



Crossings and collisions – Exploring how roe deer navigate the road network

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Abstract

Context To investigate the major impact of roads on wildlife, most studies focus on hot-spots of wildlife-vehicle collisions (WVC) to identify areas in need of mitigation measures. However, on road stretches where the frequency of WVC is low, a question arises: is this because those locations are 'safe' places for wildlife to cross the road with little risk of collisions; or is it because individuals avoid approaching and crossing the road in these locations?

Objectives In this study, we addressed this gap by evaluating how roe deer crossings are related to WVC risk across the road network.

Methods We used 56 076 WVC locations between 2013 and 2017 to predict the spatiotemporal risk zones in response to environmental, road-related and seasonal predictors using Species-Distribution

Modelling (SDM). We compared the predictive WVC risk to the location of 20 744 road crossing by 46 GPS-collared roe deer individuals.

Results We found that the risk of WVC with roe deer tends to be higher on federal roads that are present in a density of approximate 2.2 km/km² and surrounded by broad-leaved forests and demonstrate that SDMs can be a powerful tool to predict the risk of WVC across the road network. Roe deer crossed roads more frequently in high WVC risk areas. Temporally, the number of WVC changed throughout the year, which can be linked to roe deer movement patterns rather than landscape features. Within this study, we did not identify any road segments that were a complete barrier to roe deer movement.

Conclusions The absence of complete barriers to roe deer movement detected in the present study, might be due to the low spatial variation of the landscape, coupled with the high individual variation in movement behaviour. By applying our approach at greater spatial scales and in other landscape contexts, future studies can continue to explore the potential barrier impacts of roads on landscape connectivity. Exploring the relationship between crossing activity and collision risk can improve one's ability to correctly identify road stretches that require mitigation measures to improve connectivity versus reduce collisions.

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Keywords Movement ecology · Roe deer · Road ecology · Species Distribution Modelling · Wildlife-Vehicle Collisions · WVC risk

Introduction

There are more than 64 million km of roads currently on earth (IEA 2013) and by 2050 the total lane length of roads is anticipated to increase to approximately 90 million km (Laurance et al. 2014). Roads and vehicles can have detrimental impacts on wildlife, particularly by contributing to the loss of life due to collisions with vehicles or by contributing to habitat fragmentation and restricting the ability of individuals to move through the environment (Passoni et al. 2021; van der Ree et al. 2015).

Road-mortality through wildlife-vehicle collisions (WVC) tends to receive a lot of attention in the literature and in management since WVCs can be dangerous and costly for humans in addition to the wildlife involved (Bissonette et al. 2008). A vast majority of studies in road ecology use data of WVC from, e.g., surveys of roadkill, or police and accident reports, to identify ‘hot spots’, i.e., locations where wildlife are particularly susceptible to WVC, the factors that may contribute to increased risk of WVC, and, thereby, locations or conditions that need to be mitigated (e.g., Laube et al. 2023; Kent et al. 2021; Found and Boyce 2011). However, roads and traffic can also be considered barrier to movement if they prevent individuals from successfully traversing the landscape. Individuals may avoid crossing roads due to, e.g., traffic noise, light, or chemical pollution (Jaeger et al. 2005; Coulon et al. 2008), or be unable to cross due to, e.g., the substrate the road is made of or the gaps in the habitat created by the road (Kramer et al. 2016). Barriers can reduce the ability of wildlife to access necessary resources such as shelter, food and mates, which can lead to genetic isolation of populations (Westekemper et al. 2021). While hot spots of WVC may indicate areas of high WVC risk, cold spots, i.e., road sections where few accidents were recorded, may provide insights into the impact roads have on habitat connectivity. Managers tend to prioritize mitigation at locations of high WVC risk (Gunson and Zimmermann Teixeira 2015). However, by doing this, areas are overlooked that serve as such strong barriers to movement and are rarely being crossed in the first place, thus, preventing collisions. At these road stretches the lack of connectivity can and should be mitigated (Bíl et al. 2019; Laube et al. 2023).

Cold spots of WVC may either occur because the stretches of road are safe to cross and thus few collisions occur, or the road is a barrier to movement, where animals cannot approach or cross the road. They may also

reflect areas where the habitat surrounding the road is degraded in quality and wildlife cannot persist in these habitats anymore or previous road mortality led to local extirpations, resulting in local population depressions (Zimmermann Teixeira et al. 2017; Bhardwaj et al. 2017). Previous studies have used theoretical connectivity models to quantify habitat connectivity in relation to WVC (e.g., Laliberté and St-Laurent 2020; Girardet et al. 2015). However, few study the occurrence of cold spots on the road network using true movement paths of GPS-collared individuals in the landscape.

Roe deer (*Capreolus capreolus*) are one of the most widespread and abundant ungulate species in Europe (Apollonio et al. 2010). As a species with high tolerance of anthropogenic influences and the built environment, as well as a high plasticity in habitat preference (Dupke et al. 2017; Cederlund and Lindström 1983), roe deer tend to be found in human-dominated landscapes. Roe deer are also one of the most reported species in WVC in Europe. For example, 70% of the annual WVC in Croatia (Vrkljan et al. 2017), 55% of the annual WVC in Estonia (Korsten et al. 2018), and 40% of the annual WVC in Spain (Acevedo et al. 2015) involve roe deer. In Germany, roe deer were involved in approximately 80% of all WVC reported in 2022 (Brieger et al. 2022). Given roe deer are a widespread and mobile species, that are often involved in WVC, they are the ideal study species to compare spatiotemporal patterns of road crossings, as a direct measure for how often a road is successfully crossed, to the risk of vehicle collisions occurring.

In this study, we use data from southwest Germany to address the currently understudied relationship between animal road crossing behaviour and the risk of a WVC occurring, in order to separate the spatiotemporal patterns of collision risks and possible barrier effects of the road. We compare high-precision predictive risk maps of WVC to high-resolution Global Positioning System (GPS) movement data, to understand the difference between the specificity in where roe deer cross the road to where collisions tend to occur. We identify factors that contribute to increased risk of road mortality (i.e., high risk of WVC) or increased risk of barrier effects caused by the road network (i.e., low probability of crossing). We predict that crossings and collisions would have similar spatial specificity, in that roe deer WVCs would occur in areas where roe deer cross the road most frequently. Comparatively, we predict that WVC cold spots, i.e., areas with low risk of WVC, predominantly occur where roe deer do not cross the road,

indicating a barrier rather than a safe zone to cross. Temporally, we expect crossing and collision activity to vary throughout the year due to e.g., changes in movement activity depending on ecological seasons and changes in roadside vegetation. These results are among the first to show the relationship between WVC and successful road crossings in the same study. Insights will provide a first step to identify locations in the road network that are potential barrier effect pinch points, and to highlight the need to not only manage and mitigate impacts of WVC, but to also address barrier impacts and mitigate areas where connectivity is hindered.

Methods

Study area and study species

In this study, we use data from the states Hesse and Baden-Wuerttemberg in south-western Germany (Fig. 1). Hesse is 21 115 km² in size, and is

predominately made up of arable areas, meadows and broad-leaved forests, while 15.9% of the area is developed as a settlement or traffic area (Statistisches Bundesamt 2022). There are 19 689 km of roads in Hesse (ATKIS 2018), and the human population density is 296.7 inhabitants per km² (Statistisches Bundesamt 2022). Comparatively, Baden-Wuerttemberg is 35 751 km² big, predominated by arable areas, meadows and coniferous forests. Settled and traffic areas account for 14.6% of the coverage in Baden-Wuerttemberg (Statistisches Bundesamt 2022), and there are 36 643 km of roads in the state (ATKIS 2018). The states are thus both similar in land cover, human population density and roe deer population density (Appendix I).

The average roe deer population density according to the hunting bag per ha is at 0.036 and 0.043 for Hesse and Baden-Wuerttemberg, respectively. Since roe deer exhibit behavioural variation throughout the year (Found and Boyce 2011; Grilo et al. 2015), we consider the data in four separate ecological seasons: rut (mating), diapause, gestation, lactation. Roe deer

Fig. 1 Location of the five study sites in Baden-Wuerttemberg: four in the west and one in the south indicated as crossed circles. The inset map shows Baden-Wuerttemberg's (BW) location within Germany to the south of Hesse (HE)



behave and move differently in each season, which could have an impact on how much they cross roads. During the rut (16 July – 15 August), males tend to move further distances and cross roads more frequently and unpredictably as they search for females, presumably elevating collision risk (Kämmerle et al. 2017). The rut is concluded with the fertilization of females and leads into the diapause phase (16 August – 31 December), a prolonged pre-implantation period in which no differences in crossing activity are to be expected. Four months after the start of the diapause, female roe deer enter the gestation periods (1 January – 30 April; Krop-Benesch et al. 2013). Just before the females give birth, the yearlings from the previous year disperse from their natal home range increasing the chance of especially young individuals from both sexes to cross unknown roads (Linnell et al. 1998). After parturition, the lactation season starts in which females are accompanied by their new-born fawns (1 May – 15 July; Mayer et al. 2021). During this season, females are likely to move less in order to stay in close proximity to their offspring. Except for during the rut and the dispersal phase of young males, movement patterns of adult males are not expected to be strongly affected by the other periods. By separating our analysis across these four periods, we could account for the temporal difference, while the spatial variables (i.e. land cover and road characteristics) remain constant.

Analysis

To compare spatiotemporal patterns of road crossings to the risk of vehicle collisions occurring, we predicted WVC risk using a Species Distribution Modelling (SDM) and compared this to true crossing data from GPS collared roe deer (Fig. 2). We did this in a three-step method: (A) using 3 years of GPS collar data from 46 roe deer, we identified patterns in how roe deer cross different segments of roads; (B) using 5-years of WVC data, we calculated the risk of WVC according to landscape and road factors; (C) we compared the relative crossing frequencies and risks of WVC to identify spatiotemporal patterns of road crossings and WVC risk (Fig. 1). We describe these three steps in details below. To account for changes in movement behaviour of roe deer as well as the varying WVC risk throughout the year (Joyce and Mahoney 2001; Mayer et al. 2021), we built four models according

to the four ecological seasons described above. We performed all analyses in R (version 4.0.5., R Core Team 2020).

(A) Crossing activity from GPS collared roe deer

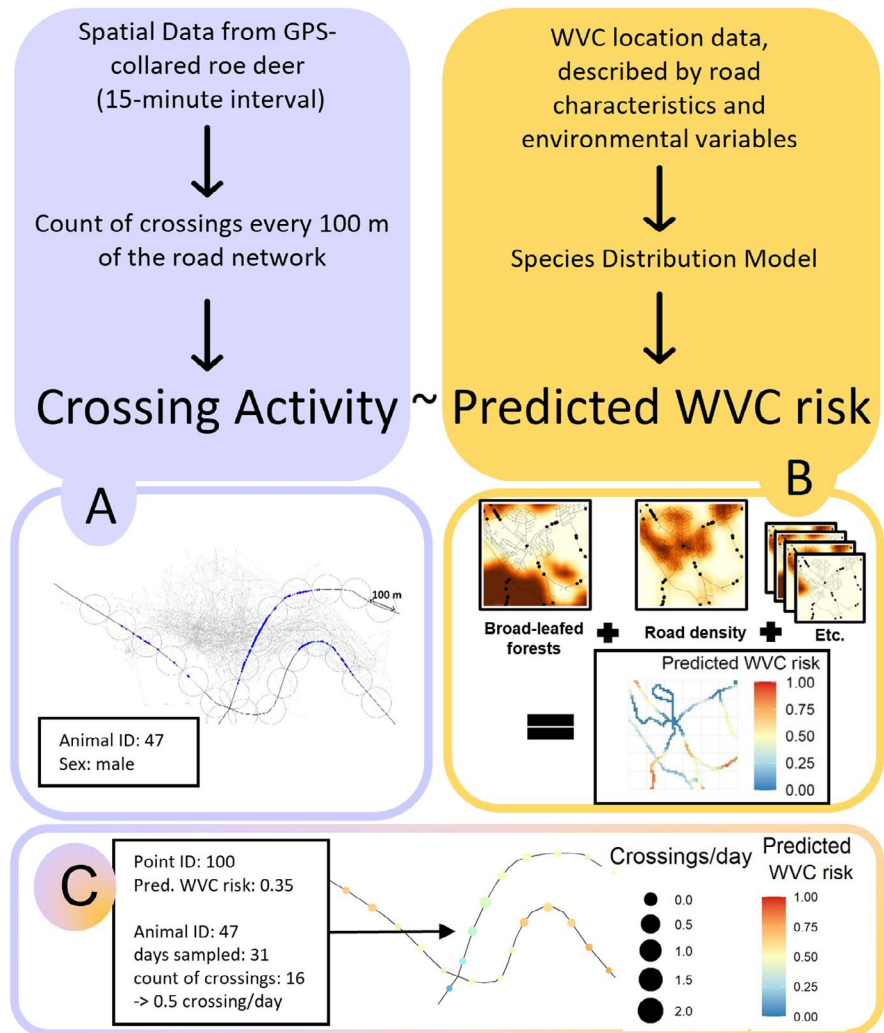
Between 2010 and 2013, 46 roe deer (17 males and 29 females) were marked with GPS collars, in five study sites in Baden-Wuerttemberg, Germany (Fig. 1; details of collaring methods provided in Appendix I, Brieger et al. 2019; Kämmerle et al. 2017). Collars sent GPS locations at a 15-min fix interval when deer were active, and at a 180-min fix interval once no movement was detected after five consecutive locations. To get an estimate of how often each roe deer individual crossed a specific part of the road network, we divided the road network within the aggregated home range (99% Minimum Convex Polygon) of roe deer into 50 m sampling buffers (centroids 100 m apart). Then, we counted the number of times each individual crossed the road through the given sampling unit per ecological season influencing roe deer behaviour (i.e., straight-line trajectory between two successive GPS-fixes that intersected a road; Kämmerle et al. 2017; Kramer et al. 2016). While the 15-min interval between fixes may be sufficient time for roe deer to walk along the road before crossing (thus contacting the road in multiple locations), we assumed the discrepancies between our estimated crossing locations and the true crossing locations were minimal, since we aggregated crossings into buffers encompassing a maximum of 100 m of road length.

(B) Predicting the risk of a WVC occurring

To estimate the risk of WVC occurrence, we generated SDMs (one model per ecological season) using known WVC locations from police reports as presence points, according to environmental predictors (i.e., roe deer population density, land cover) and road characteristics (i.e., road category, road width, road density; Table 1; Chyn et al. 2021; Jaarsma et al. 2007).

Data on the location of WVCs in Baden-Wuerttemberg were only available for one year, therefore, we used data from neighbouring state Hesse, where data is available for five years (2013 – 2017, $n=56$ 076; Brieger et al. 2021), to train the SDMs. This not

Fig. 2 Visualization of the methodology: **A** GPS data from collared roe deer (example shown for roe deer ID 47) was processed to count road crossings (blue crosses) in sampling buffers every 100 m on the road network (black line) per ecological season. **B** For the entire road network, WVC risk was predicted using the SDM of WVC presence points per ecological season and described by rasterized predictor variables. **C** The relationship between road crossings and predicted WVC risk was explored in the final analysis



only increased the sample size for the modelling process, but also allowed for a validation of the model on independent data from Baden-Wuerttemberg (2021 – 2022, $n = 12\ 617$).

Spatial predictors of risk To explore the spatial predictors of WVC risk, we created spatial raster layers with a grid size of 50×50 m, which incorporated land cover and characteristics of the road. This allowed for the best spatial accuracy for the WVC data, while also corresponding with the resolution of the road characteristics information. Land cover is a common predictor for animal abundance and dispersal (e.g. Cagnacci et al. 2011; Linnell et al. 1998), and can influence where individuals cross the road, and potentially also the driver’s visibility

of an approaching animal (Meisingset et al. 2014), thus impacting where WVC occur (Barrientos and Bolonio 2009; Malo et al. 2004; Joyce and Mahoney 2001). We characterized land cover using maps from Land Cover Project 2018 (resolution: 100×100 m; European Environment Agency 2018). Corine land cover is updated in cycles of 6 years, which makes 2018 the most accurate approximation to the temporal variation of the WVC data (ranging from 2013 to 2022), that was available for this study. We chose land cover categories based on those that are most relevant to roe deer ecology: arable areas, meadows, broad-leafed forests, conifer forest, mixed forest, complex habitats, industry, swamps and urban areas (Hothorn et al. 2012; Table 1). For each focal cell, we calculated the percentage of each land cover type within

a 100×100 m and a 200×200 m moving window as an indication of the type of habitat that surrounded the road, using the ‘raster’ package (Hijmans 2021). We chose the smaller scale to represent the habitat adjacent to the road, which may draw roe deer to the road and/or influence visibility of wildlife in roadside verges. The larger scale was chosen as it corresponds to the size of the core home range of roe deer and, therefore, represents the general occurrence of roe deer in the landscape (Saïd et al. 2009). To complement the landscape-level variables and take roe deer densities into account, we also incorporated hunting bag per game management district throughout the area (Table 1). This value does not correct for hunting effort, however, it is, to our knowledge, the most accurate and spatially consistent roe deer density estimate available.

The risk of a WVC occurring can also be influenced by road-related predictors such as ADT, speed and road density (Kent et al. 2021; Barrientos and Bolonio 2009; Jaarsma et al. 2007; Table 1). In Germany, the road network is categorized into

five categories according to ADT and speed limits (Straßenverkehrs-Ordnung §3 n.d.; Statistisches Landesamt Baden-Württemberg 2022). WVC in Hesse occurred on all road categories, with the most accidents on state roads ($n=27\,916$), followed by federal – ($n=13\,446$) and then district roads ($n=11\,859$). Motorways and community roads had the least WVC, with 1 641 and 1 214 WVC respectively. For each raster grid cell which is crossed by the road network, we extracted the largest road category and maximum road width. We also extracted the mean road density (km/km^2) using all roads within the cell and averaged the road density for each focal cell within a 100×100 m and a 200×200 m moving window. We extracted the largest road category and road width using the ‘fasterize’ package (Ross 2020), while we calculated road density using the ‘spatstat’ package (Baddeley and Turner 2005).

All predictors were masked to the rasterized road network (raster grid cells which have an according road category and maximum road width assigned) in order to limit the roadkill model to areas where WVC are expected to occur. To aid in model fitting and

Table 1 Spatial predictor names and definitions

Spatial predictor	Definition
<i>Land cover (percentage per w/100 m and w/200 m window)</i>	
Arable areas	Non-irrigated arable land
Meadows	Pastures; Areas principally occupied by agriculture with significant areas of natural vegetation and natural grasslands
Broad-leafed forests	Broad-leafed forests
Conifer forests	Coniferous forests
Mixed forests	Mixed forests
Complex habitats	Complex cultivation patterns; Fruit and berry plantations; Transitional woodland-shrubs and vineyards
Industry	Industrial or commercial units; Airports
Swamps	Moors and heathlands; Inland marshes and peat bogs
Urban areas	Urban fabric; Port areas; Construction sites; Green urban areas and sport and leisure facilities
<i>Road characteristics</i>	
Road category	Type of road based on Average Daily Traffic Volume (ADT) and speed: 1. motorways: ADT $\approx 64\,000$, recommended speed: 130 km/h (no posted limit) 2. federal roads: ADT $\approx 14\,500$, posted speed: 100 km/h 3. state roads: ADT $\approx 5\,000$, posted speed: 100 km/h 4. district roads: ADT $\approx 2\,500$, posted speed: 100 km/h 5. community roads: ADT $\approx 7\,000$, posted speed: 50 km/h (outside villages: 100 km/h)
Road width	Width of road (in m)
Road density	Mean road density (km/km^2) per w/100 m and w/200 m window
<i>Roe deer hunting bag</i>	Roe deer hunting bag per hectare as proxy of local population density

result interpretations, all non-categorical predictors were standardized.

Training and validating of SDMs Since known WVC locations are 'presence-only' data, we used Maximum Entropy Modelling (MaxEnt) to create spatially explicit predictions of WVC occurrence (Chyn et al. 2021; Merow et al. 2013). We chose SDM modelling, in particular MaxEnt, over other methods because of the predictive quality of comparable accuracy to ensemble methods, the ease of use, reduced computational time (Kaky et al. 2020) and because analyses are not as dependent on the quality and completeness of the data through the whole study area. Since each collision was recorded independently of one another, issues of spatial autocorrelation were negligible. In order to only include areas where the species are physically present and could potentially cross the roads, we created a bias grid using a two-dimensional kernel density estimate based on the coordinates of the WVC presence points and masked it to the road network (Syfert et al. 2013). We then generated 10 000 background points on this road network, with the probability of being sampled according to the bias grid, thus, biased towards areas with a higher density of presence points (Dudík et al. 2005; Elith et al. 2011; Phillips et al. 2009; Background collision positions generated using the 'MASS' package, Venables and Ripley 2002).

We trained all four seasonal models using 5-fold cross validation (80% training and 20% testing data). To reduce collinearity and model complexity, we first trained the models with all variables and then removed variables with a Spearman's rho correlation value higher than 0.7, while using the Area Under the Receiver-Operating-Characteristics curve (AUC) to compare between the simplified models (Vignali et al. 2020). We used a Generic Algorithm implementation to optimize the hyperparameter configuration (i.e., the amount of regularization, the number of iterations and the feature class combinations; Merow et al. 2013). Finally, we reduced the simplified optimized models to only include variables with a permutation importance higher than 2%, while keeping the model performance constant. The resulting estimated risk of a WVC occurrence on the 'cloglog' scale ranged between 0 and 1, which can be interpreted as the probability of a WVC to occur.

We projected the estimated risk of WVC, as predicted from the model using data from Hesse, into Baden-Wuerttemberg. Validating the model with independent WVC locations from an area outside of the geographical range of the training data performed well, and all models were able to differentiate the probable WVC risk between presence and background data. For training, optimization and evaluation of the models, we used the 'SDMtune' package (Vignali et al. 2020). Full details on how the SDMs were trained and validated as well as the evaluation performance tests are provided in supplementary information Appendix II.

(C) Relationship between crossing and collision locations

To determine the relationship between crossing and collision locations per defined sampling unit (50 m buffer with centroid every 100 m on the road network within the aggregated home range), we compared the frequency of roads crossings with the predicted WVC risk of the according road segments. The WVC risk was predicted using the model of the ecological season which corresponded with the season that the road crossings count was sourced from. We used a zero-inflated negative binomial model to analyse the possible effect of WVC risk, season and sex of the individual on number of crossings per sampling unit. The zero-inflated model allowed us to build a count model to estimate the number of crossings, and a binary model with zeros and no zeros to evaluate the probability of zeros occurring (using the package 'GLMMTMB'; Brooks et al. 2017). We offset the count model using the log-transformed value of sampling days as a covariate within the model to correct for unequal sampling periods for each individual and season length. We included sex as a predictor to account for behavioural differences among the seasons (Brieger et al. 2022), and study site as a random effect to account for other unexplained variation. As all roe deer were not monitored in all seasons, individual ID could not be included into the global model. We selected the most parsimonious model using Akaike Information Criterion (AIC) for model comparison, which evaluates the models fit on the training data while adding a penalty term for the complexity of the model (Burnham and Anderson

2004). In order to compare the fits of competing models which were in the range of a $\Delta\text{AIC} < 2$, we did ANOVA testing. This tested whether the more complex model with additional parameters included was also significantly better at capturing the data than a simpler model (Arnold 2010).

Results

Crossing activity

Each collared roe deer individual was monitored for an average of 423 ± 247 days between 2010 and 2013. Over the entire study period, collared roe deer crossed roads a total of 20 606 times (of which 8 002 crossings during gestation, 4 420 during lactation, 1 967 during the rut and 6 212 during diapause). Of the 46 collared individuals, 44 crossed roads 1 – 2 387 times (468.3 ± 557.5), indicating strong individual variation. The two remaining individuals never crossed roads, while wearing the GPS collar. Most crossings were over community roads (2 688 crossings/km; 3 091 crossings on 1.15 km of community roads within the home ranges of collared individuals), followed by state roads (680.03 crossings/km; 7 421 on 10.9 km of state roads) and district roads (536.91 crossings/km; 10 094 on 18.8 km of district roads). No motorways were crossed (2.57 km) and no federal roads occurred within the home ranges of the collared individuals and could thus not be investigated.

Risk of WVC

Broad-leafed forests, road density within a 200 m window and road category explained 55–65% of the risk that a WVC would occur (Appendix II). Specifically, the risk for a WVC is highest at a moderate ADT and speed levels (linked to federal roads) on roads that are surrounded by increasing percent cover of broad-leafed forests and at a surrounding road density of 2.2 km/km² (Fig. 3). Spatial predictors of WVC did not differ among ecological seasons.

Relationship between crossing activity and risk of WVC

The final model describing the frequency of road crossings included all predictors without interactions and the zero-inflation described by season and sex (Tables 4 and 5 in supplementary information Appendix III include further details on model selection and results). Number of road crossings per day were positively influenced by the predicted WVC risk, with more road crossings in areas with higher risk value (0.42 ± 0.17 ($\bar{E} \pm \text{SE}$), $p = 0.01$). With season influencing the crossing frequency marginally ($f(3) = 7.42$, $p = 0.06$), the highest crossing frequency of males and females was observed during the rut. Overall, males crossed roads more often than females (0.22 ± 0.10 , $p < 0.05$). In most cases, all sampling buffers within an individual's home range were crossed at least once

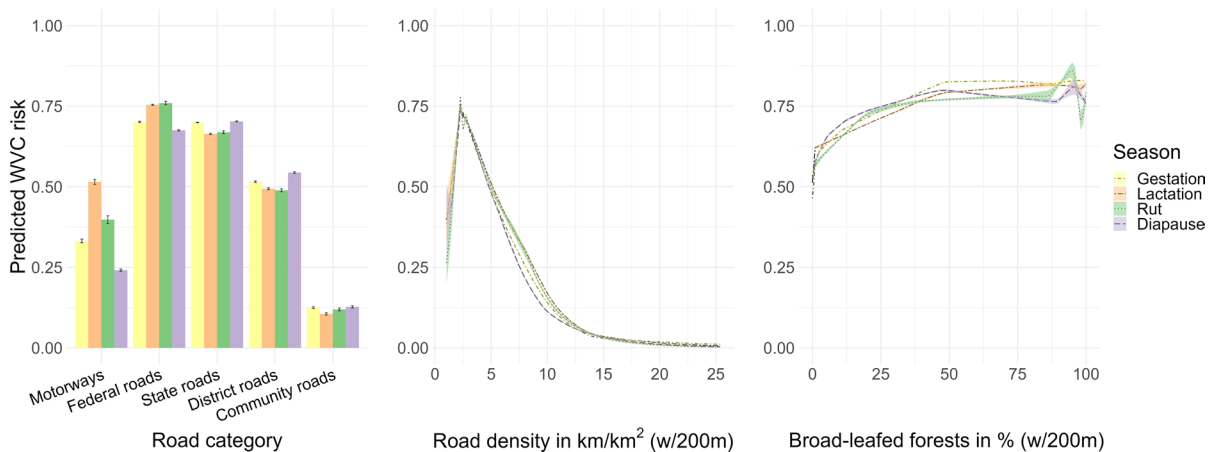


Fig. 3 Response curve on the 'cloglog' scale, which can be interpreted as the probability of occurrence for the three predictors that explain WVC risk best: **a** Road category, **b** Road density and **c** Broad-leafed forests, separated by ecological seasons

(Fig. 4), even buffers with low predicted WVC risk. Visual comparison of the walking trajectory of individual roe deer showed different movement behaviour around and over the same roads (Fig. 4). Of the 33 individuals that died while collared, 14 are known to have died in a WVC. The mean predicted risk of WVC at the collision locations of collared roe deer was 0.61 ± 0.22 , and these locations were crossed more frequently than the overall mean number of crossings during the season in which the individual was involved in the collision.

While the seasonal SDMs did not indicate a riskier season in comparison with others, we could demonstrate fluctuation in road crossing behaviour. WVC occurrence peaked in April and May, before declining in the lactation phase (Fig. 5; i.e., the period with fewest crossings by females (0.28 ± 0.14 , $p=0.04$)). WVC peaked again in August, which corresponds to the rutting season, when males and females crossed most frequently (0.3 ± 0.21 , $p=0.16$).

Discussion

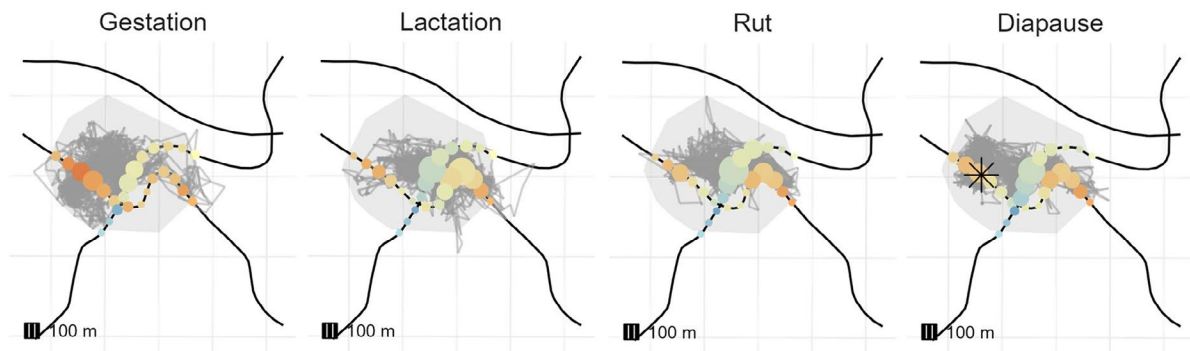
We aimed to identify locations of WVC cold spots on the road network by comparing patterns in where roe deer cross roads to the predicted risk of WVC. We found that the risk of WVC with roe deer tends to be higher on federal roads that are present in a density of approximate 2.2 km/km^2 and surrounded by broad-leaved forests (Fig. 3). Broad-leaved forests provide cover, which may promote deer occurrence in vicinity to the road (Brieger et al. 2022; Dupke et al. 2017) and may also reduce visibility into the roadside verge for drivers, increasing the risk of WVC (Malo et al. 2004; Neumann et al. 2012; Meisingset et al. 2014). The hump-shaped peak of WVC risk at roads with moderate ADT and speed, i.e., 5 000 – 14 5000 vehicles/day and a posted speed limit of 100 km/h, while declining at lower and higher road categories, follows relationships as described in the literature (e.g., Seiler 2005; Seiler et al. 2016). We also demonstrated the same relationship between road density and the risk of WVC, as the highest probability of WVCs was at 2.2 km/km^2 , an intermediate road density. This combination of ADT, speed and road density tends to occur near villages or the outskirts of cities, which also tend to support roe deer populations, by providing a heterogenous landscape of open and cover

habitats, and access to human-provided resources, such as agriculture and gardens (Apollonio et al. 2010). At lower road densities, the probability for an animal to have to cross a road is generally decreased as fewer roads transect their home ranges. Areas with higher road densities and higher ADT, may be avoided by roe deer (Benhaïem et al. 2008; Coulon et al. 2008; Kent et al. 2021), contributing to a barrier or filtering effect of the roads on the movement of roe deer in the landscape (Barrientos and Bolonio 2009; Grilo et al. 2015; Madsen et al. 2002).

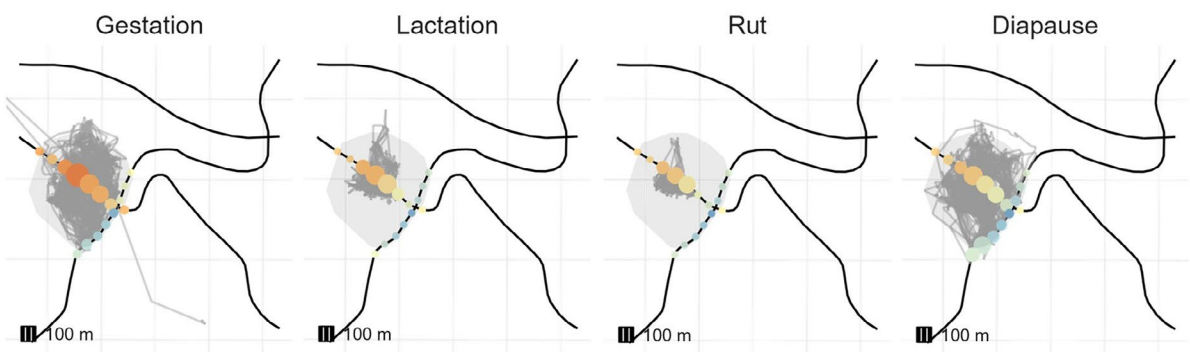
Collisions can only occur when an animal is attempting to cross a road in the same location and at the same time as a passing vehicle. Predicting the risk of WVC, thus, combines the probability of an animal choosing to cross a road as well as the risk of it being hit at a certain location (Lima et al. 2015). In line with our hypotheses, we demonstrate the linear relationship between risk of WVC occurrence and road crossings. WVC occurrence fluctuated over the year (Fig. 5). Spatial features, such as road category, road density or percentage of broad-leaved forest around the WVC did not show changing response curves per season (Fig. 3), indicating that the features in the surrounding environment are less likely to influence the seasonal fluctuations of WVC numbers. The fluctuations may be, thus, rather due to seasonal changes in crossing behaviour of individuals. Temporal peaks in WVC occurrence in April and May (Fig. 5) closely match peaks in crossings activity at the beginning of the lactation phase (Appendix II.), which is the time of the spring dispersal of yearlings (Liberg et al. 1998; Wahlström and Kjellander 1995). Spatially, roe deer crossed more frequently in high WVC risk areas, and the predicted risk of locations where collared individuals were involved in a WVC was 0.61 ± 0.22 . Increased movement activity may contribute to higher WVC risk (Brieger et al. 2019; Girardet et al. 2014). We, therefore, propose that collisions usually occur during routine movements within the territory of roe deer (Madsen et al. 2002; Kämmerle et al. 2017; Brieger et al. 2022) and the frequency of road crossings is directly influenced by the factors contributing to a high WVC risk.

Contrary to our expectations, we did not find a clear indication of a barrier effect, i.e., road segments with a low WVC risk that were not crossed at all. Instead, we found high levels of variation in the crossing behaviour among individuals, and identified roads that were barriers for some individuals while being crossed often

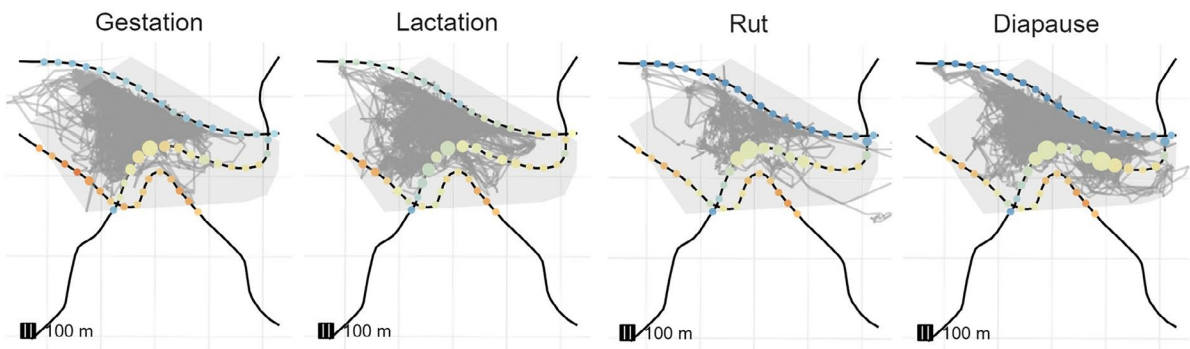
ID 47 - Sex: male



ID 43 - Sex: female



ID 58 - Sex: female



Predicted WVC risk 0.00 1.00

Crossings/day • 0.0 1.0 2.0

Fig. 4 Seasonal results for ID 43, 47 and 58, which all occurred in the same area. The grey shading represents the home range (99% Minimum Convex Polygon) for each individual, the grey lines show the walking trajectories, and the black line depicts the road network. Circles on the roads represent the sampling buffers, and their sizes correspond to the number

of crossings per day. The predicted WVC risk is represented in the colour gradient, with blue indicating low WVC risk and red indicating high WVC risk. The black star in the 'diapause' panel of ID 47 indicates the location of the WVC ID 47 was involved in. These individuals are selected for visualization purposes

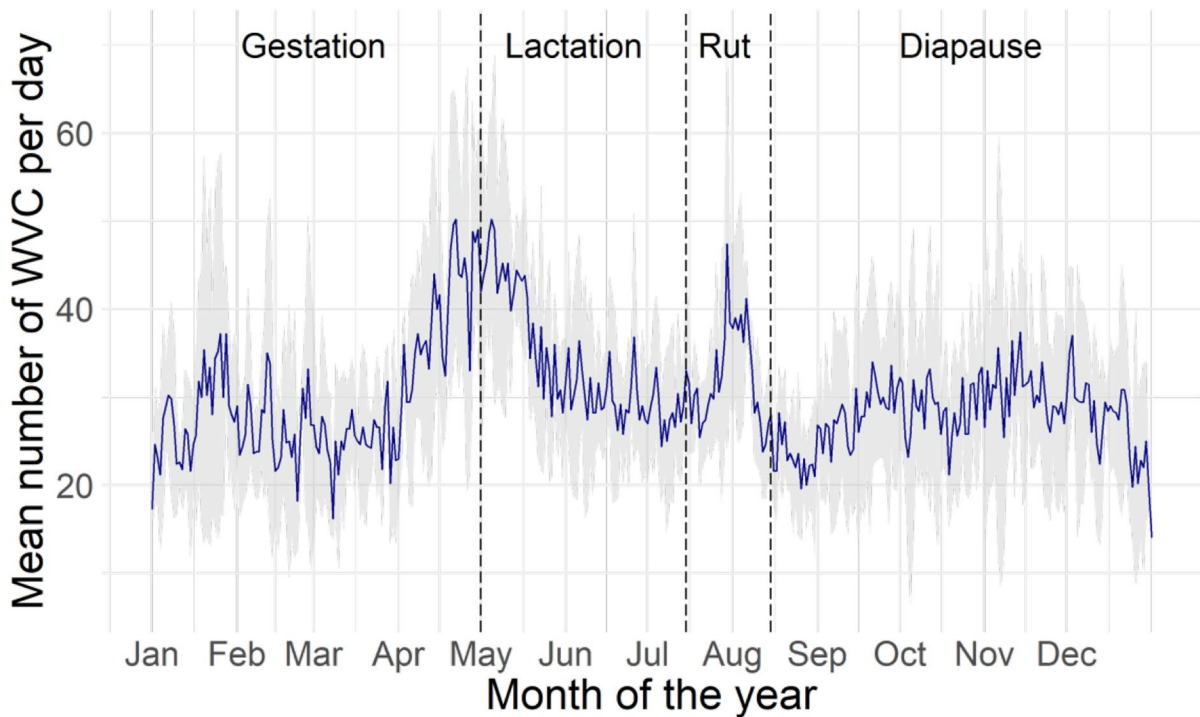


Fig. 5 Mean number of WVC per day over the year. The transitions between the four ecological seasons are indicated with the dotted lines

by others (Fig. 4 and see Kämmerle et al. 2017). This suggests strong individual variation in roads ‘crossing cold spots’, which could be due to the high behavioural plasticity reported in roe deer (Cagnacci et al. 2011; Steiner et al. 2014). Additionally, the expected barrier effect might be most prominent on federal roads and motorways, which could only be tested in a very limited way, as no federal roads and only 2.57 km of motorways occurred within the home range of the collared roe deer. Thus, the low spatial variation of the landscapes in which the collared roe deer were monitored, coupled with the high individual variation in movement behaviour, may be masking a barrier effect that have otherwise been demonstrated at greater spatial scales and in other landscape contexts (e.g., Passoni et al. 2021). Therefore, we conclude, that the scale of the study, as well as the fact that the SDM was conducted in Hesse and only validated with WVC data from Baden-Wuerttemberg, may have influenced our findings. GPS-collars allow for detailed and fine-scaled data collection on particular individuals, which are, presumably, representative of the population. Comparatively, WVC data comes from a population-scale, which is generalized across the entire

sampling area. Detailed demographic data from WVC reports, i.e., data on sex and age of the killed animal, may allow future research to explore the impact of roads on the individual-scale. Alternatively, the relationship between collisions and crossing can be up-scaled to the population/species levels by including more GPS-collared individuals at the scale of available WVC data. For example, Passoni et al. (2021) found roads in Europe can be a barrier to roe deer movement on the continental scale. Using similar data, within our methodological framework of comparing crossings to predicted WVC risks, future studies may be able to separate mortality from barrier effects of roads on wide-ranging species such as roe deer.

Analysing landscape connectivity can involve various methods and measures to understand how effectively wildlife can move and disperse across the landscape. Least-Cost-Path analysis, CircuitScape (McRae and Beier 2007) or open-source R packages such as *SiMRiv* (Quaglietta and Porto 2019) can model the most efficient route that wildlife would likely take, by considering the resistance of different habitat and road characteristics. These theoretical resistance/flow models are

strengthened and validated with telemetry data, which identify true paths individuals take, as we have done in the present study (Laliberté and St-Laurent 2020; Quaglietta et al. 2019). To improve the results of the present study, future studies can combine our approach of using telemetry data to identify paths of individuals crossing roads with resistance/flow models, to generate realistic movement models that describe how movement patterns are impacted by roads (e.g., Quaglietta et al. 2019). Further, following our framework, the results of the combined resistance/flow models and telemetry-based movement models can be compared to predicted WVC risks derived from SDM models to identify the two critical areas for wildlife movement: 1. areas of high numbers of road crossings, where animals attempt to cross the road and there is a high risk for WVCs resulting in low realized connectivity, and 2. areas where no WVC happen, due to limited movement through a fragmented habitat.

While areas of high WVC risk tend to get the most attention in the literature and in management, the ecological impacts of barrier effects can have just as negative consequences on wildlife populations as direct loss of individuals. Many transport agencies invest millions of dollars a year in mitigating the negative impact of roads on wildlife (Huijser et al. 2009). A common strategy to mitigate the impacts of roads on wildlife is to install wildlife crossing structures, i.e., structures designed to allow movement of an animal from one side of a road to another without travelling across the road surface, ultimately promoting or restoring movement across the landscapes (Smith et al. 2015). We argue, that installing crossing structures in areas of high WVC risk only addresses one part of the problem and ignores the issue of barrier effects all together (Soanes et al. 2024; Zimmermann Teixeira et al. 2017). Our approach to compare WVC risk to crossing activity is an appropriate tool to inform the correct implementation of effective measures to reduce WVC and enhance landscape connectivity, especially when demographic data of individuals involved in WVC, or when GPS-collar data across multiple populations, are available. Transportation infrastructure is one of the major challenges to the maintenance of landscape connectivity for wildlife, and new approaches to identify and address the multifaceted ecological issues due to transportation infrastructure can help to maintain viable wildlife populations as the terrestrial landscape continues to be developed and fragmented.

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Author's contribution JM and MB conceived the ideas and designed the methodology with additional input from FB. FB collected the data. JM and MB developed the modelling framework. JM performed the analysis and led writing of the manuscript. MB and FB supervised and supported the analysis and writing. All authors contributed critically to drafts and gave final approval for publication. The authors have no relevant financial or non-financial interests to disclose.

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Data availability All relevant data that can be shared are within the paper and its Supporting Information files. WVC data cannot be openly shared.

Declarations

Competing interests The authors declare no competing interests.

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