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ROE DEER POPULATION TREND AFTER REINTRODUCTION OF EURASIAN LYNX WITHIN THE PALATINATE FOREST: A FIRST INSIGHT INTO A LONG-TERM STUDY

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Abstract.

After becoming extinct approximately 250 years ago in the Palatinate Forest, the first Eurasian lynx (Lynx lynx) *were reintroduced within this area in 2016, with 20 lynx reintroduced in the following five years. We observed the roe deer* (Capreolus capreolus) *population within the Palatinate Forest before (2016) and during (2017–2019) the lynx reintroduction by estimating the population and evaluating the hunting bag. The roe deer population estimation based on the distance sampling method was conducted on ten defined transects with an average length of 48 km from 2016 to 2019, observing a 6,000 km transect length for 120 nights overall. An average of 6.54 ± 1.28 roe deer km^{-2} was estimated over the course of the four years (2016 – 2019). Since we suspect that our estimations might underestimate the roe deer population within the Palatinate Forest, hence we preferred to use the roe deer count index for further analysis. Over the first four years (2016–2019), significant differences were neither found in the roe deer count index nor for the hunting bag in relation to the reintroduction of the lynx. The data and findings presented in this study provide a first insight into a long-term observation of a predator-prey system within the Palatinate Forest, with roe deer not having experienced a natural predator over a long time. In order to make coherent interpretations, long-term data is needed to estimate the population trends of both species within the Palatinate Forest.*

Key words: *Eurasian lynx, Roe deer, population estimation, distance sampling, predator-prey*

Introduction

The recovery of large carnivores like the brown bear (*Ursus arctos*), wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) (hereafter called “lynx”) are making a comeback in Central Europe (Breitenmoser and Breitenmoser-Würsten 2008, Heurich 2019, Tracz et al. 2021). Since the 1970s, the largest European felid was reintroduced in different areas (Central and West) of Europe (Breitenmoser and Breitenmoser-Würsten 2008). With the reintroduction of the lynx in the Palatinate Forest (Germany), another step was taken towards achieving a demographically and genetically viable lynx population within the southwestern region of Europe (Jura, Northern and Southern Vosges, Black Forest).

However, the recovery of this large carnivore was accompanied by serious conflicts with traditional hunters, wildlife managers and conservationists in Central Europe (Breitenmoser et al. 2010, Lüchtrath and Schraml 2015). The impact of lynx believed or observed by local hunters on its prey population based on the increase in predator abundance, the simultaneous decline of ungulate population and the change in roe deer behaviour led to repeated illegal killings of this large carnivore (Breitenmoser et al. 2010, Heurich 2018). Poaching seems to be the most threatened mortality for lynx within the Czech Republic (Červený et al. 2002) and in the Bavarian Forest ecosystem (Heurich et al. 2018). Even nowadays, the acceptance among hunters of this large carnivore is the most important factor for the successful return of lynx within Europe (Breitenmoser and Breitenmoser-Würsten 2008). In order to assess the effects of predation on their main prey, solid and valid data are of crucial importance in this debate, and above all it should lead to public acceptance (Kutal et al. 2021).

The predation success rate and its effect on the prey species is dependent on multiple factors, such as the nutritional base, climate, diseases, competition and land use by humans (Breitenmoser and Breitenmoser-Würsten 2008). The effect of lynx on its prey has been studied in several regions with different methodological setups, resulting in a variety of outcomes, whereby it is not yet fully understood today (Molinari-Jobin et al. 2002). For instance, Haller (1992) found that the impact of lynx on the local roe deer population was quite substantial, even leading to a temporary local extinction of roe deer in the Swiss Turtmanntal. Breitenmoser and Haller (1993) concluded that in the Swiss Alps ungulates showed no antipredator behaviour in areas where their natural predators had not been present for a longer period.

Within the Bavarian Forest, roe deer density was relatively low with 1–5 animals km^{-2} and hence it resulted in a strong influence of lynx on the roe deer population due to such a low prey density (Heurich et al. 2012). These results are in line with the findings of Jędrzejewska and Jędrzejewski (2005), who found a strong pressure on ungulate numbers by large carnivores in periods of cooler climate and less productive environments. In their study, Melis et al. (2009) found that the productivity of the environment appears to be essential when evaluating the effect of a predator on its prey. In regions with a mild climate and highly productive habitat, the top-down effect of large carnivores on its prey was relatively weak, whereas in regions with low productivity and harsh winter conditions the effect increased (Melis et al. 2009, Melis et al. 2010). Lynx only show low variation in the kill rate across a large range of prey densities (Melis et al. (2010) cited after Breitenmoser and Haller (1993), Okarma et al. (1997), Molinari-Jobin et al. (2002)). This leads to the assumption that the impact of lynx may increase in low-density prey populations (Melis et al. 2010) and hence create a "predator pit" situation.

In the north-eastern part of Switzerland Schnyder et al. (2016) found a significant decrease in population estimation for roe deer and chamois (*Rupicapra rupicapra)* (based on hunting bag data and count data) and browsing intensity on European silver fir (*Abies alba*) over a time frame of 15 years (five years before and ten years after the reintroduction of lynx – lynx relocation in northeast Switzerland). Continued hunting pressure, illness and weather conditions could have cumulatively affected the ungulate population within the lynx core area (Jędrzejewska et al. 1997, Schnyder et al. 2016). In south-central Sweden, Andrén and Liberg (2015) found that lynx predation influences the roe deer population together with density-dependent factors. Additionally, the lynx kill rate was strongly affected by the lynx's social status (Andrén and Liberg 2015), revealing higher kill rates for female lynx with kittens, followed by males and solitary females.

The annual growth rate of the roe deer population decreased after a natural recolonisation of this top-predator, showing that bottom-up and top-down processes work at the same time, with both influencing the population dynamics (Andrén and Liberg 2015).

Breitenmoser et al. (2010) argues that three different kinds of impact scenarios have been observed from a predator on its prey population: a) "changing predation impact during the recolonization of areas with naive and abundant prey", b) low-to-moderate impact after re-adaption, and c) "dynamic predator-prey phase with high impact after 15 years of stability". The first scenario revealed a considerable impact of the roe deer population with a delay of three to five years, whereas in the second scenario prey within the northwestern Alps regained vigilance towards the new predator, forcing lynx to increase their home ranges. In the third scenario, the predation impact in the northwestern Alps within the mid-1990s almost tripled for the roe deer population compared with the 1980s due to the increased lynx population, e.g. lynx preyed on 36–39 % of the local roe deer population. At this point, such high predation rates were only observed in Poland, with 21–36 % consumption of the local roe deer population (Okarma et al. 1997). This high impact was explained with a numerical response of lynx due to an increased roe deer population as a consequence of several mild winters (Breitenmoser et al. 2010).

Not only should the effect of a predator be taken into consideration, but also the possible cumulative effect of human harvest on the ungulate populations. We only found a few studies comparing human harvest and a natural predator (lynx) regarding the impact on the prey population.

For instance, Krofel et al. (2014) found that lynx predation in the Dinaric Mountains was considerably lower than the human harvest in the same area. In addition, lynx predation was similar across a gradient of roe deer densities, whereas human harvest increased with increasing roe deer density (Krofel et al. 2014). In Norway, Andersen et al. (2007) found that lynx killed a random section, whereas hunters killed a disproportionally large proportion of adults, especially males. Hunters within lynx home ranges argue that the influence of lynx on the roe deer population and especially their behaviour is quite significant (Heurich et al. 2004, Heurich et al. 2012). They also dispute that the presence of the predator influences their hunting success, which leads to the request to abate the rent of the hunting areas (Tröger, personal observation).

In order to address local hunters concerns that the roe deer population might decline, we started to investigate the population dynamics of roe deer – lynx's main prey – in the Palatinate Forest even before lynx returned to the area.

The impact of a reintroduced predator on an ungulate population needs to be determined in more regions of Europe due to the strong variation in present research studies (Molinari-Jobin et al. 2002, Heurich et al. 2012).

In this study, we present the first years of an ongoing long-term study. We investigated the prey population density by estimating it before and after the presence of the predator within the study area. Additionally, hunting bag data (hunted roe deer within the state-managed forest) of the Palatinate Forest and lynx home range calculations were included within our analysis. For this purpose, we tested the following predictions:

We assume **(a)** that lynx do not affect the roe deer population (less predation risk) in the Palatinate Forest within the first four years after their reintroduction (2016–2019), when the lynx population is still at a low level and the roe deer population at a low-medium population level.

Furthermore, we predict (**b**) that roe deer hunting bag in the Palatinate Forest does not correlate with the increasing and spreading lynx population in the first years after their reintroduction.

Methods

Study area

The study was conducted in the Palatinate Forest in the southwestern part of Germany, located in the temperate zone between the Atlantic and continental climate (49°12'N, 7°45'N). The Palatinate Forest elevation ranges from 210 to 609 m A.S.L. and contains only small settlements and little infrastructure, representing approx. 3 % of its area. Approximately 90 % of the Palatinate Forest is covered by forest (MUEEF RLP 2012), which mainly comprises of *Fagus sylvatica* and *Pinus sp.*. The Palatinate Forest is an average mountain range with dense and steep carved valley systems and various hill formations (MUEEF RLP 2012). The mountain range has a north-south orientation. 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 and it has been a German Natural Reserve since 1967 (Naturpark Pfälzerwald 2018). The Palatinate Forest stretches over 1790 km² (179.000 ha) and borders the northern part of the Vosges. Established in 1998, the Palatinate Forest and Vosges du Nord was the first trans-boundary biosphere reserve in Europe. It is called the "UNESCO-Palatinate Forest-North Vosges Biosphere Reserve" (Naturpark Pfälzerwald 2018) and covers about 3018 km² in total.

Our study concentrated on the German part of the biosphere reserve, the Palatinate Forest (**Fig. 1**). The study area is inhabited by 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 mentioned ungulates are hunted within the whole study area, with one exception of a 25 km^2 area located in the middle of the Palatinate Forest. Since 2013 (1.4 % of the whole forest), this area has been closed to hunting. In 2012, wild boar density within the centre of the Palatinate Forest was estimated at around 4.5–5.0 individuals km^{-2} (Ebert et al. 2012a). Deer densities were estimated at around 3.3 red deer km^{-2} (Ebert et al. 2021) and 5.9 roe deer km^{-2} (Ebert et al. 2012b) within the same area. For the rest of the whole study area, only hunting bag data exists, which is currently only geographically assigned within state-managed parts of the forest (**Fig. 1**).

Thermal infrared imaging

The study was conducted between February 2016 and March 2019. Data acquisition for the 2020 sampling year started in February but could not be finished due to the corona virus pandemic. Normal sampling was carried out annually in winter/spring, between February and April of 2016 to 2019 (full data sets). Sampling was based on ten transects (**Fig. 1**). The starting point of each transect was randomly selected within the corresponding forestry department using the "random points" tool in ArcGIS. Transects were established as a round-course based on a drivable forestry road network, with an average length of 48 km (total transect length per round / 10 transects ~ 480 km, **Fig. 1**). We considered the hab-

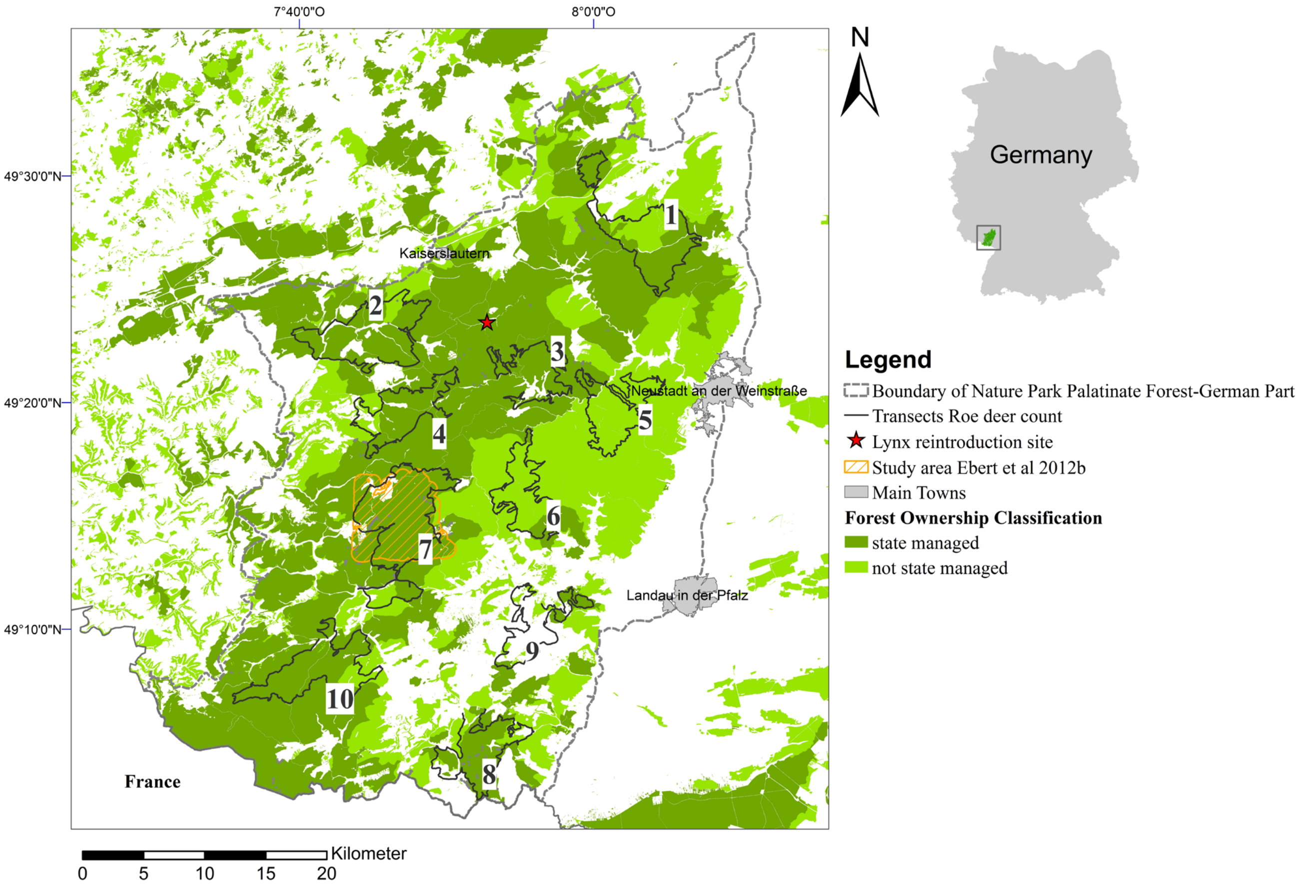

Figure 1: Overview of the study area. The location of the lynx reintroduction site and the ten transects used for the roe deer survey within the Palatinate Forest in Germany between 2016 and 2019 (2020). Forested areas are coloured for state- and not state-managed forest. The size of the study area is 1790 km². The area not coloured comprises agricultural land, settlements and infrastructure. The study area for ungulate population estimations of Ebert et al. (2012b) is highlighted within the map.

itat type distribution of the selected forestry roads, i.e. the habitat of the selected transects were representative of the surrounding forestry department. We used different qualities of forestry roads as transects, whereby a large part comprised dirt roads, followed by gravel roads and a small number of paved forestry roads. These roads were only open for the use of forestry management and hunting practice, whereas public traffic had no permit to use these roads. The forestry road network within the Palatinate Forest can be stated as high, with a path density of 50–90 m/ha forest (Simon and Kotremba 2016). Sampling was performed after dusk using a 4WD vehicle. Transects were repeated twice (three runs, total yearly winter / spring transect length ~ 1500 km), summing up to a total amount of 6000 km sampling effort over the course of 2016–2019. The distance sampling method using line transects was applied after Buckland et al. (1993). Detection time started with sunset and lasted – depending on the number of detections and transect length – until 00:00-04:00 in the morning.

Sampling was performed with two thermal infrared imagers from the FLIR Ax5-Series. Each thermal infrared imagers was mounted on the half-open window of each side of the car. The cameras were connected to laptops / tablets to display the thermal infrared image. The laptops were attached on the dashboard of the car. The sampling images were not permanently recorded. Observations were immediately placed into an access databank, which was developed specifically for this project (dundotcan and wildlifemonitoring.eu 2015). The average moving speed of the car was 10-15 km/h. When detecting an animal, the car stopped and the species was defined either by the picture of the thermal infrared imager or with the help of a spotlight. We measured the distance from the car to an individual or group of individuals using a Leica Geovid binocular with an integrated distance range tool. When measuring the distance to a group of individuals (cluster group), the mean between the nearest and the furthest individual was calculated. We recorded the angle from the transect to the individual, the habitat on large scale (50 m radius around detected animal), habitat on fine scale (5 m radius around detected animal), behaviour when first sighted and the location (using a handheld GPS device). Fawns were identified by size, whereas adult roe deer were identified by primary and secondary sexual characteristics. On the left-hand of the car, the same person carried out observations over the whole observation period (reference person). Different observers conducted detections on the right-hand side of the car. In order to meet the assumption of distance sampling, we used high beam light on the car while driving on the forestry roads to detect all individuals on the transect line.

To determine the effect of lynx on the prey population, with the help of a BACI test (Smith 2014) we compared the roe deer count index (roe deer / km) in areas with and without lynx presence. The area (impact / control) and period (before and after lynx reintroduction) were used as predictor variables, whereas the roe deer count index was the response variable. This analysis was conducted in R version 3.5.3 (R Core Team 2020).

DS Model selection

We analysed distance sampling data separately for each year. All transects were pooled together for population estimation of the whole study area. Analysis of density estimation was based on four different analytical model sets (CDS binned = Conventional Distance Sampling binned, CDS left = Conventional Distance Sampling with full left truncation, CDS unbinned = Conventional Distance Sampling unbinned and MCDS = Multiple Covariate Distance Sampling). The CDS model set-up assumes that detection probability depends only on its distance from the transect (line). We used this model setup with and without fixed binning classes (CDS binned / CDS unbinned). The CDS left truncation is applied when there are low sighting frequencies close to the centreline line/transect line or when animals are avoiding transects (forest roads) or their vicinity. We tested a full left truncation by excluding data in the first 20 m interval of the model. Within the MCDS model setup, the detection probability is modelled on covariates such as habitat, animal behaviour, cluster size and observer (Buckland et al. 2015). In our case, we used the covariates habitat on large scale, habitat on fine scale and recorded behaviour of individuals (**Appendix 1 Table 1**). Prior to analysis, observations were manually right truncated to discard outliers (< 5 %). Model selection was based on Akaike´s information criterion (AIC). When ΔAIC < 2 between models, the model with the best goodness of fit was chosen (Burnham and Anderson 2002). Model fit was tested for three different bin widths (20 m, 40 m and 50 m). We found no difference between the estimations, and hence we chose the 20 m bin width for all final analyses. All population estimation analyses were carried out using R version 3.4.1 (R Core Team 2016) and the R package Distance (Miller 2017).

In winter 2018, all transects were mapped for their visibility. We critically checked for parts of the transect where roe deer detections are not possible. Steep slopes, wide forest roads on hill sides and cambers made detection from the transect with thermal infrared imaging cameras impossible. Non-visible stretches of transects were marked with GPS points. The lengths of these transect sections was calculated in ArcGIS and then subtracted from the total transect length (corrected effort). The distance sampling models presented here are based on the corrected transect length.

Lynx reintroduction and home range calculations

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. Over a period of five years (2016–2020), 20 lynx (*Lynx lynx carpathicus*) were released with lynx originating from Slovakia (Carpathian Mountains) and Switzerland. All lynx were released in proximity to the same place in the central part of the Palatinate Forest (**Fig. 1**, reintroduction site), close to transect number two. The reintroduction started in late summer of 2016. Released lynx are either wild catches (n = 13) or orphan lynx (n = 7), which were held a certain time in captivity. GPS collars were fitted on all reintroduced lynx with an approximate battery life of around one/two years and they were differently programmed according to the status and requirements of the reintroduction project (SNU-RLP 2020). One individual received an additional collar prior to the battery expiry date of the original one, resulting in longer GPS data sets. SNU RLP provided all lynx GPS data within the boundary of the Palatinate Forest.

The first lynx offspring within the Palatinate

Forest was documented in 2017. In the first half of 2019, twelve independent (adult and subadult) lynx were verified at least temporarily by the management team (SNU-RLP 2020) within the central Palatinate Forest. In 2019/2020, a systematic camera trap monitoring in the Palatinate Forest confirmed 17–19 independent lynx within the boundary of the Palatinate Forest (Port 2020).

For home range calculations, we used kernel density estimations (KDE). KDE were used to compare hunting bags in lynx core areas before and after the lynx presence. KDE were calculated for each individual lynx for three periods within each year: a) the mating season from January to March, b) breeding time from April to August, and c) autumn/winter time from September to December (**Table 1**). No home ranges were calculated with fewer than 78 locations. We estimated home ranges using the kernel density method with the href smoothing factor (Worton 1995, Calenge 2006). All analyses were conducted in R version 3.5.3 (R Core Team 2020). The kernel home range of 50 % was defined as core areas of lynx presence.

Roe deer hunting bag

Verifiable hunting bag records are only known for the State Forest area of the Palatinate Forest (around 50 % of 1790 km², mainly located in the western part of the study area, **Fig. 1**). We collected the raw data from each forestry department and district and analysed the hunting bag of recent hunting years (2012-2019). A hunting year lasts from 1st April to 31st March of the following year. Mean hunting bags for the forestry districts were compared based on temporal lynx presence (before and after reintroduction) with the help of a Mann-Whitney-U Test

Table 1: Home ranges of reintroduced lynx in the Palatinate Forest, Germany (2016-2019). For MCP calculations, a lynx year lasts from 1st May to 30th April. MCP data of the 2019 lynx year lasts until 31st December 2019. Kernel home range calculations were split in three seasons: the mating season lasting from 1st January to 31st March, the summer season from 1st April to 31st August and 1st September to 31st December as the autumn/winter season. No home range was calculated with fewer than 78 GPS locations. All home ranges are presented in km². Several GPS locations per individual per day were included within the home range analysis. Lynx GPS Data were provided by the Foundation of Nature and Environment (SNU) Rheinland-Palatinate.* Caution: presents a very small time frame.

Lynx	**Survey period**	**Number of locations**	**Total range** (MCP 100%)	**Reduced total range** (MCP 95%)	**Home range (Kernel 90%)**			**Home range (Kernel 50%)**		
					Mating	Summer	Winter	Mating	Summer	Winter
Year 2016										
Kaja	30.07.2016 -30.04.2017	1281	158	150	-	-	173	-	-	50
Lucky	30.07.2016-30.04.2017	1526	374	344	-	-	316	-	-	94
Luna	30.07.2016-02.12.2016	795	372	272	-	-	295	-	-	103
Rosa*	13.04.2017-30.04.2017	185	80	75	-	-	-	-	-	-
Year 2017										
Cyril	20.06.2017-28.11.2017, 01.01.2018-10.02.2018	1266	523	374	-	229	340	-	64	102
Jara*	19.04.2018-30.04.2018	155	34	32	-	-	-	-	-	-
Juri*	17.04.2018-30.04.2018	420	456	383	-	-	-	-	-	-
Kaja	01.05.2017-28.07.2017	581	23	19	31	13	-	8	2	-
Labka	15.12.2017-25.02.2018	2853	181	160	-	-	44	-	-	13
Lucky	01.05.2017-30.04.2018	1294	392	316	174	156	291	48	42	105
Rosa	01.05.2017-30.04.2018	266	-	-	-	243	284	-	72	96

Table 1, continued

Lynx	Survey period	Number of locations	Total range (MCP 100%)	Reduced total range (MCP 95%)	Home range (Kernel 90%)			Home range (Kernel 50%)		
					Mating	Summer	Winter	Mating	Summer	Winter
Year 2018										
Alfi	12.09.2018-30.11.2018, 22.01.2019, 04.02.2019-05.02.2019, 25.02.2019-26.02.2019	566	365	170	-	-	173	-	-	51
Gaupa	22.02.2019-30.04.2019	274	305	252	-	-	-	-	-	-
Jara	01.05.2018-22.11.2018	1012	184	136	-	69	198	-	17	65
Juri	01.05.2018-25.11.2018	740	965	781	361	988	151	115	346	53
Labka	-	-	-	-	207	-	-	62	-	-
Libre	07.03.2019-30.04.2019	535	463	458	-	-	-	-	-	-
Lucky	01.05.2018-30.04.2019	1798	495	415	299	369	479	115	143	166
Mala	06.02.2019-30.04.2019	492	406	280	-	-	-	-	-	-
Rosa	01.05.2018-11.06.2018	79	24	19	243	122	-	86	36	-
Wrano	11.09.2018-30.04.2019	764	552	256	-	-	153	-	-	39
Year 2019										
Alfi	-	-	-	-	977	-	-	341	-	-
Brano	06.06.2019-09.10.2019	842	625	336	-	396	204	-	142	53
Gaupa	01.05.2019-31.12.2019	1232	265	167	760	66	213	210	21	58
Libre	01.05.2019-21.09.2019	1318	612	391	444	529	411	128	99	112
Lucky*	01.05.2019-13.05.2019	169	128	127	160	112	-	38	27	-
Mala	01.05.2019-03.10.2019	771	154	112	282	197	27	86	38	5
Wrano	01.05.2019-23.06.2019	78	238	185	378	471	-	118	134	-

(Mann and Whitney 1947).

Roe deer hunting bag within lynx core home ranges

We intersected the lynx core areas for each season (mating, summer, autumn/winter) for 2016 to 2019 with the single forestry district of each forestry department. Only forestry districts that were mostly/fully covered by the lynx core home range at least three times between 2016 and 2019 were grouped as lynx presence (impact area), and others as a lynx absence.

From the total number of forestry districts, the state-managed ones were filtered out due to the availability of hunting bag data for these districts. The corresponding roe deer hunting bag (unit: km^{-2}) of the 2012/2013 to 2019/2020 hunting years were then used to test for differences in the hunting bag before and after lynx reintroduction (Mann-Whitney-U Test, Mann and Whitney (1947)). We also tested for the influence of the predator on the roe deer population on the temporal and spatial scale by applying a BACI analysis (Smith 2014). Control and impact areas in relation to before and after lynx reintroduction were compared with the help of a linear model (lm). Area (control and impact), period (before and after lynx reintroduction) and forestry districts were used as predictor variables, whereas hunting bag was the response variable.

Results

Thermal infrared imaging / Density estimation with DS

A total of ~6000 km was surveyed along ten repeated transects over 120 detection nights from winter/spring 2016 to winter/spring 2019 within the Palatinate Forest. Over the whole period, an average of 1168 roe deer detections were recorded per year (min = 938, max = 1319, SD = 168.12, n = 4671). The mean encounter rate was 0.8 ± 0.12 SD roe deer per transect kilometre (min = 0.65, max = 0.91). We estimated an average of 6.54 ± 1.28 SD roe deer km^{-2} (average over all MCDS models, min = 4.75, max = 7.6; **Fig. 2**). An increase of around 15 % from 2016 to 2017 was observed, followed by a decreasing population estimations in 2017 and 2018 (2017 to 2018: - 4 %, 2018 to 2019: - 35 %, based on MCDS model, **Fig. 2**). The roe deer count index after the reintroduction of lynx did not depend on the area (control or impact area), and hence the index does not differ between lynx and lynx-free areas (BACI analysis: p = 0.21, **Fig. 3**).

Roe deer hunting bag

Hunting bag comparison before and after the reintroduction of lynx within the Palatinate Forest revealed no significant differences between the two samples (Mann-Whitney, U = 425.5, p = 0.59), hence

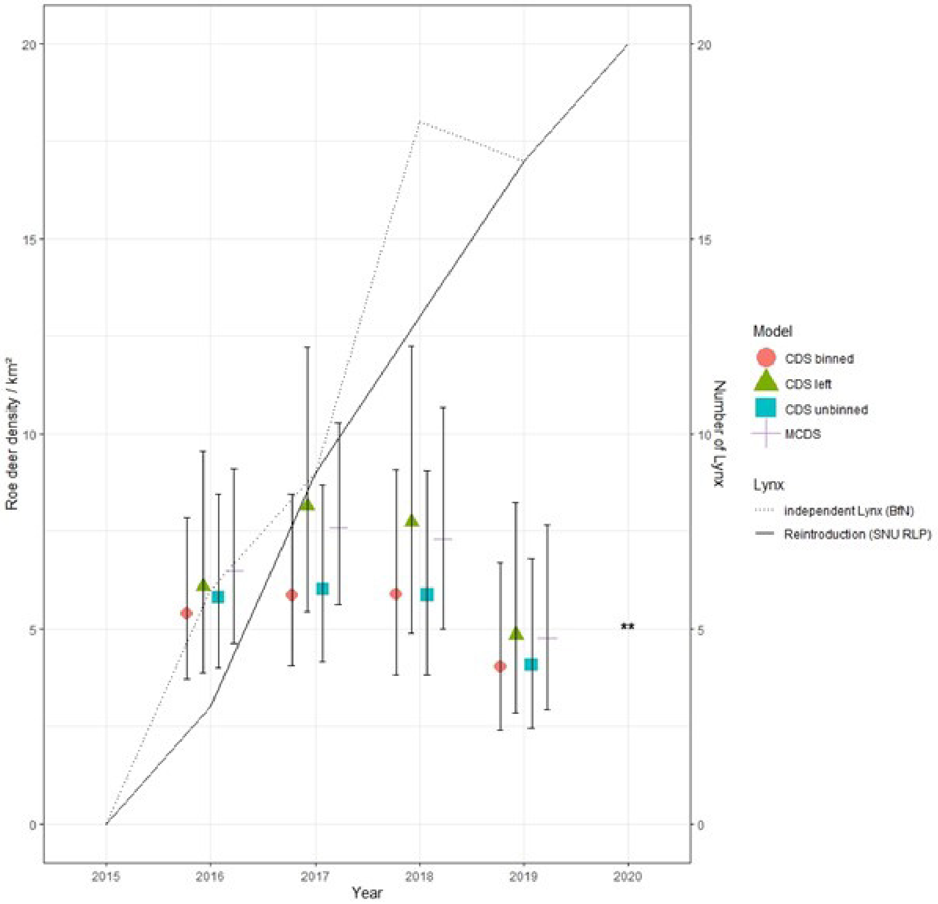

Figure 2: Density estimation of roe deer within the Palatinate Forest between 2016 and 2019. Density estimation was based on nocturnal line transect applying the distance sampling method. The lynx reintroduction within the Palatinate Forest started in 2016 over a time span of five years, introducing 20 lynx (SNU RLP). Number of lynx based on evaluations according to BfN standards and the total number of lynx reintroduced in the Palatinate Forest (SNU RLP). Four different model setups for roe deer population estimations were applied. Futher details are provided in **Appendix 1 Table 1**.

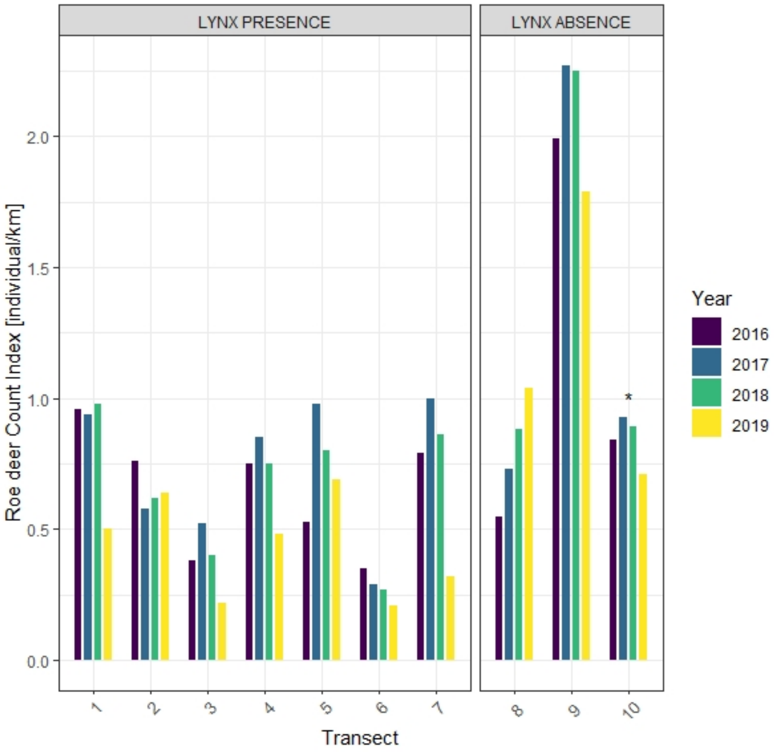

Figure 3: Roe deer count index on ten fixed transects in the Palatinate Forest, Germany, between 2016 and 2019. Based on lynx home range calculations, areas were classified into lynx presence and lynx absence.

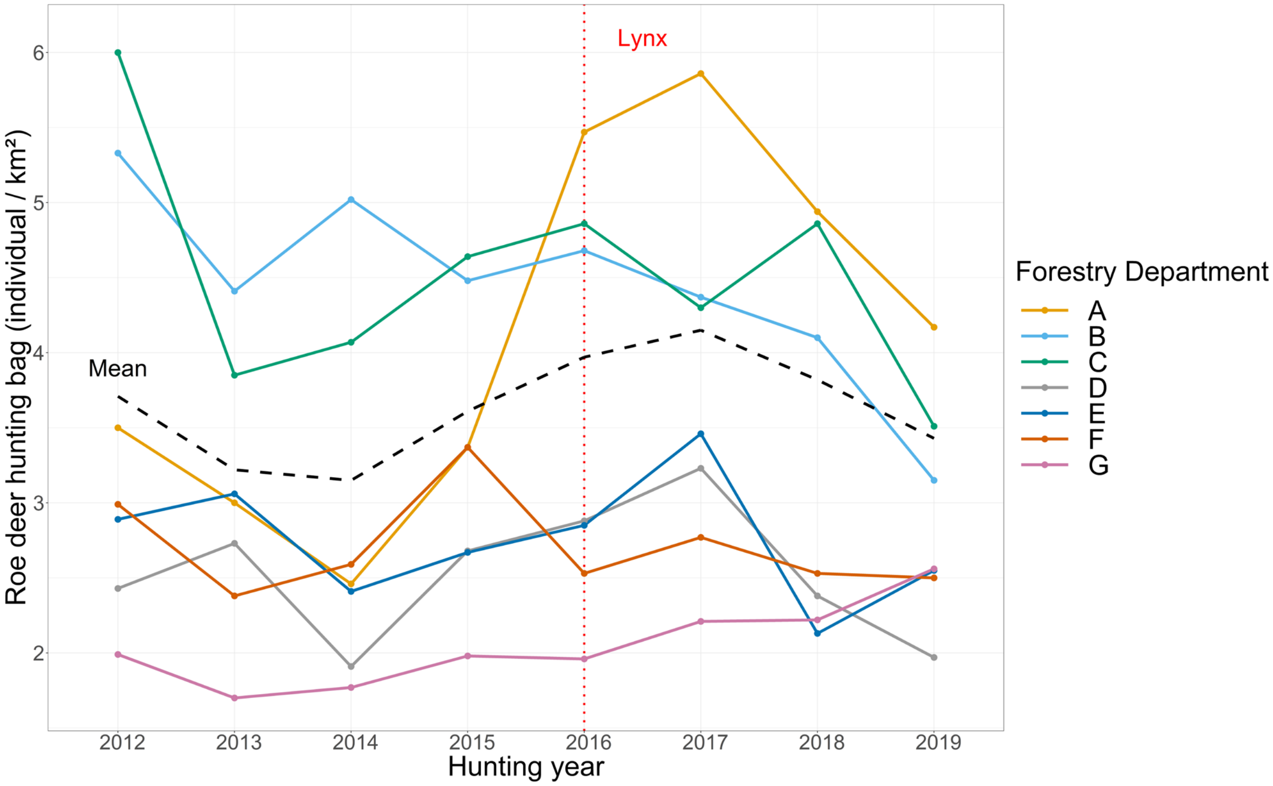

Figure 4: Overview of roe deer hunting bag of the state-managed areas in the Palatinate Forest (around 50 %) over the 2012 to 2019 hunting years. The Palatinate Forest comprises seven forestry departments, presented here with letters. The red dotted line marks the start of the reintroduction of lynx within the Palatinate Forest. The black dashed line presents the mean roe deer hunting bag over all forestry departments.

revealing similar mean hunting bags before and after the lynx reintroduction ($\text{mean}_{\text{before}}$ = 3.2 ± 0.21 se; $\text{mean}_{\text{after}}$ = 3.39 ± 0.22 se, **Fig. 4**). We found on average a lower hunting bag in 2018 and 2019 than in 2016 (mean_{2016} =3.97, mean_{2018} = 3.82, mean_{2019} = 3.43). In the 2013 and 2014 hunting years, we registered an overall drop of around 0.5 roe deer km^{-2} (**Fig. 4)**, and at this time no predator populations were present within the study area.

The mean sex ratio across all forestry departments was 1 ♂ : 0.91 ♀. We found low variation in the sex ratio of roe deer hunting bag comparing the individual forestry departments (SD = 0.23, min= 0.69, max=1.4, se= 0.09). Only one department reached a higher hunting bag for female than male roe deer (**Appendix 1 Table 2**). The sex ratio of hunted roe deer reveals similar trends before and after the lynx reintroduction ($\text{before}_{2012\text{ - }2016}$: 1 ♂ : 0.84 ♀, $\text{after}_{2017\text{ - }2019}$: 1 ♂ : 0.87 ♀). Hunters in the Palatinate Forest culled more adult than juvenile roe deer from 2012 to 2019 ($\text{mean}_{\text{adult}}$= 1422 individuals; $\text{mean}_{\text{juvenile}}$ = 356 individuals). This relates to around four (min = 3, max = 5) times more adult roe deer than juveniles within the hunting bag. Hunters bagged on average 45.4 % adult males, 34.7 % adult females and 19.9 % juvenile roe deer within the state-managed area of the Palatinate Forest (based on hunting bag of 2012–2019).

Human hunters culled on average 1,777 roe deer per year on around 900 km² of the Palatinate Forest, which – assuming the same harvesting rates on the other 50 % area – would sum up to 3,554 roe deer per year for the whole Palatinate Forest.

Roe deer hunting bag within lynx core home ranges

Overall, we found 34 forestry districts that were covered at least once by lynx core areas, of which eleven forestry districts were covered three times by the lynx core area. For eight out of these eleven forestry districts, hunting bag data was available (Kernel 50 %, **Fig. 5**, **Appendix 1 Table 3, Appendix 1 Fig. 1**). There are no differences between the hunting bag before and after the lynx reintroduction (Mann-Whitney: U = 426, p = 0.40) within these eight districts. In addition, there is one forestry district that showed no permanent lynx presence (**Fig. 5**). We found no significant differences in the hunting bag caused by the presence of lynx (BACI, p = 0.055, **Fig. 5**).

Discussion

The roe deer population estimation within the Palatinate Forest revealed an average of 6.54 roe deer km^{-2}, presenting an overall low to medium level roe deer population within a forested area in Germany (Heurich et al. 2012). We suspect that our distance sampling method applied provides an underestimation of the roe deer population within the Palatinate Forest. With an average roe deer hunting bag of three individuals km^{-2}, the yearly population growth of our estimated population would then be totally reduced. In this scenario, the reintroduced lynx would consequently reduce the roe deer population. However, this is not the case, whereby we assume that our roe deer estimations are underestimations of the real population density within the Palatinate Forest.

Our distance sampling data reveal that the detection probability at distance zero is less than one, which produces a bias in the CDS and MCDS density estimators (Buckland 2004). Detection probability depends on various variables other than distances (Buckland 2004), and it depends on the situation change with the observer, habitat, environmental conditions, season, size and behaviour of the animals (Buckland et al. 2001, Buckland 2004). In addition, a distinction can be made between perception bias and availability bias, which giving reasons for observers to overlook animals during data acquisition. Buckland et al. (2015) state that ungulate studies face challenges with the problems of non-random transect placement, responsive movement before detection and cluster size estimation. Using forestry roads as transects leads to a violation of the basic distance sampling rule that transects need to be randomly placed within the study area (Buckland et al. 2001, Buckland 2004, Buckland et al. 2015). Ungulate density can vary along roads, due to – for example – disturbance, hunting pressure and habitat availability alongside the road (Buckland et al. 2015). Additionally, forest roads are usually placed dependently to topographic or habitat structures in the area (slope parallel, valley, dry ground, avoidance of rugged terrain) (Buckland et al. 2015). Nocturnal application of distance sampling paired with thermal imagers is stated to be one possible way of circumventing responsive movement of the animals (Gill et al. 1997, Focardi et al. 2013) and hence prevent and/or reduce bias within the estimation. We cannot clarify which factor influences our density estimation the most, but in our opinion responsive movement is certainly one of the factors.

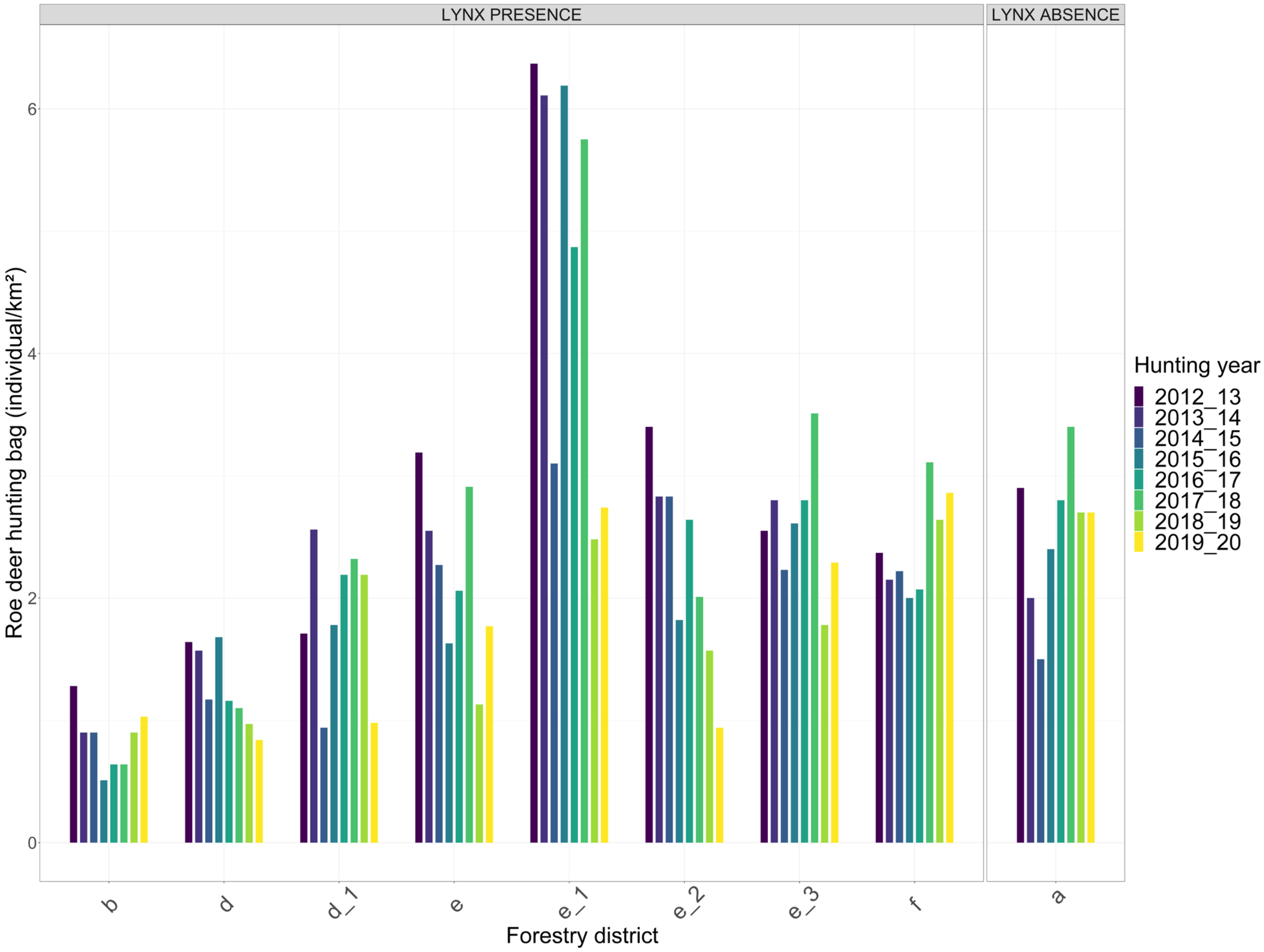

Figure 5: Roe deer hunting bag in eight forestry districts with and without permanent lynx presence in the Palatinate Forest over the time period of the 2012 to 2019 hunting year. Hunting bag data is based on state-managed forestry districts (around 50 % of the Palatinate Forest). Forestry district labels are linked to the abbreviation of forestry departments of **Fig. 4**.

Although our estimated population density is presumably lower than the real density, we still used the collected data to register changes within the index on a long-term temporal scale. However, we did not find significant differences for the roe deer count index before and after the reintroduction of lynx in the study area. Lynx reintroduction within the Palatinate Forest started in late summer 2016 with three individuals and finished with a total of 20 lynx in 2020, representing a slow but steadily increase in the abundance of lynx within the area over the five years. We hypothesised a) that lynx does not negatively affect the roe deer population during the first four years after reintroduction. Thus far, our results show no effect of the predator presence on the roe deer population on a large scale, although it should be considered that the lynx population at this time was still at a low level and not all areas of the study area were occupied at the end of 2019.

In addition, we detected on average lower numbers of culled roe deer in the 2018 and 2019 hunting years in almost all areas within the study area. Again, we were unable to find a difference within the hunting bag, which could be linked to the presence of the predator, like hypothesised in b). Furthermore, a decrease of human hunting success was detected in the 2013 and 2014 hunting years, indicating that other factors (like abiotic factors) might have influenced the roe deer population in these years and hence might have also influenced population dynamics in 2018 and 2019. Comparing hunting data on a national scale, we also found lower numbers of hunted roe deer in these years (2013/2014), which are then followed by an increase (Statista 2020), supporting the aforementioned hypothesis.

Besides the population estimation and overall hunting bag data, sex ratio and age class of hunted roe deer are also valuable information to determine the hunting mode of natural and human hunters and their influence on the population. Only a few studies have sought to compare the roe deer hunting bag of human hunters to natural predators (lynx) (Andersen et al. 2007, Krofel et al. 2014). Our hunting bag analysis revealed that recreational hunters in the Palatinate Forest (state-managed areas) harvest more male than female roe deer (sex ration: 1 ♂ : 0.91 ♀) and a higher percentage of adults than juveniles (1 adult: 0.25 juvenile).

Contrary to this, lynx in the Palatinate Forest seem to harvest more female than male roe deer (1 ♂ : 3.93 ♀ based on 153 kill sites, SNU-RLP (2020) unpublished data) and especially more adults than juveniles (2.66 adult: 1 juvenile based on 153 kill sites, SNU-RLP (2020) unpublished data).

Genetic sex ratio analyses within the study area revealed a higher percentage of females to males roe deer within the population of the central Palatinate Forest (2011: 1 ♂ : 1.4 ♀, Ebert et al. (2012b)). Hence, the sex ratio of the standing roe deer population in our study area does not reflect the sex ratio of the lynx prey to such an extent. Thus, lynx hunting mode can possibly result in a stronger impact on the prey population on a long-term scale compared with human hunting modus. Lynx qualitatively selecting prey is thus also decisive for the quantitative effect of predation on the prey population by affecting the reproduction of the population (Breitenmoser and Breitenmoser-Würsten 2008).

In the Dinaric Mountains in Slovenia, Switzerland and the Swiss Jura Mountains, lynx killed more female than male roe deer (Molinari-Jobin et al. 2002, Ryser et al. 2004, Breitenmoser and Breitenmoser-Würsten 2008, Krofel et al. 2014) and they were less likely to kill fawns and yearlings than adult roe deer (Mayer et al. 2012, Krofel et al. 2014). These results are in line with the findings in the Palatinate Forest (SNU-RLP (2020), unpublished data), whereas in contrast, lynx selectively preyed on male roe deer in the Bavarian Forest Ecosystem (Heurich et al. 2016).

Interestingly, Andersen et al. (2007) found no difference between the age structure of 151 lynx-killed roe deer compared with the standing population. However, hunters killed a significantly higher proportion of adult animals, especially males (hunter: 44 % adult males, 28 % adult females, lynx: 24 % adult males, 44 % adult females, Andersen et al. (2007)), again supporting our results for the Palatinate Forest. Recreational hunter prefer to shoot trophy males, so lynx actually kill the highest proportion of adult female roe deer (Molinari-Jobin et al. 2002, Andersen et al. 2007). This leads to the assumption that hunters harvest a non-random part of the population and hence do not replace a natural predator (Andersen et al. 2007).

Again, differences between natural and human hunters are strong and need further analyses to evaluate the effects on the prey population in further detail.

Within the 2019/2020 monitoring year, the lynx population within the Palatinate Forest was estimated at 17–19 independent lynx (on an area of 1800 km²) based on camera trapping data, resulting in a lynx density of 0.94–1.06 lynx/100 km² (Port 2020). We assume that lynx in our study area consumed around 829 to 1345 roe deer per year (based on predation rate 46.05–74.71 roe deer/year/individual after Belotti et al. (2015) and lynx individual numbers of 2020, Port (2020)), which relates to around 0.46–0.75 roe deer km^{-2} per year. Similar predation values are found in the north-western Alps with 1.2 roe deer km^{-2} per year (Breitenmoser et al. 2010) and in the Bavarian Forest with 0.78 to 1.26 roe deer km^{-2} (Wölfl 2002).

Consequently, the predation rate of lynx in the Palatinate Forest in 2016 to 2019 must have been lower than the 0.46–0.75 roe deer km^{-2} per year due to lower abundance of lynx in the area, as the lynx population estimation was carried out in 2020. Thus, this makes it difficult for our applied census method (distance sampling) to detect such low differences in population changes when we have confidence intervals of around ± 2.5 roe deer km^{-2} in our population estimation models. Therefore, we considered roe deer count index and roe deer hunting bag data to evaluate the possible effect of the reintroduced predator within our study area. As already mentioned, for both approaches we could not detect an effect of lynx on the prey population within the Palatinate Forest for the first four years after release.

The mean hunting bag within the state-managed forest was around three roe deer km^{-2} and assuming similar hunting bag rates for the rest of the Palatinate Forest, the overall hunting bag would be around 2–3 roe deer km^{-2}. Consequently, we suppose that human hunters in the Palatinate Forest are culling around

2.6–4.3 times more roe deer compared with lynx, which again is in line with the results of the Dinaric Mountains, where the human harvest of roe deer is higher than lynx harvest (Krofel et al. 2014).

Both lynx and recreational hunters select animals in good physical condition, indicating an additive effect on roe deer mortality (Andersen et al. 2007). Roe deer population may not sustain the combined mortality of hunters and lynx, especially in peripheral areas (Melis et al. (2010). The author proved that lynx presence negatively influences the long-term growth rate of a roe deer population, notably in areas with harsh conditions (Melis et al. 2010). Continuing sustainable hunting with an increasing lynx presence and the latter killing female roe deer to an increased degree could presumably also effect the roe deer population in the Palatinate Forest on a medium- to long-term scale, and hence leading to a negative population trend.

We were unable to detect any influence of the predator on its main prey within this short period. We have to bear in mind that the lynx population is yet established and the roe deer population is still naïve due to the long absence of the predator. Schnyder et al. (2016) observed decreasing population estimation values in the first years, prompting them to assume that factors/interactions like hunting, climate, illness, intra- and interspecific competition (Breitenmoser and Breitenmoser-Würsten 2008) influence the degree of predation.

In order to interpret lynx and roe deer population trends, we are dependent on long-term data (Breitenmoser and Breitenmoser-Würsten 2008). Additional camera trapping and/or GPS data of lynx within the area are helpful to determine the predation effect on the roe deer population within the Palatinate Forest. There could be possible short-term effects on a small scale, especially when female lynx have kittens and are forced to hunt on a small area for the first weeks due to the immobility of the young ones (Bouyer et al. 2015). These short-term effects are not detectable with our methodical setup applied here.

General conclusion

Scientific studies evaluating the effect of predation normally span 3 to 5 years, which represents only a short section of a trend that is very difficult to interpret (Breitenmoser and Breitenmoser-Würsten 2008). We agree with Breitenmoser and Breitenmoser-Würsten (2008) and assume that this is the exact situation encountered in the Palatinate Forest. The first reintroduction of lynx in the Palatinate Forest is not long ago. Indeed, the time scale of four years is far too short to make coherent interpretations for processes in predator-prey-systems.

The reintroduction of this large carnivore in our cultural landscape is a unique opportunity to observe the settling, dispersal behaviour and predator-prey interactions.

Other studies have proven that lynx can influence the roe deer population to different degrees (Jędrzejewska and Jędrzejewski 2005, Heurich et al. 2012, Andrén and Liberg 2015, Schnyder et al. 2016), especially in less productive environments, whereby the prey population seems to be more strongly affected (Melis et al. 2009). Due to a strong variation in the current research results of predator-prey studies, it is crucial to gain more information in different regions and hence prolong investigation periods.

Here in the Palatinate Forest, we are just at the beginning of a long-term process. We therefore plead to monitor both the predator and the prey population on a long-term scale within the Palatinate Forest. Overall, the results of this study provide further details about the dynamic in predator-prey systems and especially about the first years of the establishment of a large carnivore. Beside the importance of bringing back natural predation – which is part of biodiversity processes – it is necessary to observe the trend of the prey populations to adapt management plans of the prey species if necessary.

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Appendix 1 Table 1: Summary of distance model structures applied for 2016-2019. CDS binned refers to Conventional Distance Sampling binned, CDS left to Conventional Distance Sampling left truncation, CDS unbinned refers to Conventional Distance Sampling unbinned and MCDS refers to Multi-Covariate Distance Sampling. All transects were pooled for the yearly analysis.

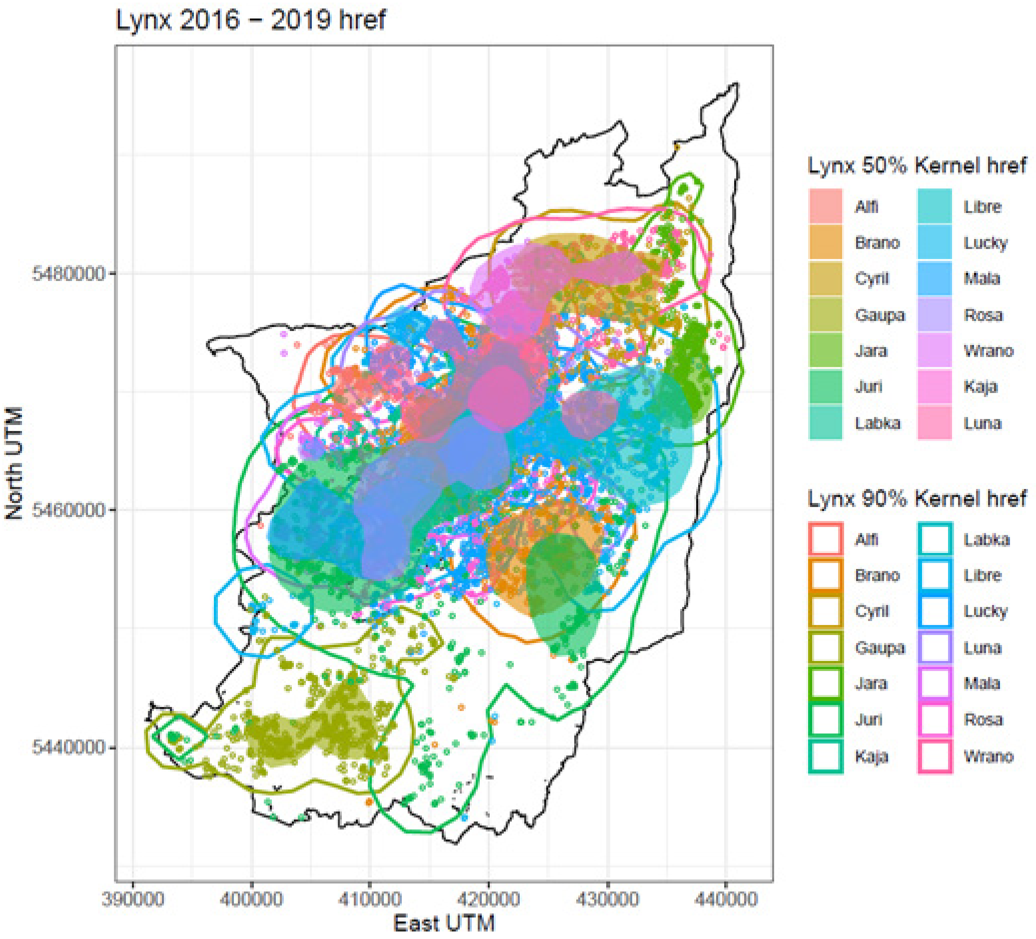
Model set up		Covariates
1) CDS	unbinned, right truncation	
2) CDS	binned (20m) , right truncation	
3) MCDS	binned (20m), right truncation	~ habitat large-scale, habitat fine-scale, behavior
4) CDS-Left	binned (20m), 20m left truncation and right truncation	

Appendix 1, Table 2: Sex ratio of roe deer hunting bag of state-managed forestry areas within the Palatinate Forest between 2012 and 2019. Forestry department numbers according to Fig. 4.

Forest department number	Forest department name	Male	Female
A	Annweiler	1	1.4
B	Bad Duerkheim	1	0.8
C	Haardt	1	0.9
D	Hinterweidenthal	1	0.87
E	Johanniskreuz	1	0.88
F	Kaiserslautern	1	0.82
G	Wasgau	1	0.69
	Mean	1	0.9

Appendix 1, Table 3: Hunting bag (number of culled individuals) of the state-managed forestry districts in the Palatinate Forest, which were covered by lynx core home range over the period from 2016 to 2019. Forestry district abbreviation are linked to Fig. 5.

Year	b	d	d_1	e	e_1	e_2	e_3	f
2012-13	10	21	28	53	72	54	40	32
2013-14	7	20	42	34	69	45	44	29
2014-15	7	15	21	36	35	45	35	30
2015-16	4	26	40	41	70	29	41	27
2016-17	5	18	49	43	55	42	44	28
2017-18	5	17	52	38	65	32	55	42
2018-19	7	15	49	43	28	25	28	33
2019-20	8	13	22	25	31	15	36	32



Appendix 1, Figure 1: Overview of the home ranges (kernel href 90 % and 50 %) of all reintroduced lynx for the period between 2016 and 2019. Lynx GPS positions are restricted to the borderlines of the Biosphere Reserve Palatinate Forest (black line). Lynx GPS data were provided by the Foundation of Nature and Environment (SNU) Rhineland-Palatinate.