



Influence of roads on space use by European hares in different landscapes

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Abstract

Context Roads are ubiquitous in human inhabited landscapes, and can impact animal movement and population dynamics, due to barrier effects, road mortality, but also by providing resources at road verges. Thus, we need a better understanding of how roads, in interaction with seasonal changes in habitat structure,

affect space use and habitat selection of the animals that persist in these landscapes.

Objectives Here, we used the European hare (*Lepus europaeus*) as model species to investigate how human-induced changes in landscape composition—measured as road density, land cover type, and field size—affect home range location, seasonal habitat selection and road crossings, which are likely to correlate with wildlife-vehicle collision risk.

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Methods We collected > 240,000 GPS positions of 90 hares from three populations (one in Denmark and two in Germany) that differed regarding agricultural intensification and road density. Using this data, we analyzed home range location and habitat selection (using step-selection functions) in relation to roads, habitat composition, and seasonality, and quantified how these factors affected road crossings by hares.

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Results In comparatively more heterogeneous landscapes, hares established home ranges in areas with lower road densities compared to the surrounding area, but not in more simple landscapes. Moreover, hares generally avoided main roads and selected for minor roads during the vegetation growth seasons, especially in areas with comparatively less heterogeneous habitat structure. Hares crossed more main roads when moving greater distances, with movement distances being comparatively larger in simpler landscapes.

Conclusions Our findings emphasize that it is important to distinguish between road types, as different roads can have different impacts on animals

(e.g., small roads providing foraging opportunities via roadside vegetation and large roads being avoided). Moreover, animals in comparatively more heterogeneous landscapes are better able to adjust their habitat selection to avoid main roads than animals inhabiting simpler landscapes. More generally, homogenous landscapes increase the space use requirements of animals, leading to increased probability of road crossings, which in turn might affect population dynamics via increased road mortality risk.

Keywords Agricultural intensification · GPS · Habitat fragmentation · Habitat selection · *Lepus europaeus* · Road ecology

Introduction

Human structures are ubiquitous in populated areas, and paved roads lead to increasing fragmentation of the landscape, representing barriers for wildlife movement (Lesbarreres and Fahrig 2012; Bischof et al. 2017). Physical barriers, such as fencing along roads, can have indirect effects on animal populations, e.g. reducing dispersal and gene flow among meta-populations, stressing the need to understand how human infrastructure impacts animal movement (Tucker et al. 2018). Furthermore, animals attempting to cross roads are often killed by vehicles. Vehicle collisions cause millions of animal deaths on European roads each year (Grilo et al. 2020), including a wide range of taxonomic groups (Erickson et al. 2005; Rao and Girish 2007; Shepard et al. 2008; Beebee 2013; Ascensão et al. 2017). This makes the reduction of road mortality a major field in conservation biology (Coffin 2007).

Apart from increasing fragmentation via roads, changes in the landscape are predominantly driven by agricultural intensification and expansion, leading to deterioration of habitat suitability for many species (Stanton et al. 2018; Raven and Wagner 2021). For example, homogenization though altered agricultural land use in Europe has led to a general decline in farmland biodiversity (Benton et al. 2003; Carmona et al. 2020). Moreover, changes in landscape composition, e.g. via increased agricultural field sizes, can also lead to extended space use by animals to meet their energetic requirements (Mayer et al. 2019). Consequently, increasing home ranges of individuals

might force them to cross roads more regularly, increasing the risk of wildlife-vehicle collisions. On the other hand, green stretches along roads may also provide wildlife habitats in rural landscapes, e.g. shown for the hazel dormouse (*Muscardinus avellannarius*) living in shrubberies along motor ways over which radio-tagged individuals frequently crossed (Kelm et al. 2015).

Depending on species and habitat constellations, roads and road-adjacent habitats may be avoided or selected for (Zimmermann et al. 2014; Kelm et al. 2015; Prokopenko et al. 2017). Thus, roads can potentially increase as well as decrease the ecological capacity of a species' habitat and in addition, might act as ecological traps. Because these relationships are complex with potential consequences for population dynamics (Kroeger et al. 2021; Fischer et al. 2022), we need to study them at the relevant spatial scales.

Here, we investigated how human-induced changes in landscape composition—measured as field size (i.e., the area of each land cover patch), land cover type and road density—affect road crossings, a potential proxy for increased wildlife-vehicle collision risk, and habitat selection in relation to roads by the European hare (*Lepus europaeus*; hereafter hare). Hares are an optimal model species for this, because they successfully adapted to live in agricultural areas, occurring in a wide range of agricultural landscapes that differ in habitat heterogeneity (Frylestam 1980; Vaughan et al. 2003). However, they have declined in most parts of Europe since 1960 as a result of agricultural intensification (Smith et al. 2005). It was previously shown that hares avoid roads, and that road density negatively affects hare abundance (Roedenbeck and Voser 2008), potentially because hares get killed by vehicles (Hell et al. 2005). However, in areas of habitat homogenization (large agricultural fields), hares might be increasingly forced to cross roads during parts of the year when crops are high. This is because high vegetation acts as a barrier and does not provide good forage, thereby forcing them to move greater distances to cover their biological needs (Mayer et al. 2018, 2019; Ullmann et al. 2018). Moreover, it is conceivable that males cross roads more often than females, because they have larger home ranges and move longer distances per time unit (Zaccaroni et al. 2013; Mayer et al. 2019). Despite a large body of literature investigating home range size

and habitat use of hares in relation to land use change and agricultural practices (Rühe and Hohmann 2004; Schai-Braun et al. 2014; Ullmann et al. 2018, 2020), we know little about the interplay of road infrastructure and habitat structure on the space use of hares and species persisting in farmland in general.

We expected that habitat homogenization via intensified agriculture (here measured as field size) affects hare space use—i.e., home range location and habitat selection—in relation to roads, as well as the frequency of road crossings. Specifically, we hypothesized that hares generally avoid roads, regarding both home range location and within-home range habitat selection. Additionally, we hypothesized road avoidance to be more pronounced in heterogeneous habitats, as these should offer sufficient resources for hares to avoid human infrastructure. Further, we expected that habitat selection in relation to roads and the frequency of road crossings changes seasonally, due to changes in vegetation height and resource availability. We hypothesized that hares use areas in closer proximity to roads, and cross roads more during times when vegetation is generally high (i.e., in summer before the agricultural harvest season) and in areas with comparatively larger fields. This hypothesis was based on the assumption that being excluded from areas with higher vegetation (e.g., cereals), hares are forced to move between fragments of shorter vegetation (such as roadsides and pastures). Finally, we expected road crossings to be affected by internal factors (sex) and spatio-temporal variables (season, road density, and field size), which are interrelated (hare movement changes seasonally and depending on landscape structure). We hypothesized that hares increasingly cross roads with increasing road density (due to increasing fragmentation), more so in late spring and summer when vegetation is high, when field sizes are larger (forcing them to move more), and that males cross roads more often than females because they have larger home ranges.

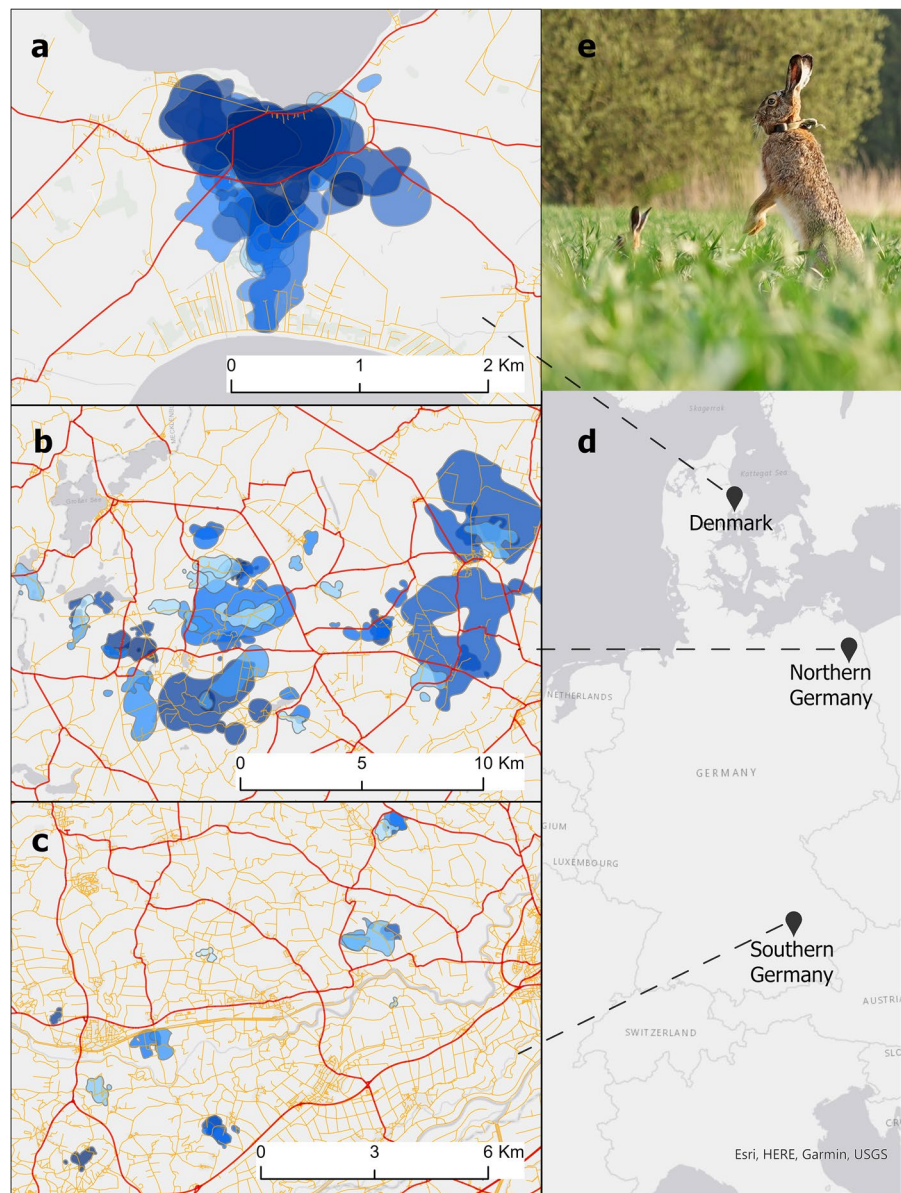
Methods

Study areas and data collection

The study areas were located in (1) Syddjurs community, Midtjylland region, Denmark (hereafter DK), (2) Uckermark, Brandenburg, Germany (hereafter

northern Germany, NG), and (3) Freising district, Bavaria, Germany (hereafter southern Germany, SG; Fig. 1). All three areas mostly consisted of arable fields, tilled with cereals, maize (German areas only), rapeseed, charlock mustard, and to a lesser degree other crops like sugar beet, beans, peas, and clover (Mayer et al. 2018). The rest of the areas mostly consisted of grassland and pastures, forest, and built-up areas. For a detailed description of the study areas see Mayer et al. (2018) and Ullmann et al. (2018). We obtained vector data of agricultural fields for DK (https://kortdata.fvm.dk/download/Index?page=Markblokke_Marker), NG (InVeKoS 2014), and SG (Vermessungsverwaltung 2014). Agricultural fields were significantly smaller in SG (mean \pm SD 4.1 \pm 4.0 ha, median 2.9 ha, range 0.02–29 ha) and DK (mean \pm SD 5.9 \pm 4.2 ha, median 4.6 ha, range 0.01–53 ha) compared to NG (mean \pm SD 19.8 \pm 37.5 ha, median 6.0 ha, range 0.1–521 ha; unpaired Mann–Whitney U tests: $p < 0.001$), whereas there was no statistical difference between SG and DK ($p = 0.434$). Similarly, within-home range habitat diversity was higher in DK (0.24 \pm 0.16) and SG (mean \pm SD: 0.21 \pm 0.16) compared to NG (0.15 \pm 0.19). This difference was significant between DK and NG (unpaired Mann–Whitney U test: $p = 0.007$) and indicated a trend between SG and NG ($p = 0.103$). Habitat diversity was calculated as Simpson's Index of Diversity, $D = 1 - [\sum(n - 1)/N(N - 1)]$ (Hill 1973), where in this context n is the area comprised by each landcover type (see below) and N is the total area (i.e., the home range of individual hares). Average vegetation height varied seasonally (Mayer et al. 2019). Consequently, we defined 4 biologically relevant seasons: (1) spring, vegetation growth period from March to May, (2) pre-harvest, highest vegetation during June to July, (3) post-harvest, mostly harvested fields from August to November, and (4) winter, from December to February. We downloaded vector data of roads from the open source database OpenStreetMap (<https://download.geofabrik.de/europe/>), creating 2 categories: (1) main roads with two or more lanes and intermediate to high traffic burden (motorways, primary, secondary and tertiary roads), and (2) minor (one lane) roads and tracks with low traffic burden (residential roads, service roads, non-paved tracks, etc.). We were unable to obtain exact numbers of traffic burden for the fine-scale resolution of this study.

Fig. 1 The study areas in **a** Denmark, **b** northern Germany, and **c** southern Germany with main (red lines) and minor (orange lines) roads and hare home ranges (blue polygons), estimated as 90% Kernel density isopleths. Different shades of blue represent different individuals. Note that the maps are on different scales and that not all home ranges are shown for hares in southern Germany (three home ranges were located outside the map extend). **d** The location of the study areas. Light grey areas depict land and dark grey water. **e** Two European hares (*Lepus europaeus*), one with a GPS collar, in Denmark. Picture: Martin Mayer



In DK, we captured 28 hares in 2014, 2018, and 2019 using box traps that were set up in pairs along the edges of agricultural fields. Three male hares died during the handling process, likely due to acute stress of handling (Mayer et al. 2021a). We captured 54 hares in NG in 2011, 2014 and 2015, and 24 hares in SG in 2014 and 2015 by driving them into nets (Rühe and Hohmann 2004; Ullmann et al. 2018). Captured hares were transferred into a canvas cone (Denmark) or a wooden box (Germany), where

they were sexed and fitted with a GPS collar (e-obs A1, e-obs GmbH, Gruenwald, Germany) without anesthesia. In DK, GPS units were programmed to record one-hourly GPS positions in 2014 and 2018, and to record one position every 15 min in 2019. In the two German areas, GPSs recorded one-hourly positions while hares were active (mostly during the night), defined by an acceleration threshold, and four-hourly positions when hares were inactive (mostly during daytime) (Ullmann et al. 2018).

Data preparation and statistical analyses

GPS data

We excluded the first four days after capture (including the capture day) to avoid potential bias of the data due to capture effects (Mayer et al. 2021a). This left us with GPS data of 90 individuals (24 in DK: 14 males and 10 females, 47 in NG: 27 males and 20 females, and 19 in SG: 11 males and 8 females). Moreover, we excluded extreme outlying GPS positions based on manual plotting that were obvious GPS errors (e.g., located in the sea). Deleted points comprised < 1% of all locations. Thus, we obtained between 104 and 22,572 usable individual GPS positions (mean \pm SD = 3951 ± 5097 , median = 2730), corresponding to 12,068 tracking days in total (range 6–390; mean \pm SD = 133 ± 85 days). The mean location error of the GPS collars was 5 ± 5 (SD) m (estimated from stationary tests in our Danish study area; unpublished results).

Home range calculation and home range location

We calculated home ranges as 90% kernel utilization distributions (UD) separately for each individual (including all GPS positions) using the R package ‘adehabitatHR’ (Calenge 2006), and using the reference method (h_{ref}) as smoothing parameter (LSCV would have led to an underestimation of home ranges). We then intersected each hares’ home range with the road vector data and calculated the length of all main roads (and all roads combined) within the home range, which was then used to estimate the road density, defined as meter (main) road per ha home range.

To investigate if hares avoid roads when selecting their home range, we shifted individual home ranges (90% UD) by 250 m in 8 different compass directions (N, NE, E, SE, S, SW, W, NW). We chose 250 m because this comparatively short distance simulated a realistic home range shift by individuals without having to remove too many home ranges due to being located in areas known to be unsuitable for hares (this was also the reason why we did not create random home ranges). We excluded shifted home ranges that intersected to > 10% with large water bodies, villages, and towns, because these areas did not constitute hare habitat (water) or we did not conduct

fieldwork there (thus including towns might have potentially biased our results, if hares are present but we did not attempt to capture them there). Further, we excluded shifted home ranges with agricultural land cover that was lower than the minimum observed agricultural land cover in any of the actual hare home ranges separately for each area (e.g., in DK, the lowest proportion of agricultural land within any hare home range was 0.71, which was then used as cut-off value for shifted home ranges). We then intersected the true and the shifted home ranges with roads and land cover, and calculated the road density (m of road per ha home range), the average field size, the proportion of agricultural land, and the number of agricultural fields within each home range. After removing shifted home ranges that were not biologically meaningful, we compared one true home range with (mean \pm SD) 6.5 \pm 1.9 shifted home ranges (range 2–8) per individual. To compare if road density, average field size, proportion of agricultural land, and the number of fields differed between true and shifted home ranges, we used paired Mann–Whitney U tests (due to non-normal data distribution).

Within-home range habitat selection

To investigate within-home range habitat selection, we used step selection functions (SSF) using the R package ‘amt’ (Signer et al. 2019). SSFs enable a realistic comparison of used and available positions by pairing each observed location with a set of random locations deemed accessible from the previously observed location (Thurfjell et al. 2014). To create movement tracks (consisting of steps between consecutive GPS positions), we subsampled tracks to one-hourly positions with a tolerance of 10 min. For the German areas, this might have induced a bias toward active hares (as inactive hares were sampled using a 4-hourly fix rate based on an accelerometer threshold). However, using hourly subsampling resulted in much less data loss compared to 4-hourly subsampling, and the average (\pm SD) time interval between GPS positions (raw data) was 1.42 ± 0.92 h in NG and 1.35 ± 0.87 h in SG, making a bias unlikely. We then created 9 random steps for each observed step using the ‘amt::random_steps’ function. Steps were categorized into day or night (which included dusk and dawn) using the ‘amt::time_of_day’ function, extracted at the end

of each step. For all observed and random steps, we then extracted the following data at the end of each step: land cover type, field size, and the distance to the closest main and minor road. We categorized land cover types of each land patch into (1) arable land, (2) pasture and grassland, (3) forest, (4) built-up area (mostly consisting of farms and holiday houses and their surrounding lawns and gardens), and (5) other land cover, such as mining sites, marshes and bogs (this last category was only present in NG).

We then used resource selection functions comparing used (=1) versus random steps (=0) as response variable using generalized linear mixed models (GLMMs) with a binomial distribution of the R package ‘lme4’ (Bates et al. 2015). We conducted six separate analyses, i.e. separate analyses for daytime and nighttime [because hares are predominantly active at night, dusk and dawn (Schai-Braun et al. 2012)] and for the three study areas (Tables S1, S2). We did this to avoid including higher-order interactions (e.g., time of day \times season \times distance to roads). We included season, land cover type, field size, and distance to main and minor roads as fixed effects, and hare ID as random intercept. To test, if selection for roads changes seasonally, we included the two-way interactions between season and the distance from main and minor roads, respectively. For the distance variables (to main and minor roads), we initially built single effect models testing if the linear, log-transformed or quadratic function fitted the data better (based on Akaike’s Information Criterion corrected for small sample size (AIC_c) (Burnham et al. 2011)). There were no correlations among the fixed effects (all $r < 0.6$) and variance inflation factors < 3 (Zuur et al. 2010). We selected the most parsimonious model based on AIC (Tables S1, S2), by conducting a stepwise backward selection starting from the full model, using the R package ‘MuMIn’ (Barton 2016). If two or more models had AIC values within delta AIC < 2 , we selected the simpler model to avoid retaining overly complicated models (Harrison et al. 2018). Estimated model coefficients that included zero within their 95% confidence interval were considered uninformative (Arnold 2010). Visual validation of the best model was made by plotting residuals against fitted values (Zuur and Ieno 2016).

Road crossings

To estimate road crossings, we created straight-line segments between consecutive GPS positions in ArcGIS Pro 2.8.2 (ESRI, Redlands, CA), and defined road crossings where a segment intersected a road. Initially, we counted the road crossings per day for each individual, and checked if the GPS fix rate had an effect on the number of road crossings. To do so, we subsampled the GPS data of Danish hares, which were sampled at a 15 min fix rate, to hourly positions. We then re-calculated the number of road crossings and compared the daily number of road crossings when sampled at 15 min versus one-hourly positions. We found that hourly GPS positions underestimated the number of daily road crossings by a factor 0.59:1 compared to the 15 min fix rate (mean \pm SD = 1.6 ± 2.0 vs 2.7 ± 3.8 daily road crossings), and consequently used the subsampled hourly data for our analyses to be comparable to the majority of data that was collected using an hourly fix rate. It is unlikely that the 4-hourly fix rate of inactive hares (in Germany only) affected the estimation of road crossings, because GPS units only recorded 4-hourly positions when hares were inactive (i.e. not moving between locations) (Mayer et al. 2018).

We analyzed the number of daily main road crossing (response variable) using GLMMs with a negative binomial response distribution using the R package ‘glmmTMB’ (Magnusson et al. 2017) to correct for overdispersion, non-normal distribution and zero-inflation of the count data (Brooks et al. 2017). We focused on main roads for this analyses, because non-paved roads generally do not present a barrier or a major road kill risk for animals (Roedenbeck and Voser 2008; Collinson et al. 2015). After testing for correlations between fixed effects (Zuur et al. 2010), we found that the number of fields within home ranges and home range size were highly correlated (Pearson rank correlation coefficient $r = 0.98$). Consequently, we included sex, season, home range size, average field size, main road density (within individual home ranges), average step length (calculated separately for each individual and day; as estimate of movement distances) and within-home range habitat diversity (measured as Simpson’s Index of Diversity) as fixed effects, and hare id nested within study area as random intercept. Additionally, we ran the same analysis using GLMMs of the R package ‘spaMM’,

with a Poisson response distribution and a log link, fitting the data with a Matérn correlation model (including the averaged x and y coordinate of each hare's GPS positions as autocorrelated random-slope term) to account for potential spatial autocorrelation (Rousset 2021). This did not affect the results (not shown). To test the assumption that hares are forced to cross main roads more when vegetation is high [thereby excluding hares from these fields; Mayer et al. (2018)] and agricultural field sizes are comparatively larger, we investigated if the probability of main road crossings (segments intersecting main roads = 1 vs segments not intersecting main roads = 0) was affected by the interaction between field size and season, separately for DK and NG (to avoid higher-order interactions). For this we used GLMMs with a negative binomial response distribution to account for overdispersion. Moreover, we accounted for sex, step length, habitat diversity and the main road density as fixed effects and hare id as random intercept. We had too little data for SG to conduct this analysis (see results). Finally, after we detected that the number and probability of daily road crossings was best explained by step length (see results), we ran an additional analysis investigating what affected step length (log-transformed response variable), using GLMMs with a Gaussian response. We included sex, season, home range size, field size, main road density, habitat diversity, and the two-way interaction of season and field size as fixed effects, and hare id nested within study area as random intercept. Model selection and validation was conducted the same way as for the habitat selection analysis (see above).

Results

Location of home ranges

Of the 90 hares, the home ranges (90% UD) of 44 individuals (48%) intersected main roads; 20 in DK (out of 24 individuals; 80%), 21 in NG (of 47 individuals; 45%), and 3 in SG (of 19 individuals; 18%). Apart from 5 individuals (2 in DK, 2 in NG, and 1 in SG), all hare home ranges intersected minor roads. Average home range sizes in NG [$187 \pm (\text{SD}) 314$ ha] were 8.1-fold and 5.8-fold, respectively, larger compared to SG (23 ± 15 ha) and DK (32 ± 19 ha). Main road density in the entire study area was 22.3 m/ha

in DK, 5.1 m/ha in NG, and 7.3 m/ha in SG. Main road density was significantly higher in shifted compared to true home ranges in DK (23.3 ± 17.6 vs 15.5 ± 11.7 m/ha; Mann–Whitney U test: $W = 1129$, $p = 0.046$) and SG (8.0 ± 12.5 vs 1.2 ± 3.3 m/ha; $W = 713$, $p = 0.032$), but not in NG (3.9 ± 5.5 vs 4.1 ± 6.2 m/ha; $W = 8633$, $p = 0.814$; Fig. 2). This general pattern was also true when investigated for all roads (Fig. 2; Table 1). There was no statistically significant difference regarding the number of agricultural fields, average field size, and the proportion

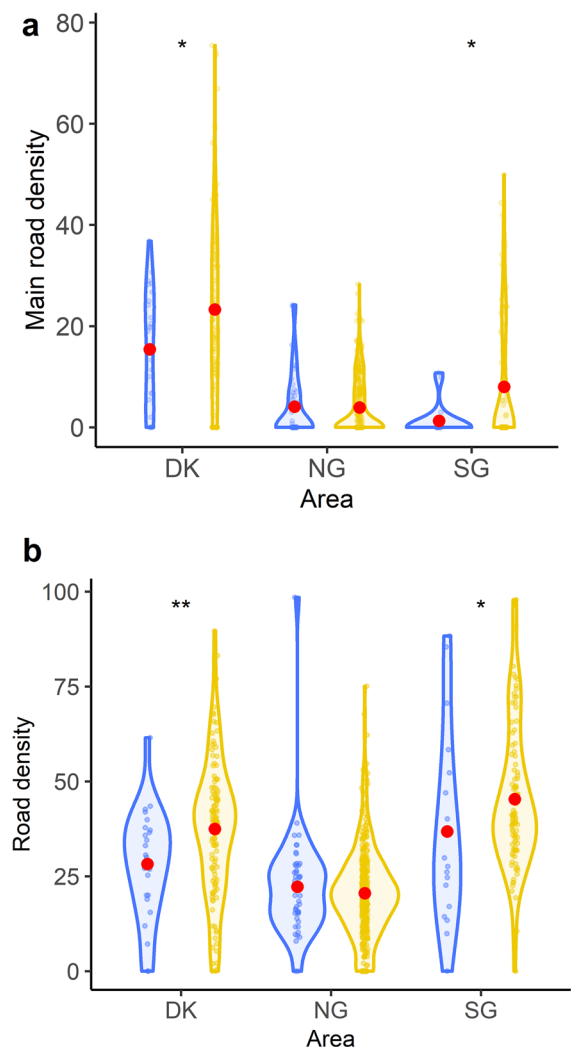


Fig. 2 Violin plots depicting the density of **a** main roads and **b** all roads inside true (blue) and shifted (by 250 m; yellow) European hare home ranges separately for the three study areas. Small dots show the raw data and large red dots show the mean for each group

Table 1 Showing the mean \pm SD of the main road density (m road/ha home range), road density of all roads, number of agricultural fields, average field area (in ha), and proportion of agricultural land separately for true and shifted home ranges (90% Kernel Density Estimates) of European hares (*Lepus europaeus*) in Denmark (DK), northern Germany (NG), and southern Germany (SG). Differences in the aforementioned variables were investigated using a Mann–Whitney U test, and significant differences are shown in bold

Area	Variable	Mean \pm SD in true home range	Mean \pm SD in shifted home range	W	P
DK	Main road density	15.39 \pm 11.7	23.3 \pm 17.59	1130	0.046
DK	Road density (all roads)	28.21 \pm 14.34	37.47 \pm 17.68	998	0.008
DK	Number of fields	40.68 \pm 20.36	38.5 \pm 21.74	1632	0.538
DK	Average field area	1.73 \pm 0.44	2.06 \pm 0.88	1178	0.083
DK	Proportion agricultural land	0.87 \pm 0.07	0.86 \pm 0.05	1847	0.083
NG	Main road density	4.06 \pm 6.24	3.91 \pm 5.47	8433	0.814
NG	Road density (all roads)	22.25 \pm 14.52	20.55 \pm 11.5	9083	0.532
NG	Number of fields	46.64 \pm 72.71	46.48 \pm 72.02	8449	0.775
NG	Average field area	19.72 \pm 13.49	19.8 \pm 14.71	8963	0.708
NG	Proportion agricultural land	0.79 \pm 0.25	0.79 \pm 0.23	9045	0.631
SG	Main road density	1.24 \pm 3.27	7.96 \pm 12.52	713	0.032
SG	Road density (all roads)	36.82 \pm 24.83	45.31 \pm 18.87	685	0.043
SG	Number of fields	17.32 \pm 10.65	19.74 \pm 9.86	778	0.174
SG	Average field area	2.89 \pm 0.88	3.13 \pm 1.12	869	0.478
SG	Proportion agricultural land	0.91 \pm 0.1	0.91 \pm 0.05	1148	0.203

of agricultural land between true *versus* shifted home ranges in any study area (all $p > 0.08$; Table 1).

Habitat selection

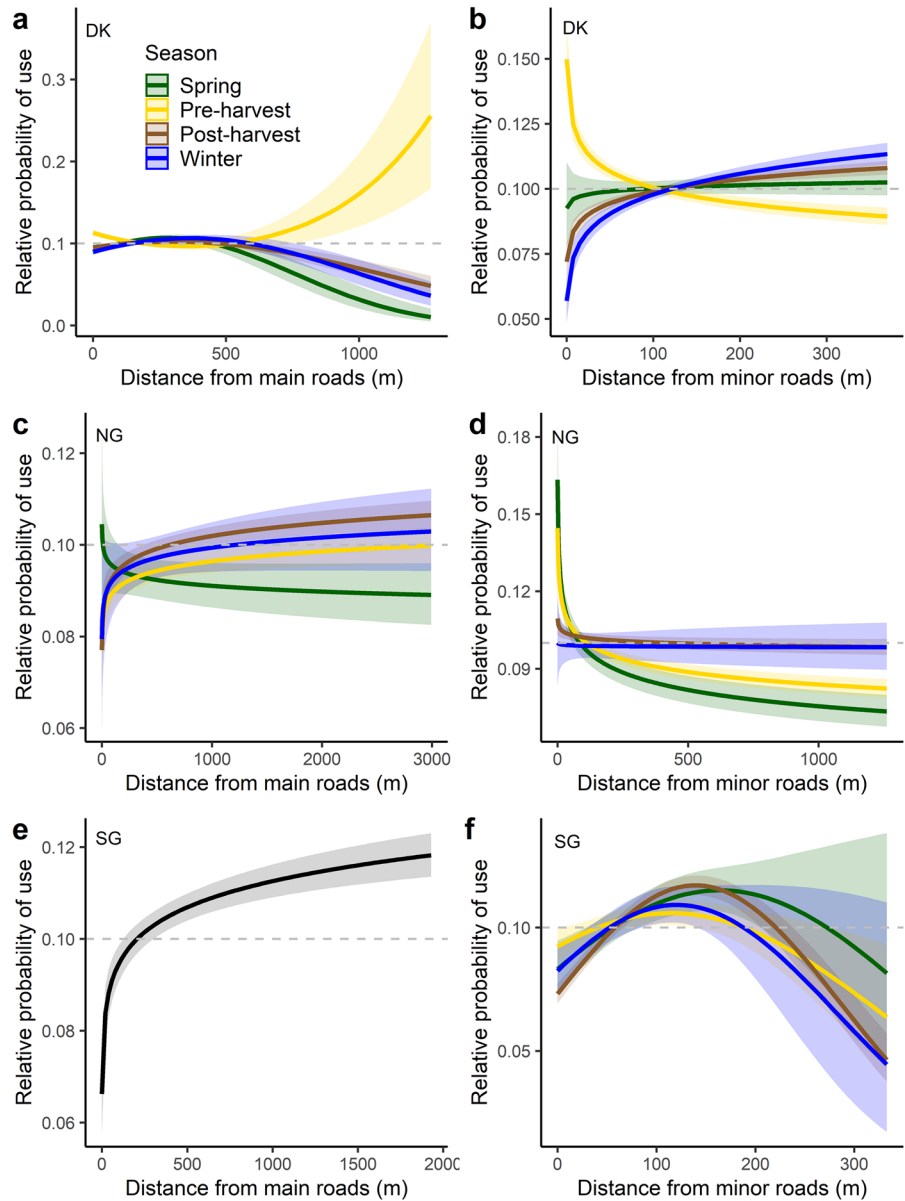
In DK, the selection for proximity to roads by hares during nighttime, dusk and dawn (their principal activity period) changed seasonally. During pre-harvest, when vegetation was highest, hares selected for proximity (< 100 m; though this effect was small) and for longer distances to main roads (> 500 m) (Fig. 3a). There was no clear avoidance or selection for proximity to main roads during the rest of the year, but hares avoided longer distances (> 500 m) to main roads (Fig. 3a; Table S3). Hares selected for proximity to minor roads during pre-harvest, showed no selection or avoidance during spring, and avoided proximity to minor roads post-harvest and during winter (Fig. 3b; Table S3). During daytime (when hares were mostly inactive), hares avoided both main and minor roads independent of the season (Table S3; Fig. S1). Moreover, independent of activity period, hares selected for comparatively smaller fields and cropland, and avoided grassland, forest and built-up areas (Table S3).

In NG, hares avoided proximity to main roads pre- and post-harvest during both day and nighttime, and showed no clear selection or avoidance

of main roads during spring and winter (Fig. 3c; Table S3). In contrast to main roads, during nighttime hares strongly selected for proximity to minor roads during spring and pre-harvest, and to a lesser degree post-harvest, but showed no selection or avoidance in winter (Fig. 3d). Similarly, during daytime hares selected for proximity to minor roads during spring and pre-harvest, but neither selected nor avoided them post-harvest and winter (Table S3; Fig. S2). Hares selected for comparatively smaller fields and grassland, used cropland according to availability, and avoided forest during both activity periods (Table S3). During nighttime, hares showed no selection or avoidance for other areas (mostly mining sites, marshes and bogs), whereas during the day, hares selected for them (Table S3).

In SG, hares avoided proximity to main roads (< 50 – 100 m) during both day and nighttime, independent of the season (Fig. 3e, S3; Table S3). Moreover, both active and inactive hares selected for intermediate distances (80–200 m) from minor roads (Fig. 3f, S3; Table S3). Avoidance of proximity to minor roads was strongest for inactive hares during winter (Fig. S3; Table S3). Finally, hares selected for smaller fields, grassland and cropland, and avoided forest during both day and nighttime (Table S3).

Fig. 3 Within-home range habitat selection depicted as the relative probability of use (based on logistic regression analyses of used and random steps created using step-selection functions) of the proximity to main (left panel) and minor (right panel) roads by European hares during nighttime, dusk and dawn in Denmark (a, b), Northern Germany (c, d), and Southern Germany (e, f). Values > 0.1 (above the grey dashed line) indicate selection, whereas values < 0.1 indicate avoidance. The 95% confidence intervals are given as shading



Road crossings

We recorded a total of 6554 main road crossings during 12,068 observation days for all 90 individuals. When only considering the 44 hares whose home ranges (90% UD) intersected main roads, we recorded 6412 main road crossings (4765 in DK, 1619 in NG, and 28 in SG) during 6145 observation days. Individuals crossed main roads mostly during their activity time between dusk and dawn (Fig. 4a–b). This pattern was absent in SG, because we only observed 28

main road crossings by the three individuals whose home ranges intersected main roads. Hares generally moved greater distances in NG compared to SG and DK (Fig. 4b–c).

Of the 44 hares whose home ranges intersected main roads, individuals crossed main roads on average 0.8 ± 1.4 (SD) times per day, with the number of daily road crossings being highest in DK (1.2 ± 1.6), followed by NG (0.7 ± 1.7), and lowest in SG (0.1 ± 0.3). The number of daily main road crossings increased with average step length and main

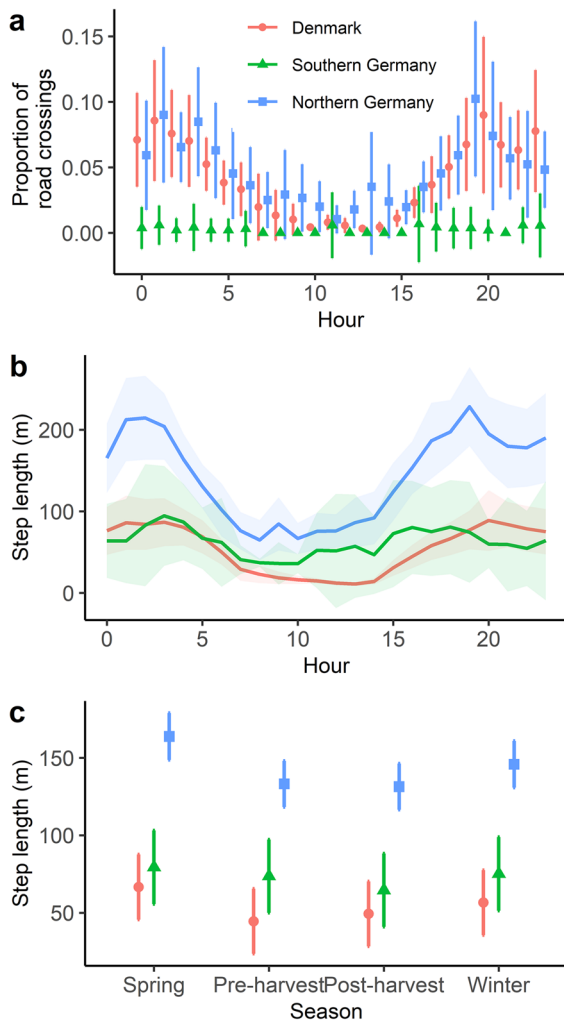


Fig. 4 **a** The probability of main road crossings by hares separately for each hour of the day, calculated as the number of segments that intersected a main road compared to all segments in a given hour (estimated separately for each individual). And the step length, calculated as straight-line distance between consecutive hourly GPS positions, in relation to the **b** time of the day and **c** season. The 95% confidence intervals are given as bars (**a**, **c**) or shading (**b**)

road density within an individuals' home range, and hares crossed roads less often pre-harvest compared to the other times of the year (though this effect was small; Fig. 5a; Tables S4, S5). Home range size was included in the best model but uninformative, and sex, average field size and habitat diversity were not included in the best model.

The probability of main road crossings by hares in DK increased with field size in spring, whereas

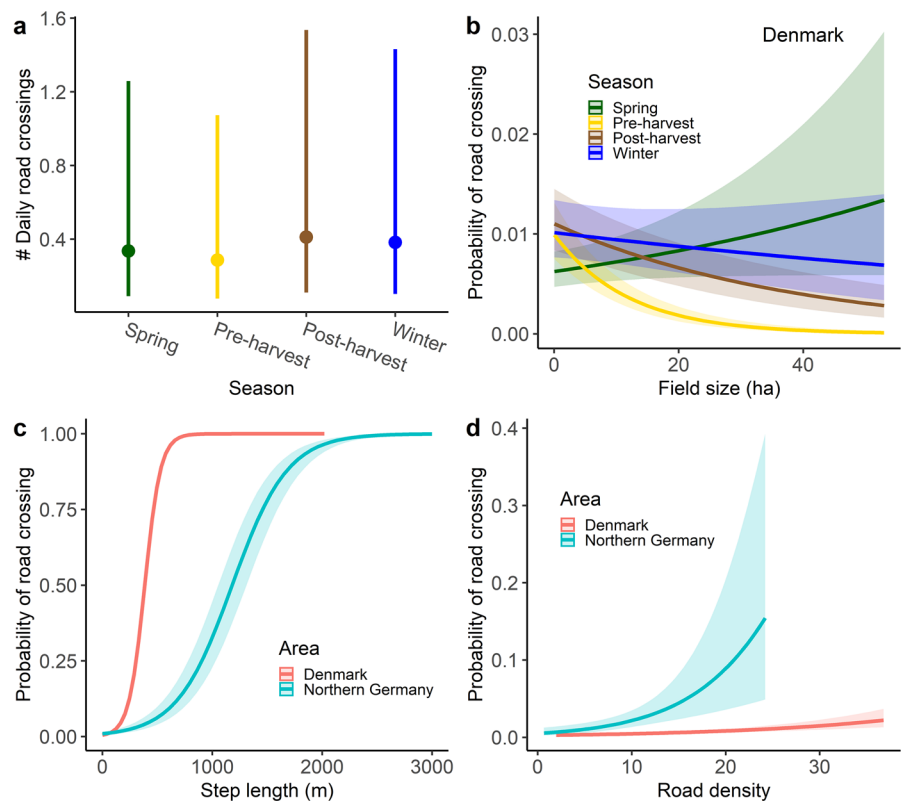
it decreased with increasing field size during pre-harvest (when vegetation was highest) and to a lesser degree post-harvest and in winter (Fig. 5b; Table S6). Moreover, main road crossing probability by hares in DK increased with step length and (to a smaller degree) main road density within the hares' home range (Fig. 5c–d). Sex and habitat diversity were not included in the best model. The probability of main road crossings by hares in NG increased with step length and main road density within the hares' home range (Fig. 5c–d) and was higher in spring compared to the rest of the year (Table S6). Sex, habitat diversity, field size and the interaction between season and field size were not included in the best model. The sample size was too small to conduct this analysis for SG. In DK, of 9 individuals with known cause of mortality, 3 (33%) were killed by a car when crossing roads. In Germany, we did not record the fate of individuals (hares were not monitored regularly there and data downloaded via base stations).

Variation in step length (analyzed across study areas) was best explained by the full model (Table S7). Hares moved greater distances with increasing field size, habitat diversity, home range size and main road density (Fig. 6a–d; Table S7). Males moved greater distances than females (Table S7). The interaction of season \times field size was included in the best model, but 95% confidence intervals largely overlapped (Fig. 6a).

Discussion

Our results support the hypothesis that more homogeneous landscapes increase the space use requirements of animals, which leads to increased probability of road crossings (after accounting for road density). In DK and SG, where landscape composition was more heterogeneous compared to NG, hare home ranges had a lower road density than in the surrounding area (whereas habitat structure was unchanged), suggesting that hares avoided establishing home ranges in areas with comparatively higher road densities. Conversely, in NG, where agricultural fields were substantially larger, hares established home ranges in areas with similar road density than the surrounding areas, likely because space use requirements prevented them from avoiding roads. This emphasizes that simple landscapes with seasonally varying

Fig. 5 The predicted effect of **a** season on the number of main road crossings per day (across study areas). **b** The predicted probability of crossing a main road for hares in Denmark in relation to field size and season. Moreover, the predicted probability of main road crossings in relation to the **c** step length and **d** road density (m road per ha) within an individual's home range separately for hares in Denmark and Northern Germany. Bars (**a**) and shadings (**b–d**) depict 95% confidence intervals



resource availability increase space use requirements by hares compared to more complex landscapes (Ullmann et al. 2018), which might lead to increased energy expenditure due to increased movements and increased mortality risk due to frequent road crossings.

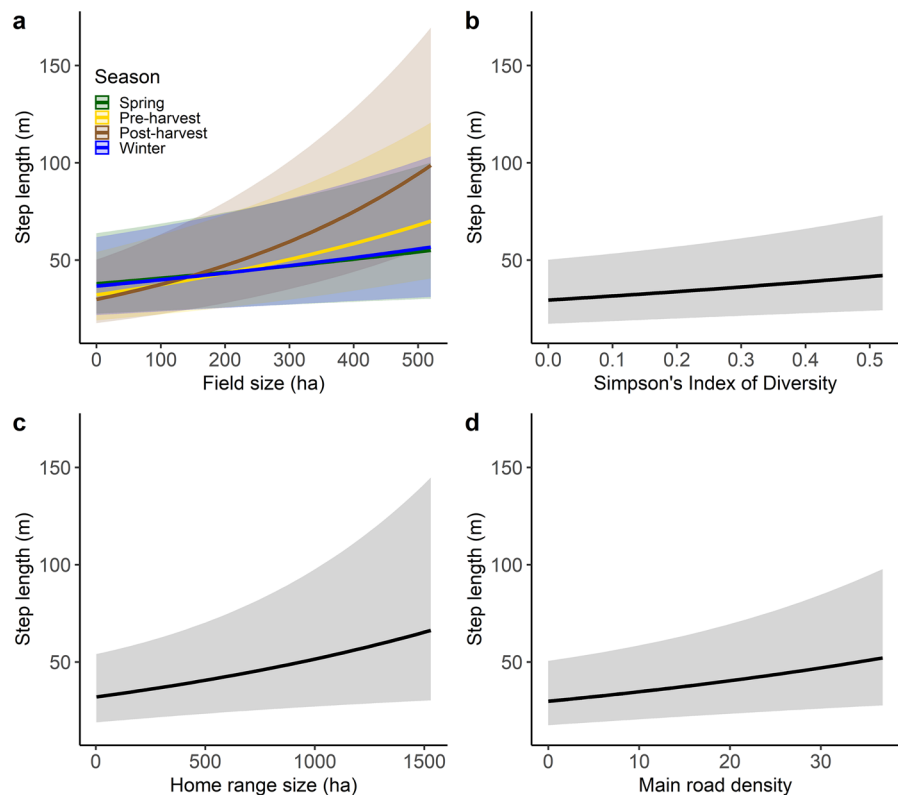
Habitat selection

Broadly, our results suggest that hares generally avoid main roads (or show no selection), and that they select for minor roads during the vegetation growth seasons, when crops were of poor food quality for hares and high vegetation was generally avoided (Mayer et al. 2018, 2019). This effect was more pronounced in areas with comparatively more homogenous habitat structure (NG). Thus, road type, as well as habitat structure, are important to consider when investigating effects of roads on animal movement (Roedenbeck and Voser 2008; Meisingset et al. 2013; Ouédraogo et al. 2020). In SG, seasonal changes had little effect on the selection for proximity to roads (with proximity generally

being avoided), probably because hares had smaller home ranges compared to the other two study areas, providing sufficient resources year-round (Ullmann et al. 2018; Mayer et al. 2019). Moreover, as hares in SG avoided establishing home ranges in areas that intersected main roads, this variable had comparatively little effect on their habitat selection.

Apart from inhibiting movement and causing direct mortality via vehicle collisions (Hell et al. 2005), main roads might also be a disturbance factor for hares and other wildlife, due to high traffic volumes, noise and light pollution. Additionally, it is possible that hares can evaluate the relative risk in relation to road type, and that proximity to main roads did not offer foraging opportunities. Independent of the cause and mechanism of road avoidance, our findings indicate that main roads potentially create barrier effects, as shown in other studies on hares (Roedenbeck and Voser 2008) and other mammals (Prokopenko et al. 2017; Scraftford et al. 2018; Carricondo-Sanchez et al. 2020). This might have consequences for the long-term viability of animal populations, if roads create dispersal

Fig. 6 The predicted effect of **a** the interaction of season and field size, **b** Simpson's Index of Diversity (as measure of within-home range habitat heterogeneity) **c** home range size and **d** main road density (m road per ha) on the step length of hares (analyzed across study areas). Shadings depict 95% confidence intervals



barriers leading to population fragmentation and genetic isolation (Dyer et al. 2002). However, this is likely not the case for hares and other small mammals that can adapt to areas with high road densities (Fey et al. 2016; Mayer and Sunde 2020).

The selection for proximity to minor roads during spring and pre-harvest by hares in DK and NG was likely related to the availability of high-quality forage, such as grasses and herbs along road verges (Jakobsson et al. 2018), whereas agricultural fields provide little high-quality food pre-harvest (Mayer et al. 2019). In line with the hypothesis that minor roads provide favorable foraging conditions, Roedenbeck and Voser (2008) showed that the density of unpaved field tracks had a positive effect on hare abundance in Switzerland. In addition, minor roads might also serve as movement corridors during spring and pre-harvest, when vegetation on agricultural fields is high. Similar to our study, Barbary macaques (*Macaca sylvanus*) showed seasonal selection for roads, avoiding roads in spring when natural food was abundant, and approaching

roads in fall and winter, as natural food availability declined and food provisioning by tourists increased (Waterman et al. 2020). This shows that animals can seasonally exploit human infrastructure to meet their biological needs. The selection/avoidance of larger distances to both main and minor roads is harder to explain in biological terms, and was probably related to other factors, such as correlation with land cover variables at large distances from roads or to the fact that comparatively few GPS positions were very far from roads (leading to biases).

Concerning habitat structure, hares generally selected for cropland and comparatively smaller fields, and avoided forests and built-up areas. A discussion of these patterns can be found elsewhere (Tapper and Barnes 1986; Roedenbeck and Voser 2008; Petrovan et al. 2013; Mayer et al. 2018). Differences in habitat selection among the study areas might also have been driven by factors not measured here, such as geographic variation in weather, predator densities, and agricultural practices. Moreover, spatio-temporal differences in traffic density (which

we could not quantify on the relevant scale) might have affected differences in habitat selection and the number of road crossings among study areas.

Main road crossings

Hares mainly crossed roads during their usual activity time, during the night, dusk and dawn, which coincided with typically lower traffic volumes (Mayer et al. 2021b), and lower human activity in general. Unsurprisingly, the road density within an individual's home range positively correlated with the number of road crossings in all study areas, which might affect the probability of animal road mortality. Importantly, within home range increases in road density led to much stronger increases in road crossings by hares in NG compared to hares in DK (this could not be assessed for SG due to a limited sample size). More generally, hares that moved comparatively larger distances crossed roads more often, and movement distances were strongly affected by agricultural field size (hares in NG had > 1.6-fold larger step lengths compared to DK and SG) and to a smaller degree habitat diversity. This suggests that animals in comparatively more heterogeneous landscapes are better able to adjust their habitat selection to avoid main roads than animals inhabiting simpler landscapes, because the latter force them to move larger distances to meet their energetic needs.

Consequently, simple landscapes might exacerbate potentially negative effects of main roads if more road crossings translate to increased risk of road mortality. For example, in DK, where road density was highest, a third of the hare mortality was caused by collisions with a vehicle, providing some evidence that road mortality constitutes a significant mortality cause. In a Slovakian study, road-killed hares represented on average 15.5% of the annual hunting bag, and in some instances as much as 75% (Hell et al. 2005). However, Roedenbeck and Voser (2008) could not show an effect of road density on road mortality rates, a pattern that might be mitigated by fine-scale habitat selection of hares. Although increased road density might have negative consequences for some animal populations (Fahrig and Rytwinski 2009), this is not necessarily the case (Kroeger et al. 2021), and road density can actually have positive impacts on species abundance in some cases due to reduced predation (Rytwinski and Fahrig 2013).

Main road crossings also changed seasonally, with hares crossing roads more often during spring and pre-harvest. During spring, this pattern was related to increased movement distances, which was likely linked to the peak mating season during spring. The finding that hares crossed roads less often pre-harvest compared to the rest of the year was in contrast to our prediction that hares move more between fragments of shorter vegetation (such as roadsides) while being excluded from areas with higher vegetation (e.g., cereals) pre-harvest (Mayer et al. 2018). While hares likely still were excluded from areas with high vegetation pre-harvest, this probably created a barrier effect, leading to fewer road crossings.

Conclusions

Overall, our findings suggest that the presence of high-quality habitat (here measured as comparatively smaller field size), providing resources throughout the year, will allow animals to establish smaller home ranges that do not intersect main roads, and reduce the number of road crossings, consequently reducing the risk of road mortality. Nevertheless, hares in DK, where road density was highest, conducted comparatively more road crossings than in the two German areas, emphasizing that increasing road density will affect the likelihood of animals crossing roads and consequently, the risk of being killed by vehicles. Our findings further highlight that it is important to distinguish between road types, as different roads can have different impacts on animals (e.g., small roads providing foraging opportunities via roadside vegetation and large roads being consistently avoided with the potential to act as barriers).

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Author contributions PS and NB acquired funding. MM conceived the study, CF, MM, and WU conducted fieldwork and prepared the data. MM conducted the statistical analyses and wrote the first draft of the manuscript. All authors critically contributed to manuscript drafts and revisions and read and approved the final manuscript.

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Data availability Data is available via the online repository Figshare <https://doi.org/10.6084/m9.figshare.21517884.v1>.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

Ethical approval In Germany, all procedures for the research were obtained in accordance with the Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and approved by the local nature conservation authority (reference number LUGV V3-2347-22-2013 and 55.2-1-54-2532-229-13). In Denmark, animal captures and handling were approved by the Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and the local nature conservation authority (reference number LUGV V3-2347-22-2013 and 55.2-1-54-2532-229-13). Fieldwork was always conducted with permission from the local landowners. All methods were carried out in accordance with relevant guidelines and regulations, complying with the ASAB/ABS Guidelines for the treatment of animals in behavioral research and teaching and with the ARRIVE guidelines.

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