpen der Schweiz 1997 - 2000. KORA-Bericht, Nr. 9, Muri in Bern, 1-88

Breitenmoser U, Breitenmoser-Würsten C (2008) Der Luchs. Salm Verlag, Wohlen/Bern, Switzerland: 1-537

Breitenmoser U, Breitenmoser-Würsten C, Capt S (1998) Re-introduction and present status of the lynx (*Lynx lynx*) in Switzerland. Hystrix - the Italian Journal of Mammalogy 10(1), 17– 30

Breitenmoser U, Breitenmoser-Würsten C, Okarma H, Kaphegyi T, Kaphegyi U, Wallmann U, Müller M (2000) Action plan for the conservation of the Eurasian lynx in Europe. Council of Europe, Nature and Environment, 112: 1-69

Breitenmoser U, Haller A (1987) Zur Nahrungsökologie des Luchses *Lynx lynx* in den schweizerischen Nordalpen. Zeitschrift für Säugetierkunde 52:168-191

Breitenmoser U, Haller H (1993) Patterns of predation by reintroduced European lynx in the Swiss Alps. Journal of Wildlife Management 57:135-144

Breitenmoser U, Ryser A, Molinari-Jobin A, Zimmermann F, Haller H, Molinari P, Breitenmoser-Würsten C (2010) The changing impact of predation as a source of conflict between hunters and reintroduced lynx in Switzerland. In: Macdonald, D.W.& Loveridge, A.J. (Eds.), Biology and Conservation of Wild Felids (pp. 493-506). Oxford: Oxford University Press.

Brown JS, Laundré JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385-399

Buckland S, Anderson D, Burnham K, Laake J (1993) Distance Sampling: Estimating Abundance of Biological Populations. Chapman & Hall, London

Buckland ST (2004) Advanced Distance Sampling. Oxford University Press, Oxford

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling. Estimating Abundance of Biological Populations. Oxford University Press, Oxford

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS (2015) Distance sampling: Methods and Applications. Vol. 431. New York, NY, USA: Springer

Bunnefeld N, Linnell JDC, Odden J, Van Duijn MaJ, Andersen R (2006) Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: Effects of sex and reproductive status. Journal of Zoology 270:31-39

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach (2nd edition). Springer-Verlag, New York

Calenge C (2006) The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516-519

Carpio AJ, Apollonio M, Acevedo P (2020) Wild ungulate overabundance in Europe: Contexts, causes, monitoring and management recommendations. Mammal Review 51:95-108

Červený J, Koubek P, Bufka L (2002) Eurasian lynx (*Lynx lynx*) and its chance for survival in central Europe: the case of the Czech Republic. Acta Zoologica Lituanica 12:428-432

Chapron G, Kaczensky P, Linnell JD, von Arx M, Huber D, Andrén H, López-Bao JV, Adamec M, Álvares F, Anders O (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517-1519

Coffin AW (2007) From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transport Geography 15:396-406

Creel S, Christianson D (2008) Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194-201

Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. Science 315:960-960

Creel S, Fox JE, Hardy A, Sands J, Garrott B, Peterson RO (2002) Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809-814

Donovan TM, Freeman M, Abouelezz H, Royar K, Howard A, Mickey R (2011) Quantifying home range habitat requirements for bobcats (*Lynx rufus*) in Vermont, USA. Biological Conservation 144:2799-2809

dundotcan, wildlifemonitoring.eu (2015) Wildlife Detection Databank vol 1.

Ebert C, Knauer F, Spielberger B, Thiele B, Hohmann U (2012) Estimating wild boar *Sus scrofa* population size using faecal DNA and capture-recapture modelling. Wildlife Biology 18:142-152

Ebert C, Sandrini J, Spielberger B, Thiele B, Hohmann U (2012) Non-invasive genetic approaches for estimation of ungulate population size: a study on roe deer (*Capreolus capreolus*) based on faeces. Animal Biodiversity and Conservation 35:267-275

Ebert C, Sandrini J, Thiele B, Hohmann U (2021) Estimating red deer (*Cervus elaphus*) population size based on non-invasive genetic sampling. European Journal of Wildlife Research 67(2):1-13

Eccard JA, Meißner JK, Heurich M (2015) European roe deer increase vigilance when faced with immediate predation risk by Eurasian lynx. Ethology 123(1):30-40

Filla M, Premier J, Magg N, Dupke C, Khorozyan I, Waltert M, Bufka L, Heurich M (2017) Habitat selection by Eurasian lynx *(Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. Ecology and Evolution 7:6367-6381

Focardi S, De Marinis AM, Rizzotto M, Pucci A (2001) Comparative evaluation of thermal infrared imaging and spotlighting to survey wildlife. Wildlife Society Bulletin:133-139

Focardi S, Franzetti B, Ronchi F (2013) Nocturnal distance sampling of a Mediterranean population of fallow deer is consistent with population projections. Wildlife Research 40:437-446

Focardi S, Montanaro P, Isotti R, Ronchi F, Scacco M, Calmanti R (2005) Distance sampling effectively monitored a declining population of Italian roe deer *Capreolus capreolus italicus*. Oryx 39:421-428

Fox J, Weisberg S (2011) An R companion to applied regression. Sage Publications, Los Angeles

Franzetti B, Ronchi F, Marini F, Scacco M, Calmanti R, Calabrese A, Paola A, Paolo M, Focardi S (2012) Nocturnal line transect sampling of wild boar (*Sus scrofa*) in a Mediterranean forest: long-term comparison with capture–mark–resight population estimates. European Journal of Wildlife Research 58:385-402

Frauendorf M (2012) Pilot Study on the microhabitat selection of the Eurasian lynx (*Lynx lynx*) concerning hunting sites in the Harz National Park, Germany. M.Sc. thesis. Van Hall Larenstein University, Sankt Andreasberg

Gaß R (2018) Habitatkartierung von Luchsrissorten im Pfälzerwald im Projekt „Interaktion von Luchs und Reh im Pfälzerwald". M.Sc. thesis. Hochschule für Forstwirtschaft Rottenburg

Gehr B (2016) Predator-prey Interactions in a Human-dominated Landscape. Doctoral dissertation. University of Zurich, Switzerland

Gehr B, Hofer EJ, Muff S, Ryser A, Vimercati E, Vogt K, Keller LF (2017) A landscape of coexistence for a large predator in a human dominated landscape. Oikos 126:1389-1399

Gervasi V, Linnell J, Berce T, Boitani L, Cretois B, Ciucci P, Duchamp C, Gastineau A, Grente O, Hilfiker D (2020) Ecological and anthropogenic drivers of large carnivore depredation on sheep in Europe. bioRxiv doi:10.1101/2020.04.14.041160

Gill R, Johnson A, Francis A, Hiscocks K, Peace A (1996) Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. For Ecol Manag 88:31-41

Gill R, Thomas M, Stocker D (1997) The use of portable thermal imaging for estimating deer population density in forest habitats. Journal of Applied Ecology 34:1273-1286

Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL (2006) Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887-898

Haglund B (1966) Winter habits of the lynx (*Lynx lynx L.*) and wolverine (*Gulo gulo L.*) as revealed by tracking in the snow. Viltrevy 4:81-229

Haller H (1992) Zur Ökologie des Luchses *Lynx lynx* im Verlauf seiner Wiederansiedlung in den Walliser Alpen.Mammalia depicta. Paul Parey, Hamburg, Berlin.

Hemami MR, Watkinson AR, Gill RMA, Dolman PM (2007) Estimating abundance of introduced Chinese muntjac *Muntiacus reevesi* and native roe deer *Capreolus capreolus* using portable thermal imaging equipment. Mammal Review 37:246-254

Herfindal I, Linnell JD, Odden J, Nilsen EB, Andersen R (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). Journal of Zoology 265:63-71

Herrero A, Heikkinen J, Holmala K (2020) Movement patterns and habitat selection during dispersal in Eurasian lynx. Mammal Research 65:523-533 doi:10.1007/s13364-020-00499-7

Heurich M (2018) Naturschutzökologische Grundlagen der Luchspopulation im Böhmerwald-Ökosystem. Naturschutz und Landschaftsplanung 50 (04):101-109

Heurich M (2019) Wolf, Luchs und Bär in der Kulturlandschaft. Konflikte, Chancen, Lösungen im Umgang mit großen Beutegreifern. Praxisbibliothek Naturschutz und Landschaftsplanung, herausgegeben von Prof. Dr. E. Jedicke. Ulmer-Verlag, Stuttgart

Heurich M, Hilger A, Küchenhoff H, Andrén H, Bufka L, Krofel M, Mattisson J, Odden J, Persson J, Rauset GR (2014) Activity patterns of Eurasian lynx are modulated by light regime and individual traits over a wide latitudinal range. PloS one 9:e114143

Heurich M, Moritz HH, Kiechle H (2004) Der Einfluss des Luchses auf Rehpopulation und Waldverjüngung. Wald und Wild 21/2004:1139-1141

Heurich M, Möst L, Schauberger G, Reulen H, Sustr P, Hothorn T (2012) Survival and causes of death of European roe deer before and after Eurasian lynx reintroduction in the Bavarian Forest National Park. European Journal of Wildlife Research 58:567-578

Heurich M, Schultze-Naumburg J, Piacenza N, Magg N, Červený J, Engleder T, Herdtfelder M, Sladova M, Kramer-Schadt S (2018) Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. Biological Conservation 224:355-365

Heurich M, Zeis K, Küchenhoff H, Müller J, Belotti E, Bufka L, Woelfing B (2016) Selective predation of a stalking predator on ungulate prey. PloS one 11(8):e0158449

Hijmans RJ (2020) Introduction to the’raster’package (version 3.0-12).

Hočevar L, Fležar U, Krofel M (2020) Overview of good practices in Eurasian lynx monitoring and conservation. INTERREG CE 3Lynx report. University of Ljubljana. Biotechnical Faculty, Ljubljana

Hohmann U, Ebert C, Huckschlag D, Hettich U, Sandrini J (2016) Jagd als Regulierungsinstrument? Untersuchungsbefunde am Beispiel zweier Schwarzwildpopulationen (*Sus scrofa*) in Südwestdeutschland. Institue for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Landesforsten RLP, Trippstadt

Hohmann U, Hettich U, Ebert C, Huckschlag D (2018) Evaluierungsbericht zu den Auswirkungen einer dreijährigen Jagdruhe in der Kernzone „Quellgebiet der Wieslauter“ im Wildforschungsgebiet „Pfälzerwald“ (Langfassung). vol Nr. 84/18. Forschungsanstalt für Waldökologie und Forstwirtschaft FAWF, Mitteilungen aus der Forschungsanstalt für Waldökologie und Forstwirtschaft FAWF

Hutto RL (1985) Habitat selection by nonbreeding, migratory land. In: Cody ML (ed) Habitat selection in birds, vol 455. Academic Press, Orlando, Fla., pp 455-476

Idelberger S, Krebühl J, Back M, Ohm J, Prüssing A, Sandrini J, Huckschlag D (submitted) Reintroduction of Eurasian lynx (*Lynx lynx carpathicus*) in the Palatinate Forest, Germany

Imperio S, Ferrante M, Grignetti A, Santini G, Focardi S (2010) Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? Wildlife Biology 16:205-214

Jędrzejewska B, Jędrzejewski W (2005) Large carnivores and ungulates in European temperate forest ecosystems: bottom-up and top-down control. In: Ray JC, Redford KH, Steneck RS, Berger J (Eds) Large carnivores and the conservation of biodiversity. Island Press (pp. 230-246),Washington DC.

Jędrzejewska B, Jędrzejewski W, Bunevich AN, Miłkowski L, Krasiński ZA (1997) Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriologica 42:399-451

Jędrzejewski W, Schmidt K, Miłkowski L, Jędrzejewska B, Okarma H (1993) Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. Acta Theriologica 38:385-403

Jiang G, Zhang M, Ma J (2008) Habitat use and separation between red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi* in relation to human disturbance in the Wandashan Mountains, northeastern China. Wildlife Biol 14:92-100

Jobin A, Molinari P, Breitenmoser U (2000) Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. Acta Theriologica 45:243-252

Kaczensky P, Chapron G, von Arx M, Huber D, Andrén H, Linnell J (2013) Status, Management and Distribution of Large Carnivores – Bear, Lynx, Wolf and Wolverine in Europe. Part 1 IUCN/SSC Large Carnivore Initiative for Europe

Karanth KU (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture - recapture models. Biological Conservation 71:333-338

Kellner C (2012) Komitee-Bericht zur Evaluierung des Nationalparks Harz. Ingenieurbüro für Planung und Umwelt - IPU

Koehler GM, Brittell JD (1990) Managing spruce-fir habitat for lynx and snowshoe hare. Journal of Forestry 88:10-14

Kopaniak L (2021) Nutzung von Wildwiesen durch Rehwild vor und nach der Wiederansiedlung des Luchses im Pfälzerwald. Masterthesis, Albert-Ludwigs-Universität Freiburg

Kramer-Schadt S, Revilla E, Wiegand T (2005) Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biol Conserv 125:169-182

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. Journal of Applied Ecology 41:711-723

Krofel M, Jerina K, Kljun F, Kos I, Potočnik H, Ražen N, Zor P, Žagar A (2014) Comparing patterns of human harvest and predation by Eurasian lynx *Lynx lynx* on European roe deer *Capreolus capreolus* in a temperate forest. European Journal of Wildlife Research 60:11-21

Krofel M, Potočnik H, Kos I (2007) Topographical and vegetational characteristics of lynx kill sites in Slovenian Dinaric Mountains. Natura Sloveniae 9:25-36

Kunz F, von Rotz J, Breitenmoser-Wörsten C, Breitenmoser U, Zimmermann F (2020) Fang-Wiederfang-Schätzung der Abundanz und Dichte des Luchses in der Zentralschweiz West IIIa im Winter 2018/19. KORA Bericht, Nr. 94, Muri in Bern, 1-18

Kutal M, Duľa M, Krojerová-Prokešová J, Belotti E, Volfová J, Bufka L (2021) Uncoordinated reintroductions of Eurasian lynx might be a threat for the species recovery in Central Europe Biodiversity and Conservation 30(12):3737-3740

Kvam T (1991) Reproduction in the European lynx, *Lynx lynx.* Zeitschrift für Säugetierkunde 56:146-158

La Morgia V, Calmanti R, Calabrese A, Focardi S (2015) Cost-effective nocturnal distance sampling for landscape monitoring of ungulate populations. European Journal of Wildlife Research 61:285-298

Landesforsten RLP Forest Taxation (2020).

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401-1409

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1-7

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48:25-34

Lima SL, Bednekoff PA (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist 153:649-659

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640

Linnell JD, Andersen R, Kvam T, Andren H, Liberg O, Odden J, Moa P (2001) Home range size and choice of management strategy for lynx in Scandinavia. Environ Manage 27:869-879

Linnell JD, Breitenmoser U, Breitenmoser-Würsten C, Odden J, von Arx M (2009) Recovery of Eurasian lynx in Europe: what part has reintroduction played? . In: M. W. Hayward & M. J. Somers (Eds.), Reintroduction of top-order predators (pp. 72-91).Oxford:Wiley-Blackwell.

Linnell JD, Promberger C, Boitani L, Swenson JE, Breitenmoser U, Andersen R (2005) The linkage between conservation strategies for large carnivores and biodiversity: the view from the “half-full” forests of Europe. In: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.). Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, DC

Linnell JD, Swenson JE, Anderson R (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Animal Conservation 4:345-349

Lüchtrath A, Schraml U (2015) The missing lynx - understanding hunters' opposition to large carnivores. Wildlife Biology 21:110-119

LVermGeoRP, GeoBasis-DE (2020) dl-de/by-2-0. lvermgeo.rlp.de.

Magg N, Müller J, Heibl C, Hackländer K, Wölfl S, Wölfl M, Bufka L, Červený J, Heurich M (2015) Habitat availability is not limiting the distribution of the Bohemian–Bavarian lynx *Lynx lynx* population. Oryx 50(4):742-752

Mann HB, Whitney DR (1947) On a test of whether one of two random variables is stochastically larger than the other. The Annals of Mathematical Statistics 18(1):50-60

Mathisen K, Wójcick A, Borowski Z (2018) Effects of forest roads on oak trees via cervid habitat use and browsing. Forest Ecology and Management 424: 378–386

Matjuschkin E (1978) Der Luchs: *lynx lynx.* A. Ziemsen Verlag, Wittenberg-Lutherstadt

Mayer K, Belotti E, Bufka L, Heurich M (2012) Dietary patterns of the Eurasian lynx (*Lynx lynx*) in the Bohemian Forest. Säugertierkundliche Informationen 45:447–453.

Meisingset EL, Loe LE, Brekkum Ø, Van Moorter B, Mysterud A (2013) Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77:181-191

Melis C, Basille M, Herfindal I, Linnell JD, Odden J, Gaillard J-M, Høgda K-A, Andersen R (2010) Roe deer population growth and lynx predation along a gradient of environmental productivity and climate in Norway. Ecoscience 17:166-174

Melis C, Jędrzejewska B, Apollonio M, Bartoń KA, Jędrzejewski W, Linnell JD, Kojola I, Kusak J, Adamic M, Ciuti S (2009) Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Global Ecology and Biogeography 18:724-734

Melis C, Szafrańska PA, Jędrzejewska B, Bartoń K (2006) Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. Journal of Biogeography 33:803-811

Michler F-U, Gilllich B, Michler A, Rieger S (2018) Interspezifisches Interatkionsverhalten von Wölfen und Rotwild in Sachsen-Anhalt - eine Projektvorstellung. Paper presented at the Conference "Wald-Wild-Wolf, was Forstleute bewegt" Freising, Germany, 2018

Miller B, Dugelby B, Foreman D, del Rio CM, Noss R, Phillips M, Reading R, Soule ME, ETerborgh J, Willcox L (2001) The importance of large carnivores to healthy ecosystems. Endangered Species Update 18:202-210

Miller DL (2017) Distance sampling detection function and abundance estimation. R package version 0.9.7, cran.r-project.org/web/packages/Distance/Distance.pdf

Ministerium für Umwelt und Forsten RLP (2002) Wildkatzen in RLP.

Moen R, Terwilliger L, Dohmen AR, Catton SC (2010) Habitat and road use by Canada lynx making long-distance movements. Center for Water and Environment, Natural Resources Research Institute, Duluth

Molinari-Jobin A, Molinari P, Breitenmoser-Würsten C, Breitenmoser U (2002) Significance of lynx *Lynx lynx* predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. Wildlife Biology 8:109-115

Molinari-Jobin A, Zimmermann F, Ryser A, Breitenmoser-Würsten C, Capt S, Breitenmoser U, Molinari P, Haller H, Eyholzer R (2007) Variation in diet, prey selectivity and home-range size of Eurasian lynx *Lynx lynx* in Switzerland. Wildlife Biology 13:393-405

Molinari-Jobin A, Molinari P, Loison A, Gaillard JM, Breitenmoser U (2004) Life cycle period and activity of prey influence their susceptibility to predators. Ecography 27:323-329

Morris D (2013) Habitat Selection. Oxford Bibliographies in Ecology, New York: Oxford University Press

MUEEF RLP (2012) Klimawandel-Informationssystem RLP: Regionale Informationen - Pfälzerwald. Ministry of Environment, Energy, Food and Forestry Rhineland-Palatinate. kwis-rlp.de/de/anpassungsportal/regionale-informationen/pfaelzerwald/. Accessed 15.01.2018

MUEEF RLP (2016) Managementplan für den Umgang mit Luchsen in Rheinland-Pfalz. Stiftung Natur und Umwelt Rheinland-Pfalz, Mainz

Mueller SA, Reiners TE, Middelhoff TL, Anders O, Kasperkiewicz A, Nowak C (2020) The rise of a large carnivore population in Central Europe: genetic evaluation of lynx reintroduction in the Harz Mountains. Conservation Genetics 21:577-587

Mysterud A (2004) Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. Wildlife Biology 10:203-211

Mysterud A, Langvatn R, Yoccoz NG, Chr N (2001) Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 70:915-923

Mysterud A, Larsen PK, Ims RA, Østbye E (1999) Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Can J Zool 77:776-783

Mysterud A, Lian L-B, Hjermann DØ (1999) Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. Can J Zool 77:1486-1493

Naturpark Pfälzerwald (2018) Biosphärenreservat Pfälzerwald-Nordvogesen. Naturpark Pfälzerwald pfaelzerwald.de/naturpark-pfaelzerwald/. Accessed 15.01.2018 2018

Niedziałkowska M, Jędrzejewski W, Mysłajek RW, Nowak S, Jędrzejewska B, Schmidt K (2006) Environmental correlates of Eurasian lynx occurrence in Poland – Large scale census and GIS mapping. Biological Conservation 133:63-69

Nilsen EB, Linnell JD, Odden J, Andersen R (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. Journal of Animal Ecology 78:741-751

Odden J, Linnell JDC, Andersen R (2006) Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. European Journal of Wildlife Research 52:237-244

Okarma H, Jedrzejewski W, Schmidt K, Kowalczyk R, Jedrzejewska B (1997) Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeral Forest, Poland. Acta Theriologica 42:203-224

Ordiz A, Støen O-G, Delibes M, Swenson JE (2011) Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166:59-67

Pebesma E, Bivand RS (2005) S classes and methods for spatial data: the sp package. R news 5:9-13

Pedersen VA, Linnell JD, Andersen R, Andrén H, Lindén M, Segerström P (1999) Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. Wildlife Biology 5:203-211

Pesenti E, Zimmermann F (2013) Density estimations of the Eurasian lynx (*Lynx lynx*) in the Swiss Alps. J Mammal 94:73-81

Pfälzerwald-Nordvogesen B (2021) Biosphärenreservat Pfälzerwald-Nordvogesen. www.pfaelzerwald.de. Accessed 01.10. 2020

Pierce BM, Bowyer RT, Bleich VC (2004) Habitat selection by mule deer: forage benefits or risk of predation? The Journal of Wildlife Management 68:533-541

Podgórski T, Schmidt K, Kowalczyk R, Gulczyńska A (2008) Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriologica 53:97-110

Podolski I, Belotti E, Bufka L, Reulen H, Heurich M (2013) Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx lynx* in relation to availability of kills. Wildlife Biology 19:69-77

Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture-recapture experiments. Wildlife Monographs 107:3-97

Poole KG, Wakelyn LA, Nicklen PN (1996) Habitat selection by lynx in the Northwest Territories. Canadian Journal of Zoology 74:845-850

Port M (2020) Systematisches Fotofallenmonitoring des Luchses im Pfälzerwald. FAWF Mitteilungen. Institute for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Trippstadt

Port M (2021) Systematisches Fotofallenmonitoring des Luchses im Pfälzerwald 2019/20 und 2020/21, unpublished report. Institute for Forest Ecology and Forestry of Rhineland-Palatinate (FAWF), Trippstadt

Port M, Henkelmann A, Schröder F, Waltert M, Middelhoff L, Anders O, Jokisch S (2020) Rise and fall of a Eurasian lynx (*Lynx lynx*) stepping-stone population in central Germany. Mammal Research 66(1):1-11

Putman RJ (1984) Facts from faeces. Mammal Review 14:79-97

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2014. R Core Team,

R Core Team (2020) R: A language and environment for statistical computing.R Foundation for Statistical Computing.Vienna.

Raesfeld F (1985) Das Rehwild. Paul Parey, Hamburg, Berlin

Rewildingeurope (2021) Return of the missing lynx. rewildingeurope.com. Accessed 02.01. 2021

Rheinland-Pfalz Kompetenzzentrum für Klimawandelfolgen (2021). www.kwis-rlp.de. Accessed 01.04 2021

Ripple WJ, Beschta RL (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766

Röhl U (2013) Komitee-Bericht zur Evaluierung des Nationalparks Bayerischer Wald. Ingenieurbüro für Planung und Umwelt - IPU

Rolley RE, Warde WD (1985) Bobcat habitat use in southeastern Oklahoma. The Journal of Wildlife Management 49:913-920

Rozylowicz L, Chiriac S, Sandu RM, Manolache S (2010) The habitat selection of a female lynx (*Lynx lynx*) in the northwestern part of the Vrancea Mountains, Romania. North West J Zool 6:122-127

Ryser A, Von Wattenwyl K, Ryser-Degiorgis M, Willisch C, Zimmermann F (2004) Breitenmoser, U. Luchsumsiedlung Nordostschweiz 2001-2003, Schlussbericht Modul Luchs des Projektes LUNO. KORA Bericht. 22, 1-60. 2004. Muri bei Bern

Samelius G, Andrén H, Kjellander P, Liberg O (2013) Habitat selection and risk of predation: re-colonization by lynx had limited impact on habitat selection by roe deer. PLoS ONE 8:1-8

Sand H, Wikenros C, Wabakken P, Liberg O (2006) Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? Proc Royal Soc B 273:1421-1427

Sandrini J (2010) Eignungsanalyse von Fotofallen-Standorten für das Monitoring von Luchsen (*Lynx lynx L.*) im Bayerischen Wald. Diplomarbeit, Universität Freiburg

Schadt S, Knauer F, Kaczensky P, Revilla E, Wiegand T, Trepl L (2002) Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. Ecological Applications 12:1469-1483

Schadt S, Revilla E, Wiegand T, Knauer F, Kaczensky P, Breitenmoser U, Bufka L, Červený J, Koubek P, Huber T (2002) Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecology 39:189-203

Schmidt-Posthaus H, Breitenmoser-Wörsten C, Posthaus H, Bacciarini L, Breitenmoser U (2002) Causes of mortality in reintroduced Eurasian lynx in Switzerland. Journal of Wildlife Diseases 38:84-92

Schmidt K (1998) Maternal behaviour and juvenile dispersal in the Eurasian lynx. Acta Theriologica 43:391-408

Schmitz OJ, Beckerman AP, O'Brien KM (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388-1399

Schnyder J, Ehrbar R, Reimoser F, Robin K (2016) Huftierbestände und Verbissintensitäten nach der Luchswiederansiedlung im Kanton St. Gallen. Schweizerische Zeitschrift fur Forstwesen 167:13-20

Schukraft R (2017) Luchs-Riss-Habitatkariterung im Projekt "Interaktion von Luchs und Reh im Pfälzerwald".M.Sc. thesis. Hochschule für Wirtschaft und Umwelt Nürtingen-Geislingen.

Seiler A (2003) The toll of the automobile: Wildlife and roads in Sweden. Doctoral thesis, Departmen of Conversation Biology, Swedish University of Agricultural Science, Uppsala, Sweden

Signer J, Filla M, Schoneberg S, Kneib T, Bufka L, Belotti E, Heurich M (2019) Rocks rock: the importance of rock formations as resting sites of the Eurasian lynx *Lynx lynx*. Wildlife Biology 2019 (1):1-5

Sih A, Crowley P, McPeek M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269-311

Silver SC, Ostro LE, Marsh LK, Maffei L, Noss AJ, Kelly MJ, Wallace RB, Gómez H, Ayala G (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38:148-154

Simon O, Kotremba C (2016) Lebensraumgutachten Rotwild in der Hegegemeinschaft Pfälzerwald-Süd KdöR - Lebensraumanalyse und Maßnahmenempfehlungen 2014/2015. Unveröffentlichtes Gutachten. Auftraggeber Rotwildhegegemeinschaft "Pfälzerwald-Süd", 1-70, Institut für Tierökologie und Naturbildung.

Smart JC, Ward AI, White PC (2004) Monitoring woodland deer populations in the UK: an imprecise science. Mammal Review 34:99-114

Smith EP (2014) BACI design. Wiley StatsRef: Statistics Reference Online doi:10.1002/9781118445112.stat07659

SNU-RLP (2018) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed Januar 18, 2018

SNU-RLP (2020) EU-LIFE Luchs Projekt. snu.rlp.de/de/projekte/. Accessed 15.11.2020

Sommer R, Benecke N (2006) Late Pleistocene and Holocene development of the felid fauna (Felidae) of Europe: a review. Journal of Zoology 269:7-19

Squires JR, Decesare NJ, Kolbe JA, Ruggiero LF (2010) Seasonal resource selection of Canada lynx in managed forests of the Northern Rocky Mountains. The Journal of Wildlife Management 74:1648-1660

Stahl P, Vandel J-M (1999) Mortalité et captures de lynx (*Lynx lynx*) en France (1974-1998). Mammalia 63:49-60

Statista (2020) Rehwildstrecken Deutschland. de.statista.com/statistik/daten/studie/219626/umfrage/jahresstrecken-von-rehwild-in-deutschland/. Accessed 18.09.2020 2020

Stenseth NC, Shabbar A, Chan K-S, Boutin S, Rueness EK, Ehrich D, Hurrell JW, Lingjærde OC, Jakobsen KS (2004) Snow conditions may create an invisible barrier for lynx. Proceedings of the National Academy of Sciences 101:10632-10634

Stubbe C (1997) Rehwild: Biologie, Ökologie, Bewirtschaftung. Parey Buchverlag, Berlin, 568 pp.

Sunde P, Stener SØ, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. Wildlife Biol 4:177-183

Taylor RJ (2013) Predation. Springer Science & Business Media, New York NY, USA

Thieurmel B, Elmarhraoui A (2019) Suncalc: Compute sun position, sunlight phases, moon position and lunar phase. R Package Version 50

Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324-336

Thomas L, Buckland S, Burnham K, Anderson D, Laake J, Borchers D, Strindberg S (2002) Distance sampling. In: ElShaarawi, A.H. and Piegorschs, W.W. (Eds). Encyclopedia of Environmetrics. pp. 544–552. John Wiley & Sons: Chichester, UK

Torres RT, Virgós E, Panzacchi M, Linnell JD, Fonseca C (2012) Life at the edge: Roe deer occurrence at the opposite ends of their geographical distribution, Norway and Portugal. Mammalian Biology 77:140-146

Tracz M, Tracz M, Grzegorzek M, Ratkiewicz M, Matosiuk M, Górny M, Schmidt K (2021) The return of lynx to northwestern Poland. Cat News Special:43-44

Valente AM, Acevedo P, Figueiredo AM, Fonseca C, Torres RT (2020) Overabundant wild ungulate populations in Europe: management with consideration of socio-ecological consequences. Mammal Review 50:353-366

Vogt K, Zimmermann F, Kölliker M, Breitenmoser U (2014) Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx *Lynx lynx*. Behav Processes 106:98-106 von Arx M, Breitenmoser-Würsten C, Zimmermann F, Breitenmoser U (2004) Status and conservation of the Eurasian lynx (*Lynx lynx*) in Europe in 2001. KORA-Bericht, Nr. 19. Muri in Bern, 1-319

von Arx M, Breitenmoser U (2004) Reintroduced lynx in Europe: their distribution and problems. ECOS: A Review of Conservation 25(3/4):64-68

Wäber K, Dolman PM (2015) Deer abundance estimation at landscape-scales in heterogeneous forests. Basic and Applied Ecology 16:610-620

Ward AI, White PC, Critchley CH (2004) Roe deer *Capreolus capreolus* behaviour affects density estimates from distance sampling surveys. Mammal Review 34:315-319

Warren R (2011) Deer overabundance in the USA: recent advances in population control. Animal Production Science 51:259-266

Weingarth K, Heibl C, Knauer F, Zimmermann F, Bufka L, Heurich M (2012) First estimation of Eurasian lynx (*Lynx lynx*) abundance and density using digital cameras and capture–recapture techniques in a German national park. Anim Biodivers Conserv 35:197-207

Weingarth K, Zeppenfeld T, Heibl C, Heurich M, Bufka L, Daniszová K, Müller J (2015) Hide and seek: extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. Biodiversity and Conservation 24:2935-2952

White S, Briers RA, Bouyer Y, Odden J, Linnell JDC (2015) Eurasian lynx natal den site and maternal home-range selection in multi-use landscapes of Norway. Journal of Zoology 297:87-98

Wickham H (2016) ggplot2: Elegrant graphics for data analysis.Springer International Publishing. 2nd edn., Cham, Switzerland

Wickham H, François R, Henry L, Müller K (2020) dplyr: a grammar of data manipulation. R package version 0.8. 0.1, CRAN.R-project.org/package=dplyr

Wikenros C, Kuijper DP, Behnke R, Schmidt K (2015) Behavioural responses of ungulates to indirect cues of an ambush predator. Behaviour 152:1019-1040

Wikenros C, Sand H, Wabakken P, Liberg O, Pedersen HC (2009) Wolf predation on moose and roe deer: chase distances and outcome of encounters. Acta Theriologica 54:207-218

Wölfl M (2002) Weite Wanderungen durch enge Horizonte. Bericht im Auftrag des Naturpark Bayerischer Wald eV und der Regierung der Oberpfalz Zwiesel

Worton BJ (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. The Journal of Wildlife Management 59:794-800

Zimmermann F, Breitenmoser-Würsten C, Breitenmoser U (2005) Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. Journal of Zoology 267:381-395

Zimmermann F, Breitenmoser U (2007) Potential distribution and population size of the Eurasian lynx *Lynx lynx* in the Jura Mountains and possible corridors to adjacent ranges. Wildlife Biology 13:406-416

Declaration of Authorship

I hereby affirm that I composed this dissertation by myself and only with the use of resources, data, personal communications and literature cited in the text. Those who provided assistance for the experiments, data analyses or writing of the manuscripts are listed as co-authors or mentioned in the acknowledgements in the respective manuscripts.

Furthermore, I confirm that I have read and fully understood the Doctoral examination regulations of the Faculty of Biological Sciences, Friedrich Schiller University Jena (September 23rd 2019) and that I produced the doctoral thesis project myself and that no third parties have received any indirect or direct financial rewards in relation with the contents of this dissertation. In addition, I also confirm that I cited the tools, personal communication, and literature having been used. The support in the preparation of the manuscripts was only received from named co-authors as well as anonymous reviewers within the peer-review processes during manuscript submission. I declare that this dissertation or parts of it have not been previously submitted as thesis for scientific survey to the Friedrich Schiller University Jena or to any other university.

Trippstadt, __________2021 ___________________

Carolin Tröger

Acknowledgments

Not only the interaction between predator and prey dynamics can be a long-term process, also the establishment of a PhD thesis can take a while. The first three years have passed in flight and we were busy recording the wildlife in the Palatinate Forest at night. The lynx sightings were the highlights in the past years. Besides all the roe deer detections, the sightings of red deer, wild cat and all the other night active animals enchanted us during the 180 nights in summer and winter time. In 2018 and 2019, we finally received the second important data set – the lynx GPS coordinates, giving me the opportunity to analyse the interaction of both species within our study area. Summarizing the data in 2020 and writing up the PhD thesis in 2021 rounded up a big chapter of my life.

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