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Research article

Risk response towards roads is consistent across multiple species in a temperate forest ecosystem

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Page 1 of 17

Roads can have diverse impacts on wildlife species, and while some species may adapt effectively, others may not. Studying multiple species' responses to the same infrastructure in a given area can help understand this variation and reveal the effects of disturbance on the ecology of wildlife communities. This study investigates the behavioural responses of four species with distinctive ecological and behavioural traits to roads in the protected Bohemian Forest Ecosystem in central Europe: European roe deer *Capreolus capreolus*, a solitary herbivore; red deer *Cervus elaphus* a gregarious herbivore; wild boar *Sus scrofa*, a gregarious omnivore and Eurasian lynx *Lynx lynx*, a solitary large carnivore. We used GPS data gathered from each species to study movement behaviour and habitat selection in relation to roads using an integrated step selection analysis. For all species and sexes, we predicted increased movement rates in response to roads, selection of vegetation cover near roads and open areas after road crossings, and increased road avoidance during the day. We found remarkably similar behavioural responses towards roads across species. The behavioural adaptations to road exposure, such as increased movement rates and selection for vegetation cover, were analogous to

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responses to natural predation risk. Roads were more strongly avoided during daytime, when traffic volume was high. Road crossings were more frequent at twilight and at night within open areas offering food resources. Gregarious animals exposed to roads favoured stronger road avoidance over faster movements. Ungulates crossed roads more at twilight, coinciding with commuter traffic during winter. Despite differences in the ecology and behaviour of the four species, our results showed similar adaptations towards a common threat. The continuous expansion of the global transportation network should be accompanied by efforts to understand and minimise the impact of roads on wildlife to assist wildlife management and ensure conservation.

Keywords: habitat selection, integrated step selection analysis, large mammals, movement behaviour, predation risk, road avoidance

Introduction

Humans have drastically changed ecosystems across the globe (Steffen et al. 2007), forcing other species to adapt to these changes. There is a striking variation in how species respond to human-altered environments, with some species adapting well and others not (Sih et al. 2011). To shed light into this complex variation studies should, for any given system, identify key behaviours that explain the animal's ability to cope with novel environments and define how evolutionary history might explain variation among and within species in both the key behaviours and their underlying sensory/cognitive ecology (Sih et al. 2011). Studying the responses of multiple species to the same source of disturbance in a given area can help clarify this variation and reveal the effect of the disturbance on the ecology of wildlife communities (Ruiz-Capillas et al. 2013, Suraci et al. 2019, Dickie et al. 2020).

One of the most important forms of landscape modification is the continuous expansion of the global road network as well as increasing traffic volume on many of these roads (Meijer et al. 2018). Roads affect animals by restricting their movement, increasing mortality through wildlife–vehicle collisions, and altering their behaviour (Trombulak and Frissel 2000, Shepard et al. 2008, Moore et al. 2023). The magnitude of the impact of roads on wildlife species varies significantly based on the intrinsic characteristics of roads and the traits, behaviour and ecological requirements of the species (Rytwinski and Fahrig 2012, González-Suárez et al. 2018, Grilo et al. 2018). Species-specific behavioural responses to roads should therefore be considered when evaluating the impact of roads on wildlife species (Jacobson et al. 2016, Grilo et al. 2018).

According to the 'risk-disturbance' hypothesis, the behaviour of wildlife species in response to human disturbances is similar to that of prey responding to the risk of predation (Frid and Dill 2002). Animals' perception of predation risk varies in space and time, generating a heterogeneous and dynamic 'landscape of fear' (Laundré et al. 2001, Palmer et al. 2022) in which prey seek to maximise food intake while minimising their exposure risk by changing other behaviours such as habitat selection (Creel et al. 2005) and movement (Frair et al. 2005). For prey to adjust their behaviour and mitigate the predation risk, the risk must vary predictably in space, time, or both (Palmer et al. 2022). The impact of roads and traffic on wildlife species can be similarly understood. The risk

of encountering a vehicle is spatially predictable, as it occurs only on the road itself, although it is temporally harder to predict, as the exact time of a vehicle passing is unknown. Nonetheless, traffic volume follows predictable temporal patterns throughout the day, which may enable animals to modulate their behaviour accordingly to avoid the perceived risk posed by vehicles.

Despite the spatial predictability of the risk posed by roads, animals with large home ranges, such as ungulates and large carnivores, cannot completely avoid them. Instead, they adopt a tradeoff between avoiding risk and reaching attractive habitat patches on the other side of the road, by adjusting their movement behaviour and habitat selection (Prokopenko et al. 2017, Scrafford et al. 2018, Poulin et al. 2023). Both ungulates and carnivores were observed to increase their movement rates when they are near roads (Neumann et al. 2013, Prokopenko et al. 2017, Scrafford et al. 2018) and when they cross them (Dussault et al. 2007, Thurjell et al. 2015), presumably to reduce their risk exposure time. Ungulates in the proximity of roads also seek vegetation cover, as it provides shelter and visual obstruction (Dussault et al. 2007, Bonnot et al. 2013, Prokopenko et al. 2017), while they preferred to cross roads within open areas that provide visibility, facilitate quick movement and offer foraging opportunities (Meisingset et al. 2013, Thurjell et al. 2015, Prokopenko et al. 2017). Other studies, however, have found that ungulates and carnivores cross roads in areas with high vegetation cover, which would offer both shelter and foraging opportunities (Dussault et al. 2007, Baigas et al. 2017, Passoni et al. 2021). Because wildlife responses to roads vary across species and ecosystems (Grilo et al. 2018, Duffett et al. 2020, Brieger et al. 2022), multiple species in the same study system should be investigated for a comprehensive understanding of the role of vegetation cover on animals moving near and across roads.

Traffic volume is typically higher during the day than at night and peaks with early-morning and late-afternoon commuter traffic (Kämmerle et al. 2017). Consistently, ungulates and carnivores avoid areas near roads and road crossings more during the day than at night (Meisingset et al. 2013, Baigas et al. 2017, Whittington et al. 2022). In Canada, wapiti *Cervus canadensis* avoid crossing roads and areas near roads throughout the day, and especially during their activity peak at twilight, when traffic volume is still high (Prokopenko et al. 2017). By contrast, the road crossing

frequency of European roe deer *Capreolus capreolus* follows their daily movement rate rather than traffic volume, with increased road crossings during their activity peak, which is typically at twilight (Kämmerle et al. 2017). Accordingly, deer-vehicle collisions also peak at twilight, coinciding with commuter traffic (Steiner et al. 2014). Although previous studies found that many species consistently avoid roads during the day, whether active avoidance coincides with their activity peak at twilight, when a high traffic volume poses a considerable threat, is unclear and should be further investigated.

Multi-species studies suggest that despite roads can affect several species (Rich et al. 2016), some species avoid roads more than others (Boyle et al. 2020) and species-specific traits explain the variation in behavioural responses to roads (Grilo et al. 2018, Duffett et al. 2020, Brieger et al. 2022). High-resolution movement data and the development of recent methods to analyse movement and habitat selection simultaneously (Avgar et al. 2016) give the opportunity to disentangle the complex behavioural response to anthropogenic infrastructures and to compare it across guilds (Dickie et al. 2020). Such models can be applied to test whether roads induce similar behavioural responses to both prey and predator species, and whether these responses are similar to those typically

induced by the exposure to natural predation risk, such as increasing movement rates, selection for vegetation cover, and temporal avoidance of risk. In this study, we applied an integrated step selection analysis (iSSA) (Avgar et al. 2016) using GPS telemetry data from four wildlife species with distinct ecological traits but inhabiting the same study system to investigate fine-scale habitat selection and movement in relation to roads. The four species selected for this study were: 1) European roe deer, a solitary and selective browser, 2) red deer *Cervus elaphus*, a gregarious mixed feeder, 3) wild boar *Sus scrofa*, a gregarious omnivore, and 4) Eurasian lynx *Lynx lynx*, a solitary large carnivore.

A priori, we assumed that the movement behaviour of all studied species varies on daily and seasonal scales and reflects animal activity patterns (Krop-Benesch et al. 2013, Heurich et al. 2014, Johann et al. 2020). Additionally, habitat selection was assumed to vary on a daily scale, with a preference for dense vegetation during the day, when human disturbance is high, and open areas at night and twilight, as they are ideal for foraging (Bonnot et al. 2013, Filla et al. 2017, Dupke et al. 2017). Following the 'risk-disturbance' hypothesis, all studied species were presumed to show spatio-temporal avoidance of roads and increased movement rates when exposed to roads (Jacobson et al. 2016). Specifically, for all studied species we predicted a priori (Fig. 1):

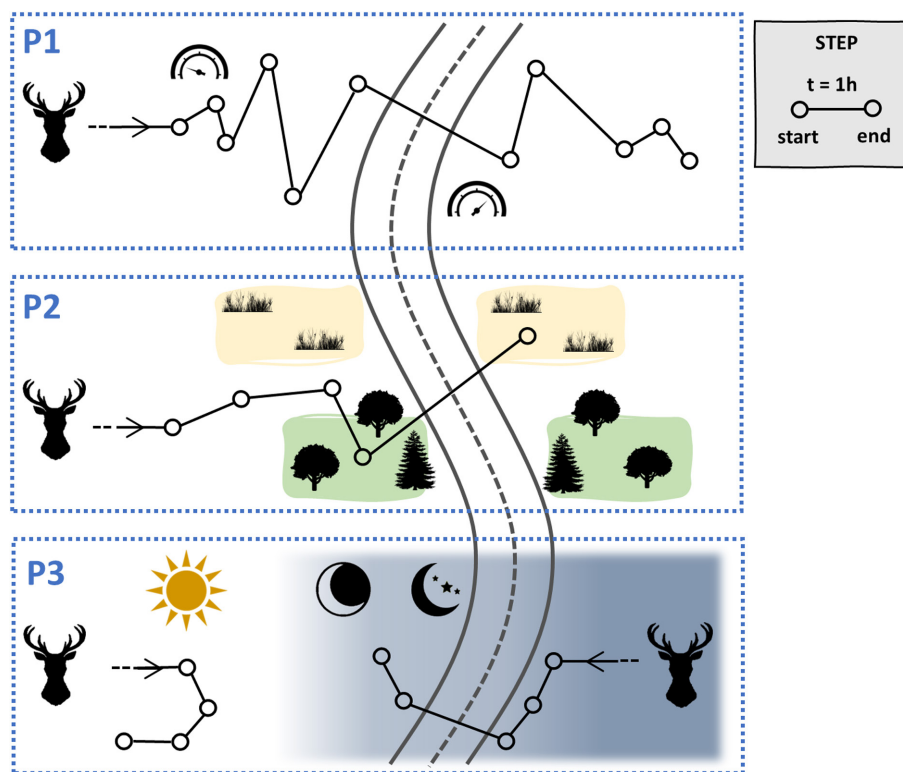


Figure 1. Graphical representation of the potential behavioural responses of wildlife towards roads according to our three predictions: (P1) wildlife species move faster when near roads and during road crossings; (P2) wildlife species select for vegetation cover when close to roads and open areas after a road crossing; (P3) reduced avoidance of roads at night and higher likelihood of road crossings at twilight.

- 1) faster movements in the vicinity of roads and during road crossings to reduce risk exposure (Frair et al. 2005, Prokopenko et al. 2017);
- 2) selection of habitats offering shelter (i.e. vegetation cover) (Bonnot et al. 2013) by animals moving near roads, and selection of more open areas providing high-quality forage or a high prey abundance after road crossings, which are guided by increased foraging opportunities (Meisingset et al. 2013, Thurjfell et al. 2015);
- 3) reduced avoidance of roads during nighttime, when traffic volume is lower and animal activity is higher than during the day (Meisingset et al. 2013, Baigas et al. 2017). Because of their crepuscular activity (Krop-Benesch et al. 2013, Heurich et al. 2014), the studied species were expected to cross roads more frequently at twilight, despite the high traffic volume, particularly during winter (Kämmerle et al. 2017).

Given the potential variations in reproductive strategies and risk aversion between females and males (Montgomery et al. 2013, Poessel et al. 2014), separate analyses were conducted for each sex to account for sex-specific differences.

Material and methods

Study area

The Bohemian Forest Ecosystem is a forested low mountain range (370–1456 m a.s.l.) located in the border region between the Czech Republic, Germany and Austria, representing one of the largest protected ecosystems in central Europe. It includes the Bavarian Forest National Park (243 km²) and Šumava National Park (681 km²) (Fig. 2), and it is surrounded by the Bavarian Forest Natural Park (3007 km²) and the Šumava Protected Landscape Area (1000 km²). Human population densities are relatively low and vary between two inhabitants/km² inside the national parks and 30–70 inhabitants km⁻² in nearby regions (Heurich et al. 2015). The two national parks have a relatively low road density (0.36 km km⁻²), with paved roads located at the edges (i.e. lower elevations). Traffic radars located on two roads within the Bavarian Forest National Park between March and November 2022 recorded an average of 1021 (location Nationalparkstrasse) and 672 vehicles per day (Jugendwaldheim), with the highest traffic volume occurring between 07:00 and 18:00 h (Supporting information).

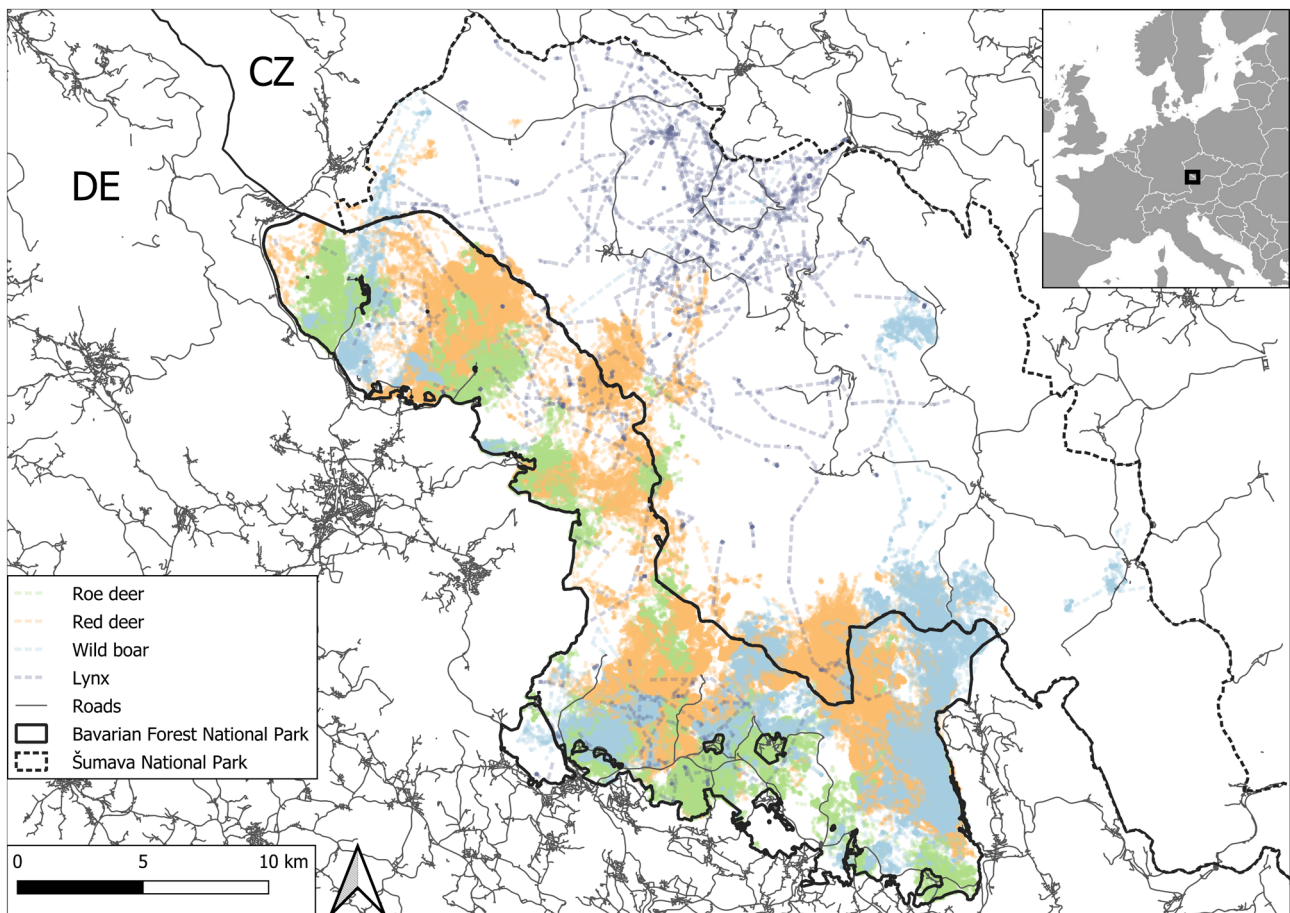


Figure 2. Study area with borders and roads of the national parks and the trajectories of the GPS-tagged roe deer, red deer, wild boar, and lynx.

Norway spruce *Picea abies* dominates the vegetation at higher elevations, where mountain ash *Sorbus aucuparia* is also found, while lower elevations are characterised by Norway spruce, European beech *Fagus sylvatica* and silver fir *Abies alba* (Cailleret et al. 2014). Roe deer, red deer and wild boar are widely distributed in the area; moose *Alces alces* are present only in small numbers, in the southern part (Janík et al. 2021). The two large predators in the area are wolf and Eurasian lynx. Lynx were reintroduced in the 1970s and 1980s (Wölfel et al. 2001) and mainly prey on roe deer (80% of detected kills) and red deer (17%) (Belotti et al. 2015). Red deer and wild boar in the Bavarian Forest National Park are managed by trained personnel inside the management zone (25% of the area), while roe deer population management was reduced in 2007 and stopped in 2012. The situation is similar in Šumava National Park: only red deer and wild boar populations are regulated, with the hunting of only a negligible number of roe deer permitted per year and only in the southern part of the park. Within the two national parks, 14 winter enclosures were established for the overwintering of red deer between October and May, thereby simulating their natural absence in montane forests during winter (Möst et al. 2015). Permanent snow cover in the study area lasts up to seven months (October–May) on the mountain tops and five months (November–April) in the valleys.

Telemetry data

Within the study area, GPS telemetry data were obtained from 138 roe deer captured between 2005 and 2012, 76 red deer captured between 2002 and 2013, 45 wild boar captured between October 2021 and March 2023 and 10 lynx captured between 2005 and 2012. Roe deer were captured using wooden box traps baited with pomace, maize or silage and fitted with GPS-GSM collars without using chemical tranquilliser. Traps were set during the evening and inspected the following morning. Red deer were captured with two approaches: 1) attracted to a baited enclosure (apple pomace, sugar beets) and fitted with GPS-GSM collars within the enclosure without chemical immobilization or 2) tranquilised using an immobilization gun with a Hellabrunn mixture (Ketamin and Xylazine) on baited sites and fitted with GPS-GSM collars. Wild boar were captured using wood-clad corral traps baited with maize and then fitted with a GPS-GSM collar without the use of anaesthetic. The traps were equipped with live cameras for monitoring, enabling handling and release of the animals within less than six hours. Lynx were captured in baited walk-through box traps at kill sites and well-known lynx trails, they were immobilised using a Hellabrunn mixture (Ketamin and Xylazine) and equipped with GPS-GSM collars immediately after capture and immobilization. Roe and red deer GPS sensors retrieved one to three fixes per hour, and wild boar sensors retrieved one fix every 30 min. Lynx sensors retrieved two fixes per day, except once every second week, when one fix per hour from 15:00 to 07:00 h of the following day was retrieved (Belotti et al. 2015). This time window was selected

because lynx is typically inactive during the central hours of the day (Heurich et al. 2014). The data were subjected to semi-automatic implemented outlier detection processes for error identification (Urbano et al. 2021). We removed red deer GPS telemetry data from the analyses during the period when the animals were located inside the winter enclosures (October–May). Since most wild boar showed long-distance displacement behaviour after capture, we removed the first week of data for this species (Brogi et al. 2019). In addition, since tagged wild boar formed distinctive groups following similar trajectories, we ensured data independence by selecting only one individual from each group for further analysis, specifically the individual with the highest number of collected GPS fixes. Because data on two pivotal covariates used in this analysis, namely canopy cover and understory, were available only within the borders of the national parks, we clipped GPS telemetry data of all species to the national parks' extent.

Animals' step calculations

We performed all data preparation and analyses using R ver. 4.1.2 (www.r-project.org). We harmonised the data across species to a one-hour GPS fix sampling rate and then transformed it into 'steps' (i.e. movement between two consecutive GPS fixes) using the R package 'amt' (Signer et al. 2019). A step is described by its length (i.e. straight-line distance between two consecutive relocations) and turn angle (i.e. angular deviations between the heading direction of two consecutive steps) (Prokopenko et al. 2017). We included only individuals with a minimum of ten steps in the analysis. To ensure that the choice of this threshold would not affect our results, we performed a sensitivity analysis by running simplified models using a gradient of increasing thresholds (therefore decreasing the number of individuals available for the model), and recorded model coefficients, which proved to be stable (Supporting information). For each species, we fitted a gamma distribution to the observed step lengths and a von Mises distribution to the observed turn angles and used these distributions to pair 15 random steps with each observed step (Signer et al. 2019). In total, data from 114 roe deer (52 females, 62 males), 68 red deer (47 females, 21 males), 22 wild boar (8 females, 14 males) and 8 lynx (3 females, 5 males) were available for modelling, with 86 816 observed and 1 302 240 random steps for roe deer, 237 580 observed and 3 563 700 random steps for red deer, 45 295 observed and 679 425 random steps for wild boar and 1133 observed and 16 995 random steps for lynx, which was the species with the most limited data. A summary statistic of steps can be found in the Supporting information.

Environmental covariates

In 2011, full waveform light detection and ranging (LiDAR) data with 10 m resolution were collected in the two national parks (Krzystek et al. 2020). LiDAR is an active remote sensing method that provides accurate and high-resolution

data on the three-dimensional vegetation structure (Ciuti et al. 2018). We included the metric ‘fractional vegetation cover’ which ranges from 0 to 1 and is defined as the projection of tree crowns onto the ground divided by the ground surface area, determined for two different height strata: 1) canopy cover, to represent high-stand vegetation density (above 2 m) and 2) understorey, to represent forest undergrowth density (below 2 m) (Ewald et al. 2014). Topography was accounted for by calculating terrain ruggedness using the R package ‘raster’ (Hijmans 2022) from a 25-m resolution digital elevation model (EU-DEM, ver. 1.1) provided by the European Environment Agency (EEA, EU Copernicus).

We downloaded OpenStreetMap road data through the R package ‘osm’ (Padgham et al. 2017), considering only paved roads (Passoni et al. 2021), which in our study area include: 1) tertiary and unclassified roads (i.e. local roads linking smaller towns, villages and hamlets; total length: 178 km); 2) service roads (i.e. accessing huts, business and national park buildings; 81 km); 3) secondary roads (i.e. regional roads linking towns; 48 km); 4) residential roads (i.e. access to housing; 18 km) and 5) primary roads (i.e. national roads linking larger towns; 12 km). We extracted two parameters often used to measure road effect: distance to roads and road crossings (Prokopenko et al. 2017). We calculated the Euclidean distance between each start and end point of a step and the nearest road and transformed the value using the natural logarithm to incorporate a decrease in the effect with distance from the nearest road (Prokopenko et al. 2017). We extracted road crossings by transforming each observed and random step to a line that could intersect the road line object and we generated a binary variable for road crossings, with a value of ‘1’ if the step crossed at least one road and a value of ‘0’ otherwise.

We included time of day as a three-level, categorical variable (day, night and twilight) using the R package ‘sun-calc’ (Thieurmel and Elmarhraoui, 2019) and following Passoni et al. (2021). To account for seasonal variance, we created a binary variable with winter (0) (November–April) and summer (1) (May–October) categories based on vegetation phenology and snow cover in the study area.

To allow for comparability and a better interpretation of the modelling results, we normalized Canopy cover, Understorey, Ruggedness and Road distance to have a zero mean and unit standard deviation. We screened all variables for collinearity using Pearson’s correlation coefficient with a threshold of $|r| > 0.7$ (Dormann et al. 2013). We did not find substantial collinearity among our variables (Supporting information).

Integrated step selection analysis (iSSA)

To investigate animal habitat selection and movement in relation to roads, we applied an iSSA. In this analysis, each observed step taken by an individual (referred to as ‘used’) was compared with random steps (referred to as ‘available’) (Fortin et al. 2005) in a Poisson model with stratum-specific fixed intercepts (Muff et al. 2020), using the R package ‘glm-TMB’ (Brooks et al. 2017). We accounted for the behavioural adaptability of an individual animal towards roads by incorporating random slopes for the variables distance to the nearest road and road crossing.

We built a full model based on the a priori assumptions and hypotheses described herein and applied it to each of the four studied species (Table 1). We developed separate models for females and males, resulting in two models per species, except for the lynx where a single model, without sex

Table 1. Model specification of the full model divided into parts, each one addressing a specific prediction. The response variable was 1/0 for observed/random steps. All extracted covariates were included in the model at the end of the step, except those marked with the subscript ‘Start’. Quadratic terms are indicated by $()^2$. $\ln()$ indicates the natural logarithm.

	Model terms	Predictions
Full model	Core model	
	$\ln(\text{Step length}) + \cos(\text{Turn angle}) + \ln(\text{Step length}) : \text{Time of day}_{\text{Start}} + \ln(\text{Step length}) : \text{Season}_{\text{Start}}$	Movement: movement behaviour varies on a daily and seasonal scale
	$\text{Canopy cover} + \text{Canopy cover}^2 + \text{Canopy cover} : \text{Time of day} + \text{Understorey} + \text{Understorey}^2 + \text{Understorey} : \text{Time of day} + \text{Ruggedness} + \text{Ruggedness}^2$	Habitat selection: selection of vegetation cover during the day and open areas during night and twilight. Quadratic terms of canopy cover, understorey and ruggedness are included to evaluate the selection of intermediate values
	Effect of roads	
	$\ln(\text{Distance to road}) + \ln(\text{Distance to road})^2 + \text{Road crossing} + \ln(\text{Step length}) : \ln(\text{Distance to road})_{\text{Start}} + \ln(\text{Step length}) : \text{Road crossing}$	P1: faster movements in road proximity and during road crossings. A quadratic term of distance to roads is included to evaluate the selection of intermediate values
	$\ln(\text{Distance to road})_{\text{Start}} : \text{Canopy cover} + \ln(\text{Distance to road})_{\text{Start}} : \text{Understorey} + \text{Road crossing} : \text{Canopy cover} + \text{Road crossing} : \text{Understorey}$	P2: selection of vegetation cover close to roads and open areas after a road crossing
	$\ln(\text{Distance to road}) : \text{Time of day} + \ln(\text{Distance to road}) : \text{Season} + \text{Road crossing} : \text{Time of day} + \text{Road crossing} : \text{Season}$	P3: weaker road avoidance at night and more road crossings during twilight
	Random effect	
	$(1 \text{Step ID}) + (0 + \ln(\text{Distance to road}) \text{Animal ID}) + (0 + \text{Road crossing} \text{Animal ID})$	Random intercepts and random slopes: account for among-individual variation in the behaviour towards roads (Muff et al. 2020)

differentiation, was built because of the limited sample size. The full model included the movement parameters natural logarithm of the step length and cosine of the turn angle. We included the natural logarithm of the step length to modify the shape parameter of the original gamma distribution used to generate the steps (Avgar et al. 2016). We extracted covariates at the end of each observed and random step to study their influence on where the animals moved (Signer et al. 2019), with two exceptions: 1) we calculated covariates interacting with the natural logarithm of the step length at the start of the step to determine how an animal moved when it started in a given habitat (Signer et al. 2019); 2) we calculated the distance to the nearest road at the start of the step when interacting with canopy cover and understorey to examine the influence of road proximity on habitat selection (Prokopenko et al. 2017) (Table 1). Road crossings from all species were overall rare because of the low road density in our study area and due to the selection of areas further away from roads. The availability of road crossings was lowest for wild boar females (0.5%; Supporting information) and due to model performance issues (unusually large coefficients; $|x| > 10$) we could not include this variable in the wild boar females' model. Lynx GPS telemetry data were not collected during the central hours of the day (Supporting information) when lynx are typically inactive (Heurich et al. 2014). Despite this gap, data from all times of day (day, night, twilight) occurred in the dataset (Supporting information), and we included this variable in the model.

We explored the inter-individual variability in the responses to roads by extracting the conditional modes of the models' random effect (also known as best linear unbiased predictors, BLUPs; Robinson 1991). The BLUPs represent the differences between the slope for each random subject and the median coefficient slope (i.e. average behaviour of the population) and are expected to span from animals showing the highest road avoidance (larger distance to the nearest road and fewer road crossings) to those showing the lowest road avoidance after taking all model predictors into account. We calculated the percentage of the population for which the random slope value (\pm conditional SD): 1) remained greater than zero (i.e. higher avoidance of areas near roads and lower avoidance of road crossings); 2) overlapped zero (i.e. median behaviour of the population); 3) remained lower than zero (i.e. lower avoidance of areas near roads and higher avoidance of road crossings).

Results

Movement

All ungulates showed low directional persistence in their movements at the low frequency of GPS fixes used in this study, and lynx showed no preference in movement directionality. Ungulates had higher movement rates (i.e. longer steps) at twilight than during the day (Table 2). Red deer and wild boar also had higher movement rates at night than during

the day, while roe deer movement rates were higher during the day than at night (Table 2). Red deer, wild boar of both sexes, and roe deer males had higher movement rates during summer, and roe deer females during winter (Table 2). Lynx movement did not show any significant response to either the time of day (data limited from 15:00 to 07:00 h) or the different seasons (Table 2).

Habitat selection

All species selected intermediate understorey and selected steps with a higher understorey during the day than at night or twilight (Table 2). Roe deer and wild boar females, and red deer of both sexes selected intermediate canopy cover values, while roe deer males and wild boar males selected high and low canopy cover values, respectively (Table 2). Lynx did not show any canopy cover preference. All deer species selected higher canopy cover during the day than either at night or at twilight, whereas wild boar selected higher canopy cover at night than during the day. Furthermore, wild boar males selected higher canopy cover at twilight than during the day (Table 2). Female roe deer selected terrain of intermediate ruggedness, while male roe deer and wild boar of both sexes selected terrain of high ruggedness (Table 2). Red deer selected terrain of low ruggedness, whereas lynx did not show any preference (Table 2).

Effect of roads on movement

As the distance from the nearest road at the start point of a step decreased, the movement rate increased for all species and groups except wild boar females, which showed a decreased movement rate near roads (Fig. 3, Table 2). The movement rates of all groups except red deer females were significantly higher during road crossings (Fig. 3, Table 2). Roe deer females and males moved ~ 50 m h⁻¹ faster when crossing roads (females: 137 m h⁻¹, 95% CI [129–146]; males: 165 m h⁻¹, 95% CI [153–177]) than during regular movements (females: 87 m h⁻¹, 95% CI [86–88]; males: 116 m h⁻¹, 95% CI [114–118]). Red deer males moved ~ 40 m h⁻¹ faster during road crossings (143 m h⁻¹, 95% CI [117–169]) than during regular movements (101 m h⁻¹, 95% CI [99–103]). Wild boar males moved ~ 130 m h⁻¹ faster when crossing roads (216 m h⁻¹, 95% CI [176–257]) than during regular movements (84 m h⁻¹, 95% CI [82–86]). Lynx moved ~ 400 m h⁻¹ faster during road crossings (875 m h⁻¹, 95% CI [638–1111]) than during regular movements (476 m h⁻¹, 95% CI [405–547]) (Fig. 3).

Effect of roads on habitat selection

When the start of a step was closer to a road, understorey selection at the end of the step increased for all deer species and in wild boar males whereas wild boar females did not show any preference (Fig. 4a, Table 2). Near roads, roe deer and wild boar of both sexes, and red deer males selected high canopy cover, while red deer females selected low canopy

Table 2. Coefficients with standard errors in parenthesis of all models. Coefficients in bold were statistically significant ($p < 0.05$). All covariates included in the model were extracted at the end of the step except for those marked with the subscript 'Start'. Quadratic terms are indicated by $()^2$. In() indicates the natural logarithm. The results of the lynx model using data at the coarser temporal scale (two GPS fixes per day) can be found in the Supporting information.

Terms	Roe deer		Red deer		Wild boar		Lynx
	Females	Males	Females	Males	Females	Males	
Movement							
ln(Step length)	0.084 (0.006)	0.048 (0.006)	-0.062 (0.004)	-0.102 (0.005)	-0.121 (0.006)	-0.101 (0.005)	0.024 (0.036)
cos(Turning angle)	-0.397 (0.007)	-0.272 (0.007)	-0.047 (0.004)	-0.043 (0.006)	-0.246 (0.009)	-0.490 (0.010)	-0.018 (0.044)
ln(Step length) : Night _{Start}	-0.096 (0.007)	-0.102 (0.007)	0.068 (0.003)	0.136 (0.005)	0.253 (0.008)	0.222 (0.008)	-0.018 (0.035)
ln(Step length) : Twilight _{Start}	0.365 (0.021)	0.516 (0.022)	0.700 (0.011)	0.646 (0.016)	0.207 (0.018)	0.175 (0.017)	0.122 (0.071)
ln(Step length) : Season _{Start}	-0.057 (0.007)	0.040 (0.007)	0.052 (0.004)	0.071 (0.006)	0.112 (0.008)	0.130 (0.009)	0.034 (0.030)
Habitat selection							
Canopy cover	-0.068 (0.014)	0.038 (0.015)	0.155 (0.006)	0.209 (0.010)	-0.188 (0.017)	-0.160 (0.020)	0.007 (0.090)
Canopy cover ²	-0.048 (0.010)	-0.001 (0.008)	-0.055 (0.005)	-0.061 (0.008)	-0.089 (0.012)	-0.018 (0.011)	-0.029 (0.052)
Canopy cover : Night	-0.156 (0.014)	-0.170 (0.014)	-0.557 (0.008)	-0.636 (0.014)	0.147 (0.023)	0.211 (0.022)	-0.127 (0.097)
Canopy cover : Twilight	-0.107 (0.029)	-0.070 (0.028)	-0.427 (0.017)	-0.378 (0.029)	0.021 (0.047)	0.099 (0.046)	0.046 (0.164)
Understory	0.234 (0.013)	0.267 (0.013)	0.345 (0.005)	0.348 (0.009)	0.410 (0.014)	0.427 (0.018)	0.723 (0.081)
Understory ²	-0.033 (0.004)	-0.034 (0.004)	-0.097 (0.003)	-0.113 (0.004)	-0.083 (0.007)	-0.018 (0.008)	-0.076 (0.024)
Understory : Night	-0.226 (0.014)	-0.278 (0.014)	-0.423 (0.007)	-0.377 (0.012)	-0.419 (0.018)	-0.517 (0.021)	-0.372 (0.077)
Understory : Twilight	-0.198 (0.031)	-0.214 (0.030)	-0.374 (0.016)	-0.247 (0.025)	-0.136 (0.035)	-0.171 (0.039)	-0.469 (0.133)
Ruggedness	0.039 (0.009)	0.043 (0.010)	-0.045 (0.005)	0.013 (0.009)	0.100 (0.015)	0.030 (0.015)	-0.059 (0.053)
Ruggedness ²	-0.020 (0.005)	-0.003 (0.004)	-0.010 (0.002)	-0.018 (0.004)	0.011 (0.005)	0.003 (0.007)	0.009 (0.021)
ln(Distance to road)	0.433 (0.094)	0.149 (0.058)	0.471 (0.108)	0.221 (0.074)	0.054 (0.124)	0.387 (0.131)	0.226 (0.182)
ln(Distance to road) ²	-0.297 (0.010)	-0.270 (0.010)	-0.094 (0.006)	-0.039 (0.007)	-0.224 (0.015)	-0.122 (0.012)	0.015 (0.023)
Road crossing	-3.594 (0.269)	-2.464 (0.246)	-1.688 (0.385)	-3.277 (0.475)	-	-5.054 (0.688)	-3.874 (0.963)
ln(Step length) : ln(Distance to road) _{Start}	-0.030 (0.004)	-0.028 (0.004)	-0.031 (0.002)	-0.041 (0.003)	0.024 (0.004)	-0.026 (0.004)	-0.042 (0.016)
ln(Step length) : Road crossing	0.516 (0.043)	0.326 (0.039)	0.004 (0.045)	0.214 (0.067)	-	0.648 (0.101)	0.401 (0.115)

(Continued)

Table 2. Continued.

Terms	Roe deer		Red deer		Wild boar		Lynx
	Females	Males	Females	Males	Females	Males	
P2							
Canopy cover : $\ln(\text{Distance to road})_{\text{start}}$	-0.066 (0.007)	-0.062 (0.007)	0.022 (0.004)	-0.033 (0.006)	-0.051 (0.011)	-0.070 (0.011)	-0.063 (0.039)
Understorey : $\ln(\text{Distance to road})_{\text{start}}$	-0.048 (0.008)	-0.077 (0.007)	-0.033 (0.003)	-0.029 (0.006)	0.001 (0.009)	-0.065 (0.011)	-0.063 (0.038)
Road crossing : Canopy cover	0.013 (0.027)	-0.006 (0.024)	-0.114 (0.037)	-0.108 (0.052)	-	-0.102 (0.076)	-0.361 (0.112)
Road crossing : Understorey	-0.103 (0.040)	-0.230 (0.038)	-0.155 (0.049)	-0.237 (0.086)	-	0.049 (0.097)	-0.074 (0.129)
P3							
$\ln(\text{Distance to road})$: Night	-0.974 (0.033)	-0.897 (0.033)	-0.552 (0.027)	-0.441 (0.040)	-0.478 (0.055)	-0.711 (0.061)	-0.307 (0.178)
$\ln(\text{Distance to road})$: Twilight	-0.788 (0.061)	-0.638 (0.058)	0.110 (0.057)	0.019 (0.075)	-0.158 (0.115)	0.127 (0.124)	0.024 (0.279)
$\ln(\text{Distance to road})$: Season	-0.143 (0.030)	-0.022 (0.031)	0.003 (0.031)	0.047 (0.047)	0.002 (0.055)	-0.145 (0.056)	-0.133 (0.106)
Road crossing : Night	0.322 (0.076)	0.120 (0.073)	1.039 (0.122)	1.026 (0.190)	-	0.742 (0.290)	1.232 (0.470)
Road crossing : Twilight	0.746 (0.128)	0.998 (0.112)	1.185 (0.196)	1.123 (0.278)	-	1.758 (0.406)	1.094 (0.656)
Road crossing : Season	-0.022 (0.068)	-0.158 (0.068)	-0.026 (0.124)	0.689 (0.173)	-	-0.830 (0.206)	-0.117 (0.253)

cover. Lynx preferred high understorey and canopy cover near roads, but this effect was not significant (Fig. 4a, Table 2).

All deer species selected lower understorey at the end of steps that crossed a road in comparison to steps that did not cross a road, while no preference was found for wild boar males and lynx (Fig. 4b, Table 2). Red deer of both sexes and lynx selected low canopy cover after a road crossing, while roe deer of both sexes and wild boar males showed no preference (Fig. 4b, Table 2).

Temporal variation in wildlife behaviour towards roads

All ungulates selected steps farther away from roads during the day than at night. Only roe deer selected steps farther away from roads during the day than at twilight (Fig. 5a, Table 2). Roe deer females avoided areas within ~ 190 m distance from roads during the day, ~ 0.20 m at twilight and ~ 10 m at night. Roe deer males avoided areas within ~ 250 m distance from roads during the day, ~ 20 m at twilight and ~ 5 m at night. Red deer females avoided areas within ~ 1300 m from roads at all times of day. Red deer males avoided areas within ~ 1200 m from roads during the day and twilight and selected areas near roads during the night. Wild boar females avoided roads within ~ 680 m during the day, ~ 370 m at twilight and ~ 120 m at night. Wild boar males avoided roads within ~ 520 m during the day and at twilight and ~ 40 m at night. Lynx did not show any significant pattern related to road proximity (between 15:00 and 07:00 h; Fig. 5a, Table 2).

All species strongly avoided taking steps that crossed a road (Table 2), but all deer species and wild boar males crossed roads more often at twilight than during the day (Fig. 5b, Table 2). Roe deer females, red deer, wild boar males, and lynx crossed roads more often at night than during the day whereas roe deer males did not show any preference (Fig. 5b, Table 2).

Roe deer females and wild boar males selected areas farther away from roads during winter (Table 2). Roe deer and wild boar males crossed roads more often during winter than during summer, while red deer males crossed roads more often during summer (Table 2). Lynx did not show any seasonal preference regarding road proximity or road crossing (Table 2).

Interindividual variability in the response to roads

The best linear unbiased predictors (BLUPs) for the ungulates showed the expected variation in the individual responses to roads (Supporting information). Most roe deer individuals showed a similar response to road proximity, with three roe deer females showing a stronger and one roe deer male a weaker avoidance of areas near roads. Similarly, only three red deer females showed a stronger avoidance of areas near roads than the median population. Most wild boar behaved similarly except for two males who showed, respectively, a stronger and a weaker avoidance of roads than the median population. The

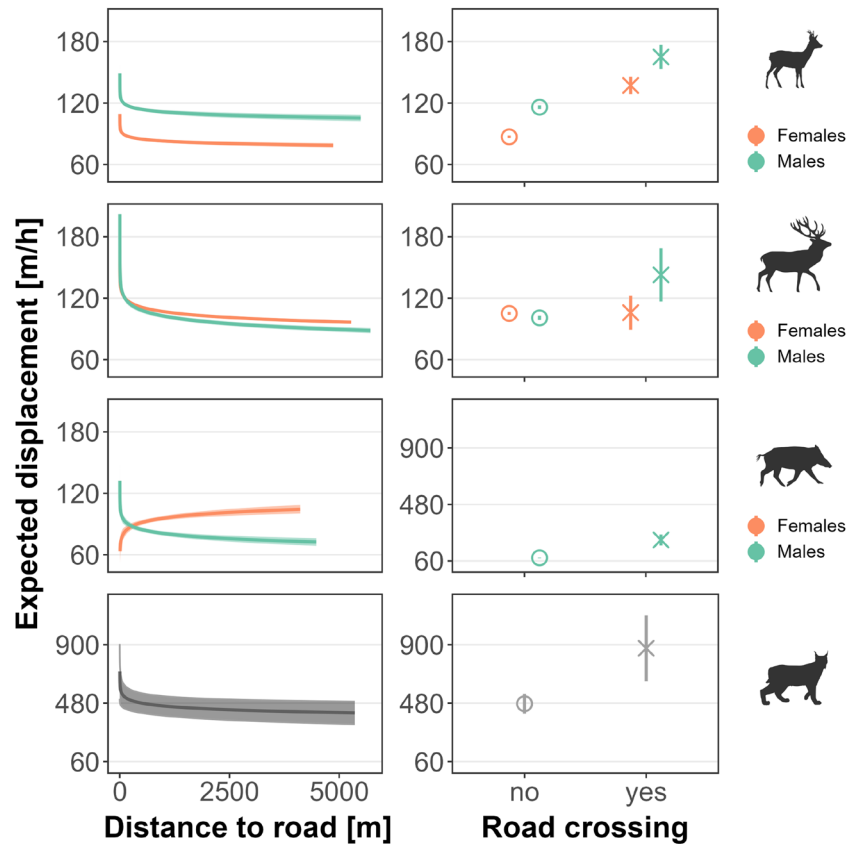


Figure 3. Comparison of the expected displacement of roe deer, red deer, wild boar and lynx as a function of the distance to the nearest roads (left-side plots) and for steps that did and did not cross roads (right-side plots). The range of distance to the nearest road values (x-axis) equals the observed ranges. Ribbons and error bars indicate the 95% confidence interval (CI). The y-axis range and scale differ for wild boar (only for the road crossing plot) and lynx, to improve plot readability. The variable road crossing was not included in the wild boar females' model.

response to road crossings was even more homogeneous, with most individuals showing a similar avoidance of road crossings. All lynx individuals showed the same behavioural response to distance to roads and road crossings (Supporting information).

Discussion

Roads affect many wildlife species, but the behavioural responses to roads are complex and can vary among and within species. Studying multiple species' responses to roads in a given area can help understand this variation and reveal the effects of roads on the ecology of the community. Our modelling approach indicated that roe deer, red deer, wild boar and lynx in the same study site perceived roads as risky, and their responses when approaching and crossing roads were consistent with the avoidance of natural predation risk. Those responses varied throughout the day according to the daily activity patterns of the species and the perceived intensity of the road-associated risk. Despite we identified subtle differences in the response towards roads between different species and between males and females of the same species, our study shows that changes in movement behaviour and habitat selection in relation to roads are consistent among multiple wildlife species within the same area.

We found that roads significantly affected movement and habitat selection of both prey and predator species. Furthermore, animals consistently selected for areas further away from roads, suggesting that the effect of roads extends beyond roads' physical footprint (Prokopenko et al. 2017, Dickie et al. 2020). While this shows that animals in our study area can adjust their behaviour to cope with roads, the avoidance of roads and their surroundings can limit animals' movement and hinder their access to critical resources such as food, mates or breeding sites (Jaeger et al. 2005). Furthermore, behavioural responses to risk can decrease the time available for animals to fulfil their requirements for survival and reproduction (Ciuti et al. 2012, Zanette and Clinchy 2020). Given the low road density of our study area (0.36 km km^{-2}), we cannot speculate that the indirect effect of roads on animals' behaviour will affect their fitness and population. However, in a continent such as Europe, with the highest road density found anywhere in the world, and with the continuous expansion of the road network, the indirect effect of roads on prey and predator fitness, summed up to the direct effect on animals' mortality through vehicle collision, can seriously threaten wildlife conservation and ecosystem functioning. Understanding species-specific behaviour towards roads is a fundamental step to optimising road planning and minimising the impact of these infrastructures on wildlife.

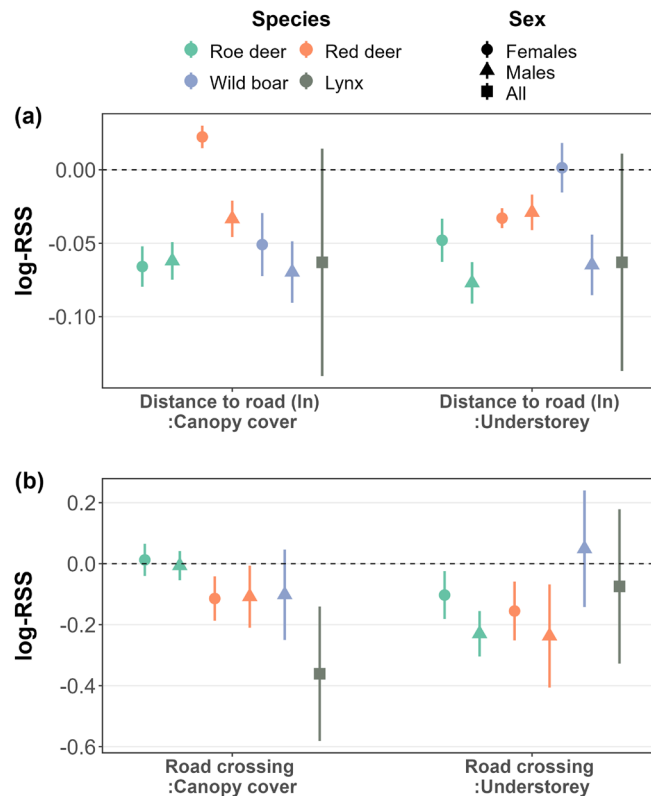


Figure 4. Coefficient estimates with 95% CI of the relative selection strength (Avgar et al. 2017) for road proximity (a) and road crossings (b) in relation to understory and canopy cover. Positive coefficients (above the zero dashed line) indicate selection, and negative coefficients (below the zero dashed line) avoidance. Coefficients equal to zero indicate no preference and the 95% CI overlapping zero indicate that the relationship is not statistically significant. The variable road crossing was not included in the wild boar females' model.

According to our first prediction, wildlife moves faster closer to roads and during road crossings in order to reduce the duration of risk exposure posed by approaching or crossing roads. Except for female wild boar and female red deer, all other groups increased their movement rate when closer to roads and during road crossings. Wild boar males and lynx showed the highest increase in movement rates during road crossings. This aligns with the behaviour-based framework proposed by Jacobson et al. (2016), which predicts that ungulates and carnivores increase their speed during road crossings to minimise the vehicle collision risk. However, this strategy might only be effective at low traffic volumes, when animals can more reliably detect gaps between passing vehicles. Studies focusing on single species found that moose, wapiti and wolverines move faster when in proximity to roads (Neumann et al. 2013, Prokopenko et al. 2017, Scrafford et al. 2018), that moose and wild boar move faster during road crossings (Dussault et al. 2007, Thurjell et al. 2015) and that lynx increase their travel speed when they are near areas with a high human disturbance (Gehr et al. 2017). However, without including data on animal activity, we cannot completely rule out the possibility that these results are, in part, due to animals resting in areas farther away from roads, which would still imply that roads are perceived as risky.

The responses of female wild boar and female red deer differed significantly from those of the other studied species,

whether male or female. The movement rate of female wild boar decreased near roads. Female red deer moved faster near roads but not during road crossings. This is in line with observations in our study area, where red deer often stand still at the roadside, possibly waiting for optimal conditions to safely cross. Another distinct behaviour observed only in female wild boar and female red deer was a stronger selection for areas located farther away from roads at all times of day, suggesting a more cautious behaviour that presumably reflects a decision taken in advance to minimise risk. There are two possible explanations for this behaviour. First, females of polygynous and dimorphic species typically exhibit less risk-taking behaviours than males, as they prioritise offspring survival (Trivers 1985, Main et al. 1996, Ruckstuhl and Neuhaus 2000), as previously observed in deer (Crawford et al. 2019) and suids (Saïd et al. 2012). Second, female wild boar and female red deer are highly gregarious and exhibit cooperative vigilance, resulting in greater accuracy in their anti-predator behaviour (i.e. reacting only to genuine threats) and thus fewer unnecessary flight responses (Duffett et al. 2020). Furthermore, gregarious species have more opportunities for non-lethal exposure to mortality risks, which enhances their ability to learn and then adjust their behaviour accordingly (Sih et al. 2011, Thurjell et al. 2017).

Our second prediction stated that wildlife seeks out vegetation cover close to roads but open areas after a road

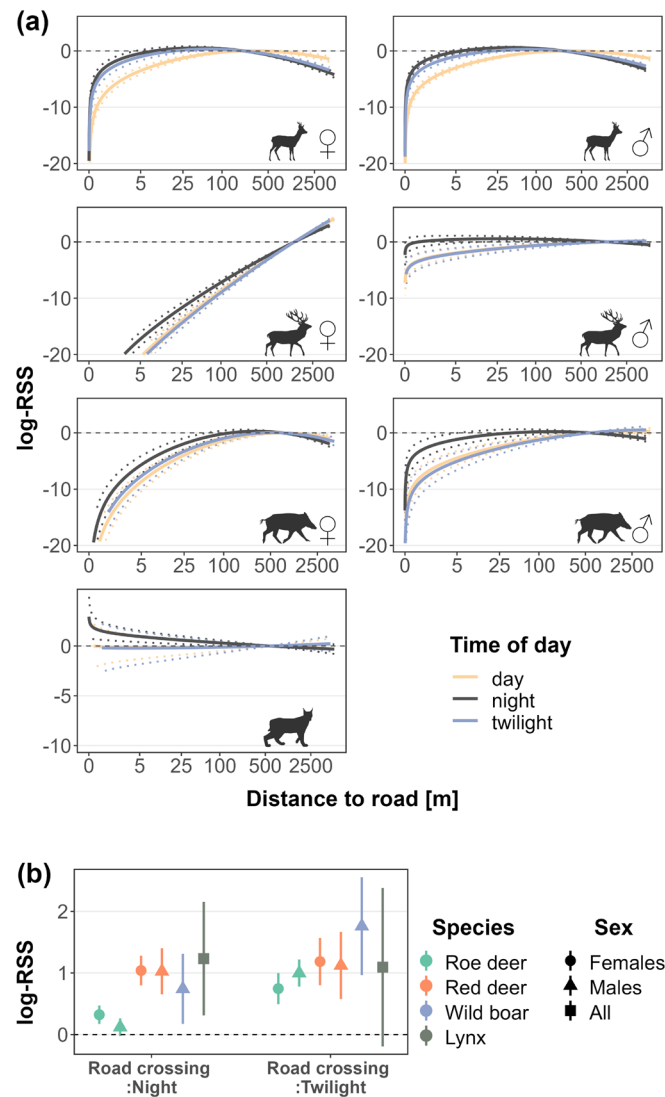


Figure 5. (a) Effect of distance to roads on the relative selection strength (log-RSS) (Fieberg et al. 2021) of roe deer, red deer, wild boar and lynx at different times of day. The figure shows the relative rates of use of two locations that were equally accessible by the animals and had identical values for all explanatory variables except for distance to road, which varies along the observed range. Dashed lines indicate 95% CI. The x-axis is log-transformed to improve the interpretability of the results within 0- and 500 m distance from the nearest road. The y-axes are cut to provide a better comparison between groups, although the minimum observed log-RSS was -24 for wild boar males, -32 for roe deer females, -57 for wild boar females and -59 for red deer females. (b) Coefficient estimates with 95% CI of the relative selection strength (Avgar et al. 2017) for road crossings at night and twilight vs. daylight. Positive coefficients (above the zero dashed line) indicate selection, and negative coefficients avoidance. Coefficients equal to zero indicate no preference; 95% CI overlapping zero indicate that the relationship is not statistically significant. The variable road crossing was not included in the wild boar females' model.

crossing. This was indeed the case for all studied ungulates, but not for lynx. These findings support the hypothesis that ungulates perceive roads as risky, such that when they are close to roads they seek habitat that provides shelter, similar to their response to natural predation risk. A study of wapiti in Canada showed that animals selected areas with high vegetation cover when moving near roads (Prokopenko et al. 2017). In a study of roe deer in France, the animals' selection for open areas decreased with increasing proximity to roads (Bonnot et al. 2013). Similarly, caribou in Alberta showed less avoidance of roads when moving near dense forest cover (Dyer et al. 2001). Contrary to our expectations, female red

deer selected low canopy cover when close to roads and this may be due to two, non-mutually exclusive mechanisms: 1) these animals risk being closer to roads only if they are moving towards more open areas providing high-quality forage, and 2) they prioritise better visibility over thicker vegetation cover when moving near roads.

After a road crossing, a low understorey was selected by both deer species, and a low canopy cover by red deer and lynx. Again, this behaviour may reflect a calculated risk in order to access high-quality foraging sites in open areas, as also found for wild boar in Sweden (Thurfjell et al. 2015), red deer in Norway (Meisingset et al. 2013) and wapiti in Canada

(Prokopenko et al. 2017, Poulin et al. 2023). Furthermore, crossing roads in more open areas would also provide greater visibility and enable quicker movement (Prokopenko et al. 2017). Lynx is a stalk-and-ambush predator that needs enough vegetation cover to approach prey without being perceived (Lone et al. 2014, Schmidt et al. 2023). In our study site, areas with a low canopy cover may still offer enough vegetation (e.g. understorey, lying dead wood, high grass) for lynx to hide (Filla et al. 2017).

We also predicted that road avoidance would be weaker at night – when the studied species are more active and traffic volume is lower – than during the day and that road crossings would be more frequent at twilight, during the activity peak of the studied species. As expected, ungulates were more often found closer to roads during the night, when the low traffic volume allowed them to exploit the high-quality forage offered near roads (Meisingset et al. 2013, Neumann et al. 2013). The absence of a similar significant pattern for lynx could be attributed to the fact that lynx data were mostly obtained during twilight and night, when this species is active. However, moving towards roads does not imply crossing them, and a vehicle collision risk is only associated with road crossings. Roe deer females, red deer, wild boar males and lynx crossed roads more frequently at night than during the day, which should decrease the risk of vehicle collisions. Similarly, roe deer in Germany crossed roads more frequently at night and during crepuscular hours (Kämmerle et al. 2017), red deer in Norway crossed roads more at night (Meisingset et al. 2013) and Canada lynx crossed roads more at dusk and night (Baigas et al. 2017). Road crossings by all ungulates increased at twilight, when the traffic volume and thus the collision risk is high (Supporting information), especially during winter (Kämmerle et al. 2017). Indeed, the daily peak of ungulate–vehicle collisions is during crepuscular hours (Lagos et al. 2012, Steiner et al. 2014, Reisinger et al. 2024).

We found that roe deer showed a weaker avoidance of areas near roads in comparison to the other studied species, especially during the day and at twilight. Furthermore, roe deer males were the only group that showed no significant difference in the frequency of road crossings during day and night. In the Bavarian Forest National Park, roe deer was the species most frequently involved in wildlife–vehicle collisions in the last 10 years (77%; Reisinger et al. 2024), reflecting patterns in Germany (200 000 roe deer individuals per year; German Hunting Association 2021). These high numbers may be explained by roe deer abundance and a stronger use of habitat near roads that could result in more road crossings for some individuals (Kämmerle et al. 2017, Brieger et al. 2022). In our study area, red deer have been more abundant than roe deer in the last few years (Palmero et al. 2021), which excludes the first hypothesis. We suggest that the reason for high roe deer road mortality could be related to a lower avoidance of areas near roads and road crossings especially at times where roads are riskier. We hereby demonstrate that multi-species studies can reveal key behavioural differences among species that determine the risk of mortality. Further

studies should consider the direct relationship between animals' behaviour and road mortality to shed light on positive and negative behaviour towards roads.

All ungulates showed the expected variation in individual behaviour, with most animals behaving similarly except for some individuals showing more extreme responses (Griffin et al. 2022). The road crossing behaviour was particularly homogeneous among individuals. This is not surprising since crossing is the ultimate risk that animals take when facing roads, and higher risk can lead to lower inter-individual variability (Balaban-Feld et al. 2022). All lynx individuals showed the same response towards roads. Large carnivores have been heavily persecuted in the past two centuries (Ripple et al. 2014), and overexploitation of wildlife population can decrease interindividual variability by selecting specific behavioural traits (Ciuti et al. 2012).

Conclusions

Our study revealed similar reactions to roads of two herbivores, one omnivore and one large carnivore inhabiting the same study system and that those reactions were strikingly similar to the behavioural changes exhibited in response to predators. These findings supported our hypothesis that the risk posed by roads is perceived as a risk of predation by species with very different biological and ecological traits.

An awareness of species-specific behaviours towards roads is fundamental to optimising road planning and to minimising the impact of roads on wildlife. For example, mitigation to reduce road mortality in our study area should be focussed on roads that cross patches of dense vegetation that alternate with more open areas. Since most species increased their speed during road crossings, measures aimed at reducing driving speeds, such as warning signs, speed bumps and radar, would aid animals in detecting gaps between passing vehicles (Danks and Porter 2010, Meisingset et al. 2014). The enforcement of speed reductions, especially during nighttime and twilight hours, when most species approach and cross roads to pursue foraging opportunities, would facilitate safer road crossings. We caution though that areas with frequent road crossings may not coincide with road mortality hotspots (Neumann et al. 2012), thus, wildlife–vehicle collision data should be used in combination with movement data to identify the road sections requiring management effort. The use of up-to-date telemetry or camera trapping data in combination with wildlife–vehicle collision data would also prevent misleading conclusions due to population depression caused by road mortality (Zimmermann Teixeira et al. 2017).

Efforts to mitigate and reverse the negative impact of roads must be based on a comprehensive understanding of how species respond to them. Our findings are a significant step towards a more complete understanding of the factors influencing the behaviour of wildlife species in relation to roads. Especially in areas of the world with high road density or where roads are expanding and traffic volumes are increasing, the scope of studied species should be broadened to

minimise road mortality and road avoidance behaviours that can have enduring consequences on biodiversity patterns and ecosystem functioning.

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Permits – Animal captures were conducted in accordance with European, Czech and German animal welfare laws. The experiments were designed to minimize animal stress and handling time and to ensure animal welfare, as defined in the guidelines for the ethical use of animals in research. Animal captures and experimental procedures were approved by the Ethics Committee of the Government of Upper Bavaria and fulfil their ethical requirements for research on wild animals (permit no.: 55.2-1-54-2531-82-10; 55.2Vet-2532.Vet_02-17-190; 55.2-2532.Vet-02-20-149). Permits for the capture of wild animals were also received from the Czech Ministry of Environment (permit no.: 41584/ ENV/10-1643/620/10-PP8; MZP/2018/630/694), the Czech Central Commission for Animal Welfare (permit no.: 44048/2008-17210, 44048/200810001) and the Government of Lower Bavaria (permit no.: 55.1-8621.1-57).

Author contributions

Matteo Luca Bastianelli: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Christian von Hoermann:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Writing – review and editing (equal). **Katrin Kirchner:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Johannes Signer:** Formal analysis (equal); Methodology (equal); Visualization (equal); Writing – review and editing (equal). **Claudia Dupke:** Formal analysis (equal); Methodology (equal); Visualization (equal); Writing – review and editing (equal). **Maik Henrich:** Data curation (equal); Investigation (equal); Resources (equal); Writing – review and editing (equal). **Elodie Wielgus:** Data curation (equal); Investigation (equal); Resources (equal); Writing – review

and editing (equal). **Christian Fiderer:** Data curation (equal); Investigation (equal); Resources (equal). **Elisa Belotti:** Investigation (equal); Resources (equal); Writing – review and editing (equal). **Luděk Bufka:** Investigation (equal); Resources (equal); Writing – review and editing (equal). **Simone Ciuti:** Supervision (equal); Writing – review and editing (equal). **Carsten Dormann:** Supervision (equal); Writing – review and editing (equal). **Tobias Kuemmerle:** Supervision (equal); Writing – review and editing (equal). **Ilse Storch:** Supervision (equal); Writing – review and editing (equal). **Clara Grilo:** Visualization (equal); Writing – review and editing (equal). **Marco Heurich:** Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3xsj3txp9> (Bastianelli et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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