

Analysis of roe deer (*Capreolus capreolus*) vehicle collisions in Lower Bavaria including the Bavarian Forest National and Nature Park

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Abstract

Densely populated regions such as Europe face dramatically increasing numbers of wildlife-vehicle collisions due to growing animal populations, traffic volume, and vehicle speeds. Identifying temporal and geographical collision hotspots can help mitigate wildlife-vehicle collisions (WVCs) and improve animal welfare and human safety. In this study, an analysis of roe deer (*Capreolus capreolus*)-vehicle collisions (RDVCs) throughout Lower Bavaria, the Bavarian Forest Nature Park (BFNatP) and the Bavarian Forest National Park (BFNP) reveals ultradian, circannual, and geographical hotspots. The highest density of RDVCs occurs in May, followed by the short but intense rutting season in August and a third, longer-lasting peak from September until November. Spring and fall migration and the dispersal of young roe deer greatly influence the annual patterns of RDVCs. The diurnal RDVC-distribution could be linked to the crepuscular activity patterns of roe deer, with the short temporal periods of dusk and dawn accounting for 55% of all RDVCs. In the BFNatP, federal roads have the highest relative number of RDVCs per kilometer followed by secondary roads. High-risk areas for RDVCs were identified in grassland patches within densely forested areas and in forest patches within grassland areas. Our results demonstrate that geographical analyses can help reveal vehicle collision hotspots and form the basis for mitigation measures.

Key words: wildlife-vehicle collisions, kernel density estimation, roe deer, temporal and spatial accident hotspots, Bavarian Forest National Park

INTRODUCTION

Habitat loss and the fragmentation of natural habitats are the most important factors of worldwide biodiversity loss (SALA et al. 2000, LESBARRÈRES & FAHRIG 2012). Protected areas such as the Bavarian Forest National Park (BFNP) and the Bavarian Forest Nature Park (BFNatP) in southeast Germany are essential in preventing both the extinction of species (BÄSSLER et al. 2011) and the loss of the ecosystem functions they perform (TILMAN et al.

2006). Extension of the road network is a major conservation concern, as roads contribute to reduced gene flow within and between populations (HOLDEREGGER & DI GIULIO 2010, CEIA-HASSE et al. 2018) through habitat fragmentation and direct mortality through wildlife-vehicle-collisions (WVCs) (D'AMICO et al. 2015, ÖZCAN & ÖZKAZANC 2017). Each year, roughly one million deer in the USA and another million in Europe are killed in WVCs (CONOVER et al. 1995, LANGBEIN et al. 2010). In Germany, wildlife-vehicle collisions cause injury to 2 500 people and 20 fatalities yearly (ADAC 2019), in the USA, WVCs are responsible for 100–200 deaths (RONDEAU & CONRAD 2003).

The density and distribution of deer species in Germany and Europe have increased considerably in recent decades (APOLLONIO et al. 2010). The associated increase in WVCs has led to enormous economic loss (GROOT-BRUIDERINK & HAZEBROEK 1996). According to the ASSOCIATION of GERMAN INSURANCES (2018), in 2017 ~275 000 (~200 000 due to roe deer) reported WVCs occurred on roads throughout Germany, resulting in a loss of ~744 million Euro.

Across Germany, roe deer account for up to 85% of all recorded WVCs (HOTHORN et al. 2012). Roughly 200 000 roe deer are killed every year by vehicle collisions, which correspond to ~20% of the total roe deer shot by hunters in Germany (HOTHORN et al. 2012). On average, nearly 23 roe deer are killed per hour in vehicle collisions in Germany. As most accidents in the BFNatP and the BFNP involve roe deer (GERMAN HUNTING ASSOCIATION 2021), we focused our study on this omnipresent cervid species.

Research has shown the strong impact of animal circannual and ultradian activity rhythms on WVCs (GROOT-BRUIDERINK & HAZEBROEK 1996, STEINER et al. 2014, KUŠTA et al. 2015, IGNATAVICIUS & VALSKYS 2017). Animal circannual activity rhythms follow the changing seasons and the accompanying changes in climate, vegetation, and food resources (KAPPELER 2012). They can be studied using large data sets containing high-quality data. The availability of data sets covering periods over 10 years has enabled precise temporal movement analyses of many animal species, including those involved in WVCs. Studies of animal circannual rhythms can provide information on their activity patterns and the effect of human disturbance (KROP-BENESCH et al. 2013). Previous studies have shown that roe deer temporal behavior reflects adaptations to environmental changes (REMMERT 1969) and is decisive for their survival (DE COURSEY 2004, KAPPELER 2012). Ultradian activity rhythms are cycles that repeat within 24 hours and often uniquely depend on physiological processes (SCHEIBE et al. 2001). European roe deer exhibit highly species-specific activity patterns devoted to foraging and rumination on an ultradian scale (TURNER 1979, SCHEIBE et al. 1999, KROP-BENESCH et al. 2013). Although roe deer were originally diurnal, they have in part become nocturnal with peaks of activity during dusk and dawn (GUTHÖRL 1994, WIESMAYR et al. 2005) due to the increased anthropogenic disturbance of the last decades (KURT 1991, BERGER et al. 2003). Consequently, roe deer-vehicle collisions (RDVCs) have increased considerably during dusk and dawn (STEINER et al. 2014).

NELLI et al. (2018) showed that deer-vehicle accidents are more likely to occur in forested areas, but there have been few studies focused on densely forested areas such as the BFNatP (up to 50% woodland). Roads in the BFNatP and the BFNP increase habitat fragmentation and animals' mortality due to WVCs. Identifying potential geographical WVC-hotspots could be important for reducing the number of accidents, improving the stability of wildlife populations, the welfare of both animals and humans, and reducing the associated economic burden.

In our study, we first focus on time-based correlations of the number of RDVCs over the year concerning activity patterns, mating season, and breeding season of roe deer and secondly determine whether RDVCs correlated with moon phase and annual time shifts from winter to summer. Furthermore, we visually analyzed the geographical patterns of those RDVCs as a function of the predominant land use classes.

Specifically, we predict:

- 1) A higher collision risk during dusk and dawn and a strong variation in RDVCs throughout the year depending on the annual cycle of roe deer and changes in abiotic factors.
- 2) A predominance of RDVC hotspots in areas with a high edge density because we expect higher roe deer densities and movement at the edge between forests and open areas.

MATERIALS AND METHODS

Study area



Fig. 1. Overview of the BFNatP. It covers the administrative districts of Regen and Freyung-Grafenau, Straubing-Bogen, and Deggendorf north of the Danube River, excluding the BFNP. The center of the Bavarian Forest Nature Park is characterized by hills and mountain ridges such that the main land uses are dairy farming and forestry. The forested part of the strictly protected Bavarian Forest National Park amounts to 98% and it mostly consists of mixed mountain forest. 2% are open-raised bogs, abandoned mountain pastures, water bodies, or boulder fields (HEURICH et al. 2010). The state border with the Czech Republic, including the Šumava National Park forms the border on the northeast side.

Our study was conducted in Lower Bavaria (10 325 km²) with a focus on the BFNatP (3 036 km²) and the adjacent BFNP (245 km²). The altitude of the road infrastructure ranges from 300 to 1 118 m a.s.l. The BFNatP consists primarily of nature and landscape protection areas and hosts a large diversity of species and biotopes. Together with the Bavarian Forest National Park, Šumava National Park and the Šumava Landscape Protected Area (Czech Republic), this region forms the largest strictly protected continuous forest expanse in Central Europe, the so-called Bohemian Forest Ecosystem, with a population density of approximately 70 residents/km² in Germany but significantly lower in the Czech Republic (PODOLSKI et al. 2013). A continental climate prevails, with a slight maritime influence from the west. Annual precipitation ranges from 400 mm in the valleys to 2 500 mm along the mountain ridges. In the valleys of the Inner Bavarian Forest the landscape is mainly dominated by meadows and forest. Large mammals in the BFNP and BFNatP include the herbivores roe deer, wild boar (*Sus scrofa*), and red deer (*Cervus elaphus*) and the carnivores Eurasian lynx (*Lynx lynx*) (HEURICH et al. 2018) and grey wolf (*Canis lupus*) (STIEGLER et al. 2020).

Data

Data was collected over ten years by the Bavarian police and documented 92 924 GPS-referenced RDVCs throughout Lower Bavaria and 21 084 across the BFNatP, including the BFNP with 203 RDVCs. In Bavaria, accidents involving wild animals of any kind must be reported to the police, which is required by the insurance, before damage compensation to the vehicle owners is granted. In addition to the date, exact time of the accident, and species involved (European hare (*Lepus europaeus*), deer (not further differentiated), European badger (*Meles meles*), red fox (*Vulpes vulpes*), wild boar, and birds) are noted. From 2009 some of the data have also included GPS positions; since 2011 all the data have GPS positions. The precision inaccuracy of the GPS positions is estimated to be within a maximum of 200 m; by contrast, the time and date information are very accurately recorded.

Roe and red deer are not differentiated in the analyzed dataset. However, we assume this did not compromise our analyses focused on the omnipresent roe deer. In fact, the more recent WVC statistical report 2019/20 for Bavaria differentiated between deer species and listed 720 red deer vehicle collisions (1.4%) compared to 53 180 roe deer vehicle collisions (GERMAN HUNTING ASSOCIATION 2021). Although there is an established red deer population in the BFNP (LUDWIG et al. 2012, HEURICH et al. 2015), hunting management ensures that red deer are almost totally absent in the BFNatP and Lower Bavaria to avoid high browsing damages in commercial forests and agricultural land.

To enable direct comparisons of the number of accidents within the BFNP- and BFNatP and to take into consideration that the radius of animals' movement (migration and dispersal) varies, we defined a 5 km buffer zone surrounding and including the BFNP (BFNP*: 2 476 accidents). We also conducted a geographical hotspot analysis to collect data on the spatial clustering of RDVCs (BİL et al. 2015).

In general, accidents caused by wildlife can occur:

- a) due to a direct collision between the animal and the vehicle,
- b) when the driver tries to avoid a collision with an animal and instead hits another object (e.g., a pole, a nearby tree or an oncoming car).

Thus, not all accidents result in the death of the involved animal. However, in cases of direct collisions between animals and vehicles (subitem a), most of the animals die from their injuries sometime later. However, the place of the animals' death did not affect our analysis as we were interested in identifying wildlife accident-sites. Accordingly, the spatial accuracy of the crossing site, including the probability of future crossings, was of primary interest.

Temporal analysis

The circannual and ultradian distribution of RDVC events were analyzed based on the interpretation of scatter diagrams. The circannual patterns were represented descriptively by line diagrams. Because circannual trends occurring over longer periods are clearly visible and consequently more robust in pattern analyses, all accidents relating to roe deer that had taken place over 10 years were used for this calculation.

To represent daylight phases of RDVCs, we calculated the sun angle at each georeferenced and timestamped RDVC-site using the function `sunAngle()` from the R package 'oce' (version 1.1-1). Regarding the diurnal RDVC distribution, the four different periods were defined and calculated as follows: night (solar angle $\leq -18^\circ$), day (solar angle $\geq 0^\circ$), and dusk and dawn (civil twilight: solar angle $> -6^\circ$ and $< 0^\circ$, nautical twilight: solar angle $> -12^\circ$ and $\leq -6^\circ$, astronomical twilight: solar angle $> -18^\circ$ and $\leq -12^\circ$). The solar angle in Bavaria varies during the year and has daily changes in winter from 18° to -64° (21st of December, shortest day of the year) and in summer from -18° to 64° (21st of June, longest day of the year) (HOFFMANN 2023).

Moon phases were calculated for each RDVC-site with the function `getMoonIllumination()` (available in the R package 'suncalc' (version 0.5.0)). They vary from 0.0 to 1.0 as follows: 0: new moon (waxing crescent), 0.25: first quarter (waxing gibbous), 0.5: full moon (waning gibbous), 0.75: last quarter (waning crescent). All RDVCs were grouped in terms of their occurrence during new moon, rising moon, full moon, and waning moon phase.

Spatial analyses

All spatial analyses were conducted using ArcGIS Pro (ArcGIS Pro, version 2.5.0). High-resolution OpenStreetMap (OSM) data for Lower Bavaria was downloaded from GEOFABRIK (2021). Road length was calculated using Python-code [`!shape.length @meters!`].

As roads are stored as polylines, we used 10 m road-buffer (diameter = 20 m) for intersecting the different road categories and the RDVCs. Due to slight overlap issues in our 10 m road buffer at road crossings or bridged intersections, road categorization was subject to a low-precision error. Therefore accidents were excluded due to intersection errors/exclusion (~9.5%). We considered paved and public roads that represent a significant risk for roe deer, namely: motorways (i.e. major divided highways); federal (i.e. national roads often link larger towns); secondary (i.e. regional roads often link towns); tertiary (i.e. local roads often link smaller towns and villages).

The kernel function in ArcGIS Pro (function: kernel density, population field: none, output cell size: 10, search radius/bandwidth: 400, symbology: equal interval, 5 classes) was used to calculate roe deer-vehicle collision hotspots. Kernel density estimation (KDE) is a non-parametric method to estimate the probability density function of a random variable.

It takes the form of a fundamental data-smoothing possibility in which inferences about the population are made based on a finite data sample (GUIDOUM 2015).

Land cover was derived from Corine Land Cover 2015 (PFLUGMACHER et al. 2018) among the best available European open-source land cover datasets. The classification of land cover classes across Europe was based on Landsat-8 data acquired over three years (2014–2016). The pixel cells have a spatial resolution of 30×30 m and were produced using Landsat imagery.

Statistical analysis

We performed one-way Analysis of Variance (ANOVA) (FISHER 1918, 1925) to infer whether the amount of roe deer-vehicle collisions significantly differed across days of the week, times of the day, moon phases and road categories. ANOVA allows for testing differences between groups and whether dividing the data into groups reduces unexplained variability (DORMANN 2020). We grouped data into levels of the categorical variable of interest and years (from 2009 to 2018) to calculate the amount of RDVCs occurring under those conditions in each year. For road category, we calculated the amount of RDVCs occurring in each type of road divided by the total length of the road category. We tested ANOVA's assumptions of normality with the Shapiro-Wilk test and for homogeneity of variance across groups with the Levene's test. If one of the two or both assumptions were violated, we used the Kruskal-Wallis test (KRUSKAL & WALLIS 1952) as a non-parametric alternative to check whether the result has been falsified by the violation (DORMANN 2020). If ANOVA or the Kruskal-Wallis test indicated significant differences between groups ($p < 0.05$), we performed post-hoc analysis through pairwise t-test (if ANOVA was used) or pairwise Wilcoxon test (if Kruskal-Wallis test was used) with 'BH' correction (BENJAMINI & HOCHBERG 1995) to test for differences between levels. The 'BH' correction limits false positive and false negative rates by controlling the false discovery rate (JAFARI & ANSARI-POUR 2019). We performed all statistical tests with R (R CORE TEAM 2021, version 4.1.2).

RESULTS

The Kruskal-Wallis test performed on the weekly distribution of RDVCs proves that the amount of RDVCs does not differ significantly between the seven days of the week ($\text{Chi}^2 = 3.06$, $\text{df} = 6$, $p > 0.05$).

From 2011 to 2018, the number of RDVCs in the BFNP* (+69.5%), BFNatP (+70.4%) and Lower Bavaria (+54.6%) increases steadily (Fig. 2). The circannual pattern of RDVCs remains stable on a yearly basis (Fig. 3), with clear local minima in January, February and March, the beginning of June until the end of July, and at the end of August. The first pronounced peak occurs in mid-April and lasts until the end of May. A second strong peak lasting less than a month emerges at the end of July/beginning of August. From September on, RDVCs increase steadily until the end of October. On a cumulative basis, the lower peaks coincide with date-fixed public holidays within Germany (e.g., 3rd of October or Christmas), with fewer roe deer accidents on these dates over 10 years.

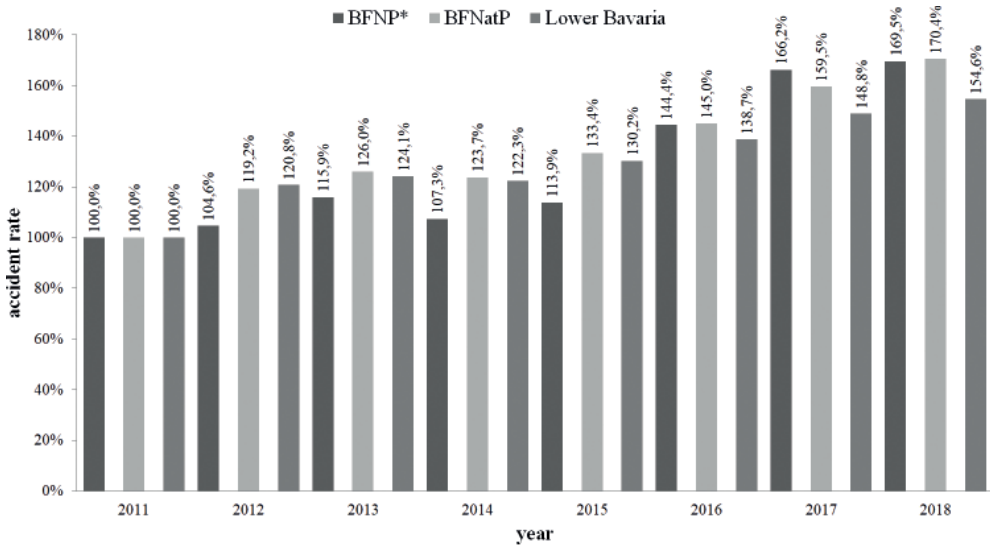


Fig. 2. Overview of the annual increase in RDVCs throughout the BFNP* and BFNatP and Lower Bavaria. The years 2009 and 2010 were excluded only for quantitative time series calculated and depicted in Fig. 2 (in all other analyses both years were included), because many accidents were not georeferenced during this period. The RDVCs in 2011 were defined as 100%.

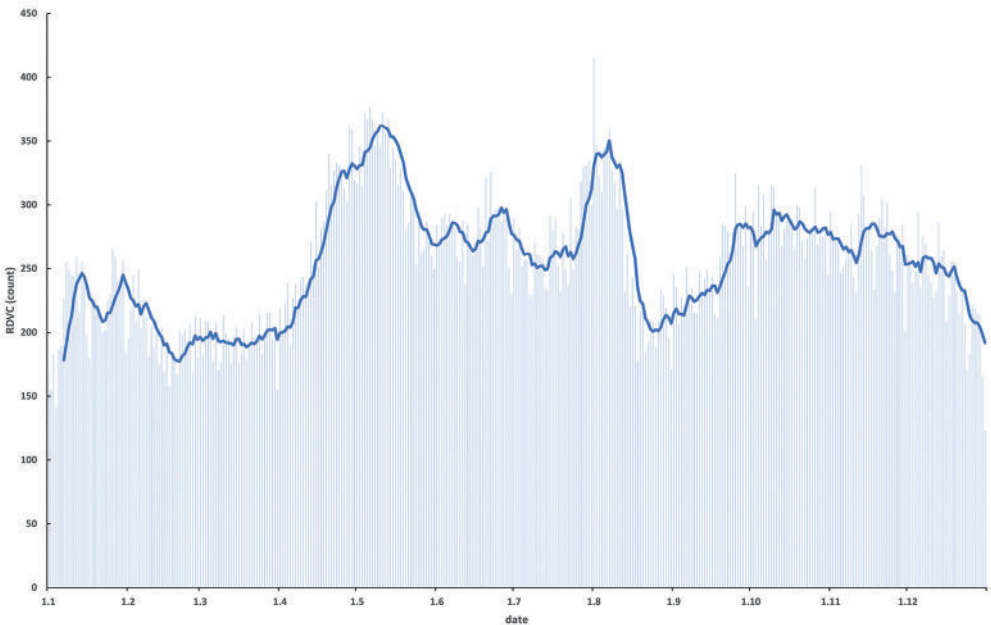


Fig. 3. Cumulative number of RDVCs across the BFNatP between 2009 and 2018. The first day of each month marks the x-axis. A 10 year time-period was selected to minimize the effects of yearly changes due to external factors (weather, snow-cover, etc.) and thus reveal the circannual rhythmic pattern of roe deer. We used a trendline-period of 7 days to overcome outliers.

The diurnal distribution of RDVCs clearly presents a bimodal crepuscular pattern (Fig. 4) and time shifts (time steps in the sunrise/sunset line) from winter to summer and vice versa (March/October). The RDVC density is particularly high during dusk and dawn in spring (beginning/mid-April) and summer. There is no quantitative increase in deer-vehicle collisions after the yearly time changes in our dataset. Bimodal roe deer activity and the corresponding clear jump in the data point distribution at sunrise and sunset, are clearly visible (Fig. 4).

The ultradian distribution of RDVCs in Lower Bavaria (Fig. 5) displays that most collisions take place during dusk, followed by night and dawn, while the lowest number of collisions occurs during the day. Dusk and dawn account for 55% of the collisions. The Kruskal-Wallis test points out that the amount of RDVCs occurring each year in Lower Bavaria differs significantly between the four times of the day ($\text{Chi}^2 = 14.59$, $\text{df} = 3$, $p < 0.01$). However, the amount of RDVCs does not differ between dusk and night and between dawn and day (post-hoc Wilcoxon test with BH correction, $p > 0.05$).

The complete RDVC dataset from Lower Bavaria is used in the moon-phase analysis. As seen in Fig. 6, the peak in RDVCs during full moon is pronounced. However, the Kruskal-Wallis test reveals that the amount of RDVCs occurring does not differ significantly between the four moon phases ($\text{Chi}^2 = 2.98$, $\text{df} = 3$, $p > 0.05$).

Most of the RDVCs in Lower Bavaria occur on tertiary roads (43.4%, Table 1). Secondary roads are the second most frequently involved type of road (32.7%), followed by federal roads (11.5%). Motorways have both the shortest total length and very few RDVCs (0.8%) (Table 1).

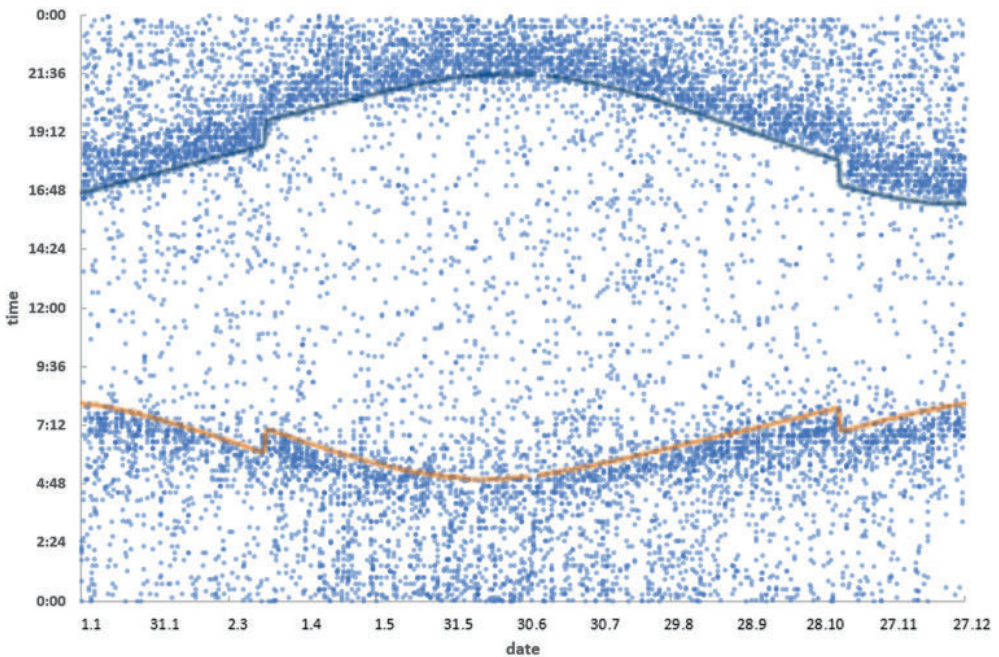


Fig. 4. Bimodular, crepuscular occurrence of RDVCs during 2018. Over the 10 year period, the diurnal RDVC-pattern distribution was very similar between single years (not shown in the figure). The orange line defines the sunrise and the blue line the sunset across the year. The denser the dot-cloud, the higher the collision rate.

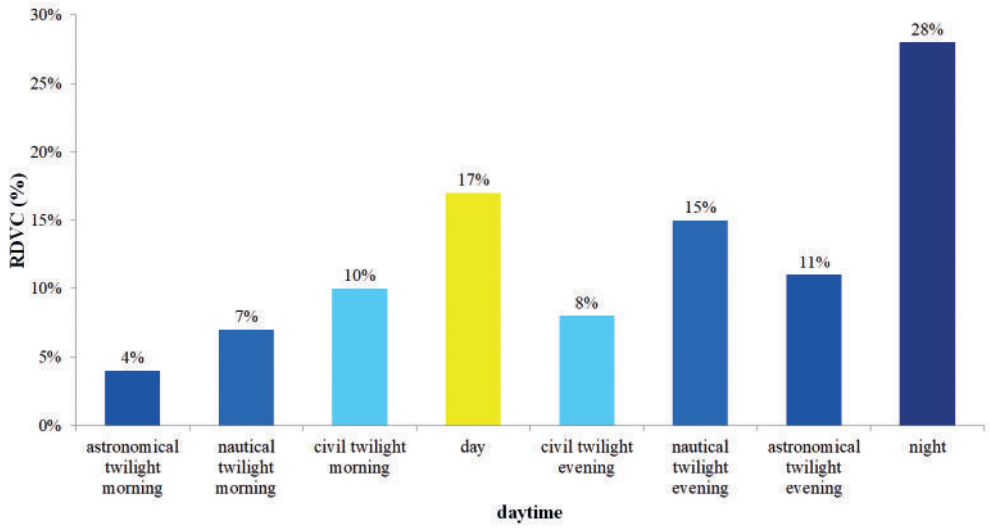


Fig. 5. Diurnal distribution of RDVCs. The short periods of dusk and dawn account for 55 % of all accidents.

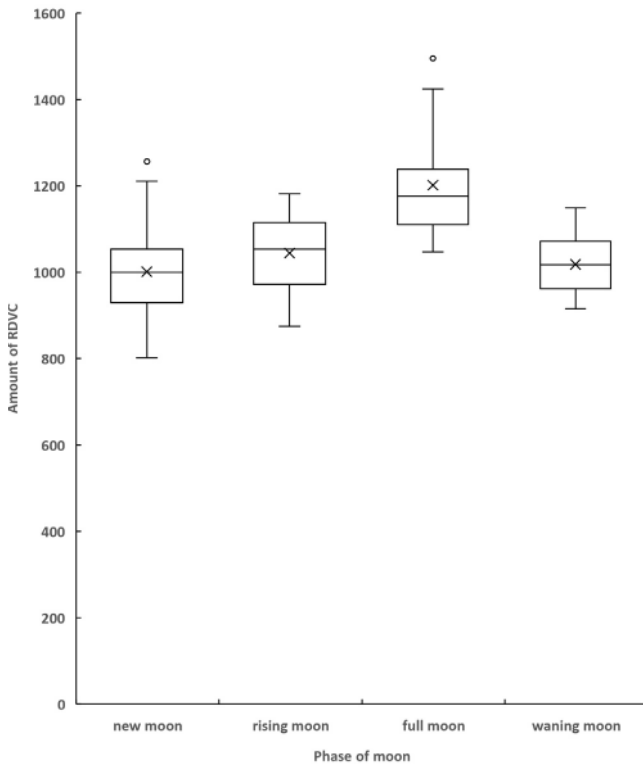


Fig. 6. Phase of moon in relation to the amount of roe deer vehicle collisions.

Table 1. Roe deer-vehicle-collisions categorized by road type. Cumulative data for 10 years are shown. The category “other” including residential, service, track, trunk (not considered part of the general-purpose road network) and unclassified roads were excluded in this Table.

	Federal roads	Secondary roads	Tertiary roads	Motorways
Lower Bavaria including the BFNatP^a				
Road length in km	854	2 269	4 040	566
RDVC total	9 672	27 635	36 595	651
RDVC per km	11.33	12.18	9.06	1.15
Bavarian Forest Nature Park including the BFNP^a				
Road length in km	229	620	956	126
RDVC total	3 070	7 075	7 395	121
RDVC per km	13.41	11.41	7.74	0.96

^a Buffer radius of the road polyline for intersection reasons: 10 m.

The highest amount of RDVCs per kilometer on roads in Lower Bavaria occurs on secondary and federal roads, followed by tertiary roads and motorways (Table 1). In the BFNatP, the number of RDVCs per km is very similar to that in Lower Bavaria. The biggest differences can be found for federal roads, where the number of RDVCs per km has the biggest variation (2.08 accidents per km more in the BFNatP than in Lower Bavaria, Table 1). The Kruskal-Wallis test shows that the amount of RDVCs per kilometer occurring in Lower Bavaria diverges significantly between the four road categories ($\text{Chi}^2 = 26.19$, $\text{df} = 3$, $p < 0.001$). However, the amount of RDVCs per km does not vary between federal and secondary roads (post-hoc Wilcoxon test with BH correction, $p > 0.05$).

The spatial analysis displays a hotspot clustering with landscape similarities in the surrounding areas. Figures 7.1 and 7.2 show the BFNP’s road with most RDVCs (length: 20.9 km, Fig. 7.1) and the border road between BFNP and BFNatP from Bayerisch Eisenstein to Buchenau (18.7 km, Fig. 7.2). Both roads pass mostly through dense forests and meadows. The traffic volume is highest from Bayerisch Eisenstein to Ludwigsthal and decreases thereafter. The traffic volume for the National Park Road declines from west to east, due to a reduction in human population density and because a road connection to the town of Freyung diverts most of the traffic volume in another direction 7.2 km before Mauth is finally reached.

DISCUSSION

Our analysis revealed increasing RDVCs throughout Lower Bavaria from 2011 until 2018, including the BFNatP and BFNP. This pattern might result from the increase in roe deer population densities throughout Lower Bavaria. For instance, in Bavaria from 2009/10 till 2019/20, the hunting quota of roe deer (including animals killed by disease, starvation or low temperature) increased from 298 784 to 338 418 roe deer individuals. Another explanation could be a general increase in road density and a general increase in traffic volume and vehicle speed (GROOT-BRUIDERINK & HAZEBROEK 1996, HUBBARD et al. 2000, MYSTERUD 2004).

However, the Bavarian State Ministry of Living, Construction and Traffic could not confirm any increase in traffic volume for the same time for the B85 primary road, which crosses the BFNatP.

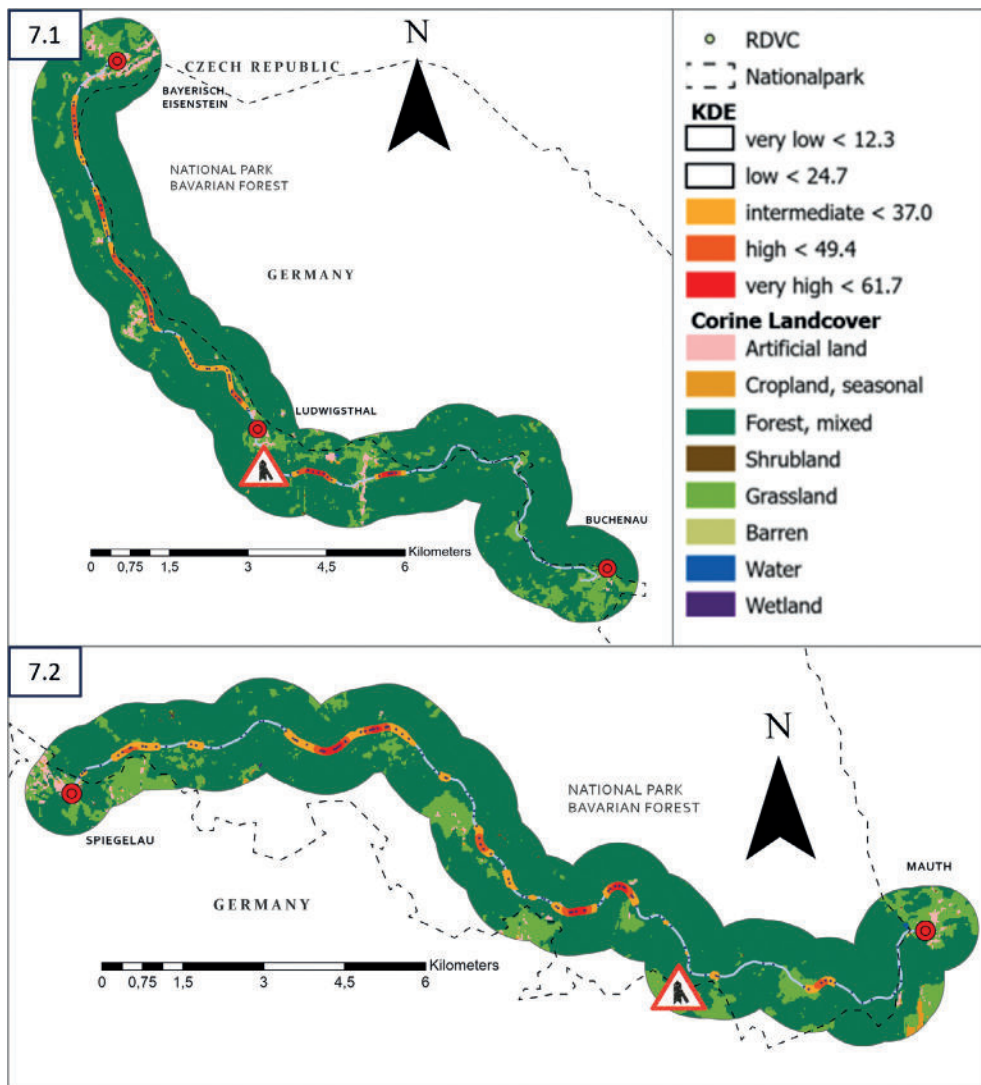


Fig. 7. Locations of RDVCs hotspots calculated using Kernel density estimation (KDE). A buffer of 800 m (radius) was used to outline the main area of interest. The KDE-classes “very low” and “low” are transparent for presentation purposes. (7.1): Course of the National Park Road from Spiegelau to Mauth (149 RDVC; FRG 4/5/16/19/21). (7.2): Border road from Bayerisch Eisenstein to Buchenau (134 RDVC; federal road: Bayerisch Eisenstein–Ludwigsthal, 9.7 km; tertiary road: Ludwigsthal–Buchenau, 9.0 km).

As expected, our results show a strong annual variation in RDVCs (Fig. 3). The first clearly visible RDVC-peak is in spring (end of April/beginning of May), coinciding with the break up of roe deer groups and the higher quantity and quality of food provided by the greening of the vegetation. The increased activity (CAGNACCI et al. 2011, STACHE et al. 2012, KROP-BENESCH et al. 2013, WOLF 2013) of roe deer might also be responsible for the higher number of RDVCs during spring. Furthermore, migration from winter to summer habitats may require more road crossings than usual (STUBBE 2008, CAGNACCI et al. 2011, STEINER et al. 2014). Contrary to that, KÄMMERLE et al. (2017) found only an average number of roe deer road-crossing sites in southwest Germany between April and May, compared to other months, and thus potentially lethal situations. In line with this, we assume that the search for new territories by less “road-crossing experienced” yearlings becoming independent causes such a marked increase in lethal collisions due to a higher crossing-mortality risk (ETTER et al. 2002, MADSEN et al. 2002). Unfortunately, there is no information regarding age or sex of animals involved in RDVCs in our dataset to explore this pattern. During the breeding season starting at the end of May, roe deer females remain settled because of the limited mobility of their fawns (IGNATAVICIUS & VALSKYS 2017), likely resulting in a sharp decrease in road crossings. This would explain the reduced number of RDVCs between the end of May until the end of July. The second pronounced peak of RDVCs observed in our study at the beginning of August and mid-August is explained by increased roe deer activity (and therefore road crossings) during the rutting period (KÄMMERLE et al. 2017). The core rutting period of roe deer is from 15 of July – 28 of August and 41.8% of roe deer females (18.1% of roe deer males) have at least one excursion outside their normal home range during that time (DEBEFFE et al. 2014). Furthermore, KÄMMERLE et al. (2017) reported a prominent high movement of roe deer males during the rutting season. These findings support a strong linkage between roe deer behavior and vehicle collisions. The third and last of the annual peaks occurred from September to November (Fig. 3) and is likely related to roe deer migration. In fact, CAGNACCI et al. (2011) reported a peak of roe deer migration in the Bavarian Forest at the end of October/beginning of November. VON HOERMANN et al. (2020) found out that roe deer are more likely to be involved in collisions in areas less familiar to them, which would partly explain the increase in RDVCs during spring and autumn migration periods. Furthermore, MADSEN et al. (2002) observed that 61% of young roe deer killed in an accident died in autumn, possibly due to a lack of experience. A further explanation for this third peak in RDVCs could be that in this season, the peak of roe deer activity at dusk and dawn coincides with commuter traffic, which is temporally stable throughout the year, while the deer adapt their activity patterns to the changing light conditions (KÄMMERLE et al. 2017). The reduced activity of roe deer during winter could explain the low RDVC-rate in that period (STACHE et al. 2012).

RDVCs show a distinct ultradian pattern, with increasing frequency during dusk and dawn, as also shown in other studies (CAGNACCI et al. 2011, STACHE et al. 2012, PAGON et al. 2013, WOLF 2013, IGNATAVICIUS & VALSKYS 2017, KÄMMERLE et al. 2017). Overall, the scattered pattern of RDVCs in the BFNatP (Fig. 4) well matches roe deer diurnal and seasonal activity patterns (STACHE et al. 2012, PAGON et al. 2013, WOLF 2013). In Lower Bavaria, the rate of RDVCs during the day is low (17%), despite the high traffic volume. The traffic-related disturbance close to roads during the day might induce deer to avoid those areas. KUŠTA et al. (2015) also reported a strong negative correlation between traffic intensity and WVCs.

The probability of an accident peaks during the short period of dusk (34%). Dawn accounts for 21% of all roe deer collisions and shows minimal vehicle-collision numbers during the short period of astronomical twilight morning (4%), which can be explained by a low traffic volume at this time of day. This indicates that time is one of the most important factors in RDVCs. Another important factor to consider is the traffic volume (CASE 1978, HUBBARD et al. 2000), which peaks in accordance with the daily commute to and from work. However, our analysis showed very few collisions during periods of high traffic intensity. Thus, the activity patterns of roe deer seem to be the most important factor determining the occurrence of RDVCs throughout the day.

We found a tendency of more accidents during full moon, but that difference was not significant. The reason is a greater activity of roe deer during full moon, potentially leading to a higher risk of RDVCs. COLINO-RABANAL (2018) showed more frequent lethal collisions (71.3%) during full moon than during new moon nights.

Federal roads within the BFNatP have the highest collision density per km. This may reflect the large traffic volume (MADSEN et al. 2002) and the high vehicle speeds (HARTWIG 1993) associated with this type of road. Elsewhere in Lower Bavaria, the number of RDVCs on federal roads is lower, presumably due to road fencing, a mitigation measure that is not widespread in the BFNatP (PAGANY & DORNER 2019). Fencing of federal roads may also explain why in Lower Bavaria, RDVCs per km are highest on secondary roads (mostly not fenced), despite the difference being insignificant. Less roe deer vehicle-collisions per km happen on tertiary roads, where both the speed limit and expected traffic volume are lower than on federal roads. The very small number of RDVCs on motorways (Table 1, BFNatP: 0.96 accidents per km; Lower Bavaria 1.15 accidents per km) was most likely attributable to extensive fencing. However, as holes and interruptions in the fence-infrastructure inevitably occur, motorways are not free of roe deer accidents (39.3% of all WVCs on motorways involve RDVCs).

The National Park Road is a RDVC-hotspot, especially in those areas at the end or beginning of forested habitats or narrow stretches of woodland within meadows. Furthermore, in the BFNatP, very few RDVCs occur in areas with dense forest, except those with bordering grassland patches. This is in line with other studies reporting that ideal roe deer habitats comprise agricultural and forested land, meadows, young forests, and forest patches (DUPKE et al. 2017) and forest edges (STUBBE 2008). PUGLISI et al. (1974) confirms that RDVCs mostly occur at the edge of forests. In contrast, NELLI et al. (2018) showed that RDVCs are more likely to appear on roads close to (or crossing) areas of woodland or forest. These differences between our findings and those of NELLI et al. (2018) can be explained by the different landscape structures and scales, as the latter confined their analysis to major roads in England, considering a minimum woodland size of 5 ha to avoid including small areas such as hedgerows. Therefore we assume that also small woodland patches influence RDVC-hotspots. Differentiating between mainly forested areas with grassland patches and mainly grassland areas with forested patches can provide insights into the two different results, as our analysis of KDE hotspots with the highest KDE-values on the road consistently distinguishes these two landscape types.

A limitation of our study is the resolution of the land cover map (30 × 30 m) which did not allow for the inclusion of small habitat patches or detailed cartographic objects. This hindered the recognition of small groups of trees, ponds, and small grassland patches with possibly

decisive effects within forested or grassland areas. The land classification characteristics of the hotspots depicted in our analysis are mainly very similar, thus justifying the use of this approach. However, information on the precision of the GPS-positions would improve the KDE and allow a more precise identification of hotspots, which could help to mitigate RDVCs. In addition, data on the age and sex of roe deer killed by a collision would allow testing our hypothesis that the high collision rates in May and October are due to the behavior of inexperienced yearlings. Therefore, we suggest reporting sex and age class of individuals killed by a collision for a more precise and comprehensive RDVC dataset facilitating future analysis.

Mitigation measures

Information on the locations of temporal and spatial hotspots can be used to provide dynamic alerts for high-risk time slots in hotspot areas with a high frequency of RDVCs. Low-cost mitigation methods such as reflectors are available, but their efficiency is debated (BENTEN et al. 2018). The use of repellants, by contrast, has shown to reduce RDVCs (KUŠTA et al. 2015, BÍL et al. 2017). Speed reduction can reduce RDVCs (MEISINGSET et al. 2014) by shortening the braking distance, allowing for better awareness of the surroundings, and delaying a possible collision. Warning signs are commonly used to alert drivers of the risk of road crossings by large animals, but there is no evidence of an effect of permanent warning signs (GROOT BRUIDERINK & HAZEBROEK 1996), as drivers become habituated to their presence.

Fences guarantee safety for both humans and wildlife, but they also increase habitat fragmentation, with adverse impacts on biodiversity. Furthermore, fencing is an expensive mitigation measure, which makes it not feasible for low-traffic road categories, but are indispensable for roads with high traffic volume and speed such as motorways. Fences are also used on federal and secondary roads with high traffic volume. However, their use in the BFNatP and especially in the BFNP is not supported because they would limit the movement of many species and act as barrier to gene flow between populations, needed to maintain genetic variability (LESBARRÈRES & FAHRIG 2012, CEIA-HASSE et al. 2018). Nonetheless, in combination with wildlife over- and underpasses, fences offer a good mitigation possibility in areas of high frequencies of RDVCs.

As the highest risk of RDVCs in the BFNP occurs in May, annual adaptations in speed limits and a system to notify road users, such as dynamic wildlife warning signs based on ultradian and annual changes, could contribute to mitigate accidents. For example, given the high collision rates at dusk and dawn, strategically placed dynamic signs could warn the drivers during these periods. New technologies such as LiDAR or RADAR, used in autonomously driving cars, and GPS-based technologies also hold promise in the detection and precise data recognition of wildlife crossing hotspots and therefore in the mitigation of RDVCs. Other promising mitigation tools are preventions systems which detect animals in the vicinity of roads and delivers warning signals directly to drivers (e.g. ANIMOT 2023).

CONCLUSION

This study describes the circannual variations in RDVCs. A high incidence of RDVCs during dusk and dawn is ubiquitous. Especially regarding the relatively short period of dusk and dawn when 55% of all accidents occurred. We found a strong seasonal variation with pronounced peaks during spring and the rutting period in August.

While, according to literature, RDVCs mostly occur on roads within dense forests, our landscape analysis reveals that most RDVCs took place at the edge of forests, which often occur in the BFNatP. As expected, the highest density of RDVCs can be found on federal and secondary roads. The temporal and spatial pattern found in this study will provide important information for the planning of mitigation measures.

Acknowledgements. We thank the German federal ministry of transport and digital infrastructure (BMVI) for funding of the mFund project “WilDa—Dynamic Wildlife–vehicle–collision warning, using heterogeneous traffic, accident and environmental data as well as big data concepts” grant number 19F2014B. We are grateful to W. Ran for the linguistic advice.

REFERENCES

- ANIMOT, 2023: Animot motion expert. AniMot, Neunkirchen. Online <https://animot.eu/en/> (accessed on 21 March 2023).
- APOLLONIO M., ANDERSEN R. & PUTMAN R., 2010: *European ungulates and their management in the 21st century*. Cambridge University Press, 604 pp.
- ASSOCIATION OF GERMAN INSURERS, 2018: Gesamtverband der Deutschen Versicherungswirtschaft [Association of German Insurers]. Online <https://www.gdv.de/de/medien/aktuell/zahl-der-wildunfaelle-so-hoch-wie-noch-nie-36172> (accessed on 21 June 2022) (in German).
- BÄSSLER C., MÜLLER J., JEHL H., LEIBL F. & PÖHLMANN R., 2011: Biologische Vielfalt im Nationalpark Bayerischer Wald [Biodiversity in the Bavarian Forest National Park]. Nationalparkverwaltung Bayerischer Wald, 226 pp. Online https://www.nationalpark-bayerischer-wald.bayern.de/natur/doc/sonderband_biologische_vielfalt.pdf (accessed on 21 June 2022) (in German).
- BENJAMINI Y. & HOCHBERG Y., 1995: Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal statistical society: series B*, 57: 289–300.
- BENTEN A., ANNIGHÖFER P. & VOR T., 2018: Wildlife Warning Reflectors’ Potential to Mitigate Wildlife-Vehicle Collisions - A Review on the Evaluation Methods. *Frontiers in Ecology and Evolution*, 6: 37.
- BERGER A., SCHEIBE K.-M., BRELURUT A., SCHOBER F. & STREICH W.J., 2003: Seasonal Variation of Diurnal and Ultradian Rhythms in Red Deer. *Biological Rhythm Research*, 33(3): 237–253.
- BÍL M., ANDRÁŠIK R., SVOBODA T. & SEDONÍK J., 2016: The KDE+ software: a tool for effective identification and ranking of animal-vehicle collision hotspots along networks. *Landscape Ecology*, 31:231–237.
- BÍL M., ANDRÁŠIK R., BARTONIČKA T., KRIVÁNKOVÁ Z. & SEDONÍK J., 2017: An evaluation of odor repellent effectiveness in prevention of wildlife-vehicle collisions. *Journal of Environmental Management*, 205: 209–214.
- CAGNACCI F., FOCARDI S., HEURICH M., STACHE A., HEWISON A.J.M., MORELLET N., KJELLANDER P., LINNELL J.D.C., MYSTERUD A., NETELER M., DELUCCHI L., OSSI F. & URBANO F., 2011: Partial migration in roe deer: migratory and resident tactics are end points of a behavioral gradient determined by ecological factors. *Oikos*, 120: 1790–1802.
- CASE R., 1978: Interstate highway road-killed animals: a data source for biologist. *Wildlife Society Bulletin*, 6: 8–13.
- CEIA-HASSE A., BORDA-DE-ÁGUA L., GRILO C. & PEREIRA H.M., 2017: Global exposure of carnivores to roads. *Global Ecology and Biogeography*, 26: 592–600.
- COLINO-RABANAL V.J., LANGEN T.A., PERIS S.J. & LIZANA M., 2018: Ungulate: vehicle collision rates are associated with the phase of the moon. *Biodiversity and Conservation*, 27:681–694.

- CONOVER M., PITT W., KESSLER K., DUBOW T. & SANBORN W., 1995: Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. *Wildlife Society Bulletin*, 23(3): 407–414.
- D'AMICO M., ROMÁN J., DE LOS REYES L. & REVILLA E., 2015: Vertebrate road-kill patterns in Mediterranean habitats: Who, when and where. *Elsevier Biological Conservation*, 191: 234–242.
- DE COURSEY P.J., 2004: The behavioral ecology and evolution of biological timing systems. In: *Chronobiology: Biological timekeeping*, DUNLAP J.C., LOROS J.J. & DE COURSEY P.J., Sinauer Associates, Sunderland, pp. 27–65.
- DEBEFFE L., FOCARDI S., BONENFANT C., HEWISON A.J.M., MORELLET N., VANPÉ C., HEURICH M., KJELLANDER P., LINNELL J.D.C., MYSTERUD A., PELLERIN M., SUSTR P., URBANO F. & CAGNACCI F., 2014: A one-night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. *Oecologia*, 176: 431–443.
- DORMANN C., 2020: *Environmental Data Analysis: An Introduction with Examples in R*. Springer Nature, 150 pp.
- DUPKE C., BONENFANT C., REINEKING B., HABLE R., ZEPPENFELD T., EWALD M. & HEURICH M., 2017: Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. *Ecography*, 40: 1014–1027.
- ETTER D.R., HOLLIS K.M., VAN DEELEN T.R., LUDWIG D.R., CHELSVIG J.E., ANCHOR C.L. & WARNER R.E. 2002: Survival and movements of white-tailed deer in suburban Chicago, Illinois. *Journal of Wildlife Management*, 66 : 500–510.
- FASTRICH K., 2022: Wildunfall: Das müssen Autofahrer wissen [Deer accidents: What motorists need to know]. ADAC, press release. Online <https://www.adac.de/verkehr/verkehrssicherheit/tiere/wildunfaelle/> (accessed on 24 November 2022) (in German).
- FISHER R., 1918: The correlation between relatives on the supposition of Mendelian inheritance. *Philosophical Transactions of the Royal Society of Edinburgh*, 52: 399–433.
- FISHER R., 1925: *Statistical methods for research workers*. Edinburgh: Oliver & Boyd, 36 pp.
- GEOFABRIK, 2021: Download OpenStreetMap data for this region: Lower Bavaria. Geofabrik GmbH & OpenStreetMap Contributors. Online <https://download.geofabrik.de/europe/germany/bayern/niederbayern.html> (accessed on 23 October 2021) (in German).
- GERMAN HUNTING ASSOCIATION, 2021: Jagd- und Wildunfallstatistik [Hunting and wildlife accident statistics]. Deutscher Jagdverband, Berlin. Online <https://www.jagdverband.de/jagd-und-wildunfallstatistik> (accessed on 21 September 2022) (in German).
- GROOT BRUINDERINK G.W.T.A. & HAZEBROEK E., 1996: Ungulate traffic collisions in Europe. *Conservation Biology*, 10: 1059–1067.
- GUIDOUM A.C., 2015: Kernel Estimator and Bandwidth Selection for Density and its Derivatives. The kedd Package. R package version 1.0.3. Department of Probabilities & Statistics, University of Science and Technology Houari Boumediene, BP 32 El-Alia, U.S.T.H.B, Algeria, 22 pp.
- GUTHÖRL V., 1994: Aktivitätsmuster von Rehen (*Capreolus capreolus* Linne, 1758) in einem Stadtwald mit starkem Erholungsverkehr [Activity patterns of roe deer (*Capreolus capreolus* Linne, 1758) in an urban forest with heavy recreational traffic]. *Zeitschrift für Jagdwissenschaft*, 40: 241–252 (in German).
- HARTWIG D., 1993: Auswertung der durch Wild verursachten Verkehrsunfälle nach der Statistik für Nordrhein-Westfalen [Evaluation of traffic accidents caused by game according to the statistics for North Rhine-Westphalia]. *Zeitschrift für Jagdwissenschaft*, 39: 22–33 (in German).
- HEURICH M., BEUDERT B., RALL H. & KŘENOVÁ Z., 2010: National parks as model regions for interdisciplinary long-term ecological research: The Bavarian Forest and Šumava National Parks underway to transboundary ecosystem research. In: *Long-Term Ecological Research, Between Theory and Application*, MÜLLER F. et al. (eds), Springer, pp. 327–344.
- HEURICH M., BRAND T.T., KAANDORP M.Y., ŠUSTR P., MÜLLER J. & REINEKING B., 2015: Country, cover or protection: what shapes the distribution of red deer and roe deer in the Bohemian Forest Ecosystem? *Plos One*, 10: e0120960.
- HEURICH M., SCHULTZE-NAUMBURG J., PIACENZA N., MAGG N., ČERVENÝ J., ENGLER T., HERDTFELDER M., SLADOVÁ M. & KRAMER-SCHADT S., 2018: Illegal hunting as a major driver of the source-sink dynamics of a reintroduced lynx population in Central Europe. *Biological Conservation*, 224: 355–365.
- HOFFMANN T., 2023: Berechnung Sonnenverlauf für [Calculation of solar course for]. Solar Course, Eisenberg, home page. Online <https://www.sonnenverlauf.de/#/48.9947,13.0408,7/2023.03.22/14:57/1/0> (accessed on 20 March 2023) (in German).

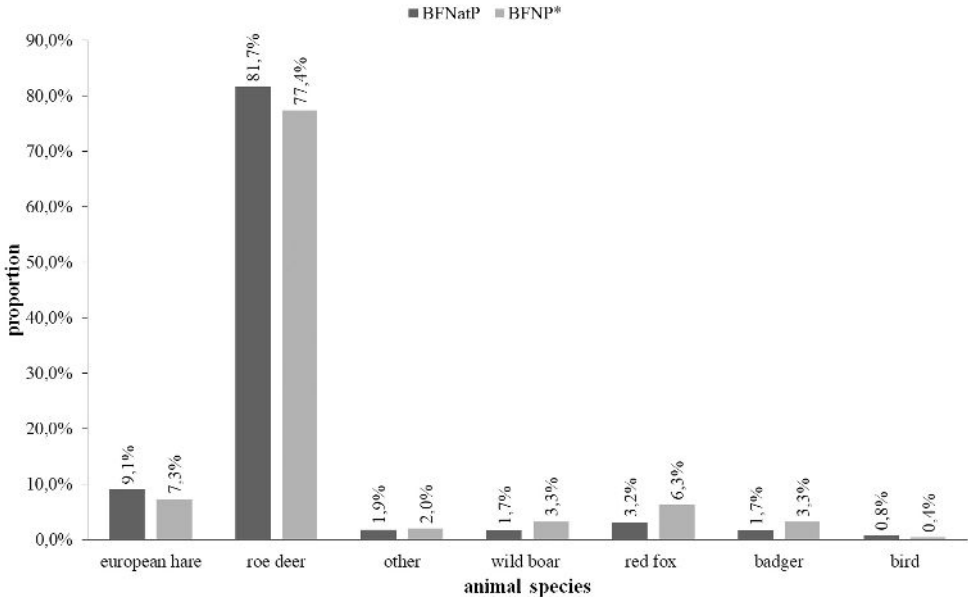
- HOLDEGGER R. & DI GIULIO M., 2010: The genetic effects of roads: A review of empirical evidence. *Basic and Applied Ecology*, 11: 522–531.
- HOTHORN T., BRANDL R. & MÜLLER J., 2012: Large Scale Model-Based Assessment of Deer-Vehicle Collision Risk. *Plos One*, 7: e29510.
- HUBBARD M.W., DANIELSON B. & SCHMITZ R., 2000: Factors influencing the location of deer–vehicle accidents in Iowa. *Journal of Wildlife Management*, 64: 707–713.
- IGNATAVICIUS G. & VALSKYS V., 2017: The influence of time factors on the dynamics of roe deer collisions with vehicles. *Landscape and Ecological Engineering*, 14: 221–229.
- JAFARI M. & ANSARI-POUR N., 2019: Why, when and how to adjust your P values? *Cell Journal (Yakhteh)*, 20: 604.
- KÄMMERLE J.-L., BRIEGER F., KRÖSCHEL M., HAGEN R., STORCH I. & SUCHANT R., 2017: Temporal patterns in road crossing behaviour in roe deer (*Capreolus capreolus*) at sites with wildlife warning reflectors. *Plos One*, 12: e0184761.
- KAPPELER P., 2012: *Verhaltensbiologie [Behavioural biology]*, 4. Auflage. Springer Spektrum, Göttingen, 104 pp. (in German).
- KROP-BENESCH A., BERGER A., HOFER H. & HEURICH M., 2013: Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-collars. *Italian Journal of Zoology*, 80: 69–81.
- KRUSKAL W.H. & WALLIS W.A., 1952: Use of ranks in one-criterion variance analysis. *Journal of the American statistical Association*, 47: 583–621.
- KURT F., 1991: *Das Reh in der Kulturlandschaft – Sozialverhalten und Ökologie eines Anpassers [The deer in the cultural landscape – social behavior and ecology of an adaptor]*. Parey, Hamburg, 36 pp. (in German).
- KUŠTA T., KEKEN Z., JEŽEK M. & KÚTA Z., 2015: Effectiveness and costs of odor repellents on wildlife-vehicle collisions: A case study in Central Bohemia, Czech Republic. *Elsevier Ltd. Transportation Research Part D*, 38: 1–5.
- LANGBEIN J., PUTMAN R. & POKORNY B., 2010: Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation. *Ungulate Management in Europe: problems and practices*: 215–259.
- LESBARRÈRES D. & FAHRIG L., 2012: Measure to reduce population fragmentation by roads: what has worked and how do we know? *Elsevier Ltd. Trends in Ecology and Evolution*, 27: 374–380.
- LUDWIG M., GRÜNINGER F., ROTHFUSS E. & HEURICH M., 2012: Discourse analysis as an instrument to reveal the pivotal role of the media in local acceptance or rejection of a wildlife management project: A case study from the Bavarian Forest National Park. *Erdkunde*, 66: 143–156.
- MADSEN A.B., STRANDGAARD H. & PRANG A., 2002: Factors causing traffic killings of roe deer *Capreolus capreolus* in Denmark. *Wildlife Biology*, 8: 55–61.
- MEISINGSET E.L., LOE L.E., BREKKUM O. & MYSTERUD A., 2014: Targeting mitigation efforts: The role of speed limit and road edge clearance for deer-vehicle collisions. *Wildlife Management*, 78: 679–688.
- MYSTERUD A., 2004: Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. *Wildlife Biology*, 10: 203–211.
- NELLI L., LANGBEIN J., WATSON P. & PUTMAN R., 2018: Mapping risk: Quantifying and predicting the risk of deer-vehicle collisions on major roads in England. *Mammalian Biology*, 91: 71–78.
- ÖZCAN A.U. & ÖZKAZANÇ N.K., 2017: Identifying the hotspots of wildlife-vehicle collisions on the Cankiri-Kirikkale highway during summer. *Turkish Journal of Zoology*, 41: 722–730.
- PAGANY R. & DORNER W., 2019: Do crash barriers and fences have an impact in wildlife-vehicle collisions? – An artificial intelligence and GIS-based analysis. *International Journal of Geo-Information*, 8: 66.
- PAGON N., GRIGNOLIO S., PIPIA A., BONGI P., BERTOLUCCI C. & APOLLONIO M., 2013: Seasonal variation of activity patterns in roe deer in a temperate forested area. *Chronobiology International*, 30: 772–785.
- PFLUGMACHER D., RABE A., PETERS M. & HOSTERT P., 2018: Pan-European land cover map of 2015 based on Landsat and LUCAS data. PANGAEA, Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research (AWI)/Center for Marine Environmental Sciences, University of Bremen (MARUM). Online <https://doi.pangaea.de/10.1594/PANGAEA.896282> (accessed on 24 September 2021) .
- PODOLSKI I., BELOTTI E., BUFKA L., REULEN H. & HEURICH M., 2013: Seasonal and daily activity patterns of free-living Eurasian lynx *Lynx lynx* in relation to availability of kills. *Wildlife Biology*, 19: 69–77.
- PUGLISI M.J., LINDZEY J.S. & BELLIS E.D., 1974: Factors associated with highway mortality of white-tailed deer. *Journal of Wildlife Management*, 38 : 799–807.

- R CORE TEAM, 2021: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online <https://www.R-project.org/> (accessed on 18 December 2022).
- REMMERT H., 1969: Tageszeitliche Verzahnung der Aktivität verschiedener Organismen [Diurnal interlocking of the activity of different organisms]. *Oecologia*, 3: 214–226 (in German).
- RONDEAU D. & CONRAD J., 2003: Managing urban deer. *American Journal of Agricultural Economics*, 85: 266–281.
- SALA O.E., CHAPIN F.S., ARMESTO J.J., BERLOW E., BLOOMFIELD J., DIRZO R., HUBER-SANWALD E., HUENNEKE L.F., JACKSON R.B., KINZIG A., LEEMANS R., LODGE D.M., MOONEY H.A., OESTERHELD M., POFF N.L., SYKES M.T., WALKER B.H., WALKER M. & WALL D.H., 2000: Global biodiversity scenarios for the year 2100. *Science*, 287: 1770 – 1774.
- SCHEIBE K., BERGER A., LANGBEIN J., STREICH W.J. & EICHHORN K., 1999: Comparative analysis of ultradian and circadian behavioural rhythms for diagnosis of biorhythmic state of animals. *Biological Rhythm Research*, 30: 216–233.
- SCHEIBE K., BERGER A., EICHHORN K. & STREICH W.J., 2001: Zeit und Rhythmen – Umweltfaktor und biologische Struktur [Time and rhythms – environmental factor and biological structure]. *KTBL-Schrift*, 407: 64–75 (in German).
- STACHE A., HELLER E., HOTHORN T. & HEURICH M., 2012: Activity pattern of European roe deer (*Capreolus capreolus*) are strongly influenced by individual behavior. *Folia Zoologica*, 62: 67–75.
- STEINER W., LEISCH F. & HACKLÄNDER K., 2014: A review on the temporal pattern of deer-vehicle accidents: Impact of seasonal, diurnal and lunar effects in cervids. *Accident Analysis and Prevention*, 66: 168–181.
- STIEGLER J., VON HOERMANN C., MÜLLER J., BENBOW M.E. & HEURICH M., 2020: Carcass provisioning for scavenger conservation in a temperate forest ecosystem. *Ecosphere*, 11(4): e03063.
- STUBBE C., 2008: *Rehwild: Biologie, Ökologie, Hege und Jagd* [Roe deer: biology, ecology, management and hunting]. Kosmos, 398 pp. (in German).
- TILMAN D., REICH P.B. & KNOPS J.M.H., 2006: Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441: 629–632.
- TURNER D.C., 1979: An analysis of time-budgeting by roe deer (*Capreolus capreolus*) in an agricultural area. *Behaviour*, 71: 246–290.
- VON HOERMANN C., PAGANY R., KIRCHNER K., DORNER W., HEURICH M. & STORCH I., 2020: Predicting the risk of deer-vehicle collisions by inferring rules learnt from deer experience and movement patterns in the vicinity of roads. IEEE Conference Proceedings, 10th International Conference on Advanced Computer Information Technologies (ACIT): 368–373.
- WIESMAYR M., SCHONERT B., KALZ B., BERGER A., BUKER A., EICHHORN K., SCHEIBE A. & SCHEIBE K., 2005: Ableitung von Richtlinien und Kriterien für Wildruhezonen auf Grundlage indirekter und direkter Verfahren. Jahresbericht 2005 und abschließender Bericht für die Jahre 2002–2005 [Derivation of guidelines and criteria for wildlife rest areas based on indirect and direct procedures. Annual report 2005 and final report for the years 2002–2005]. Leibniz-Institut für Zoo- und Wildtierforschung (IZW), 14 pp. (in German).
- WOLF S., 2013: Räumliche und zeitliche Aktivitätsmuster von Rehen (*Capreolus capreolus*) im Naturpark Hoher Fläming [Spatial and temporal activity patterns of roe deer (*Capreolus capreolus*) in the Hoher Fläming Nature Park]. Ms., diploma thesis, Alberts-Ludwigs-University Freiburg, 30 pp. (Faculty of Environment and Natural Resources, Institute of Forest Sciences, Ludwigs-University, Freiburg) (in German).

Received: 3 May 2021
Accepted: 2 May 2023

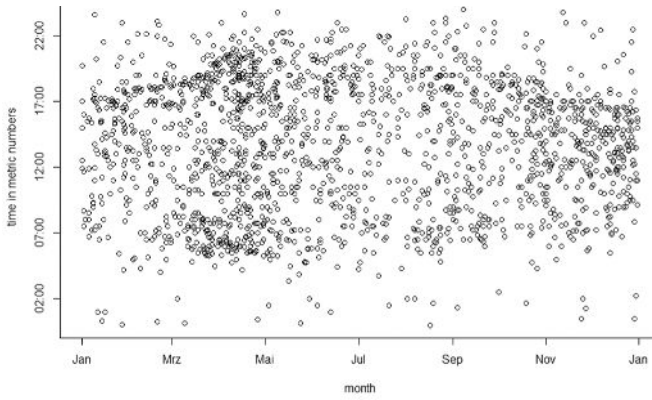
APPENDIX

Roe deer accounted for most (77.4%) of the WVCs in the BFNP*, with a much smaller proportion contributed by red fox (6.3%), European hare (7.3%), wild boar (3.3%) and European badger (3.3%). The proportion of RDVCs in the BFNatP was similar (81.7%) whereas, except for hare (9.1%), the proportion made up by other species, i.e., fox (3.2%), badger (1.7%), and wild boar (1.7%), decreased (Appendix 1).

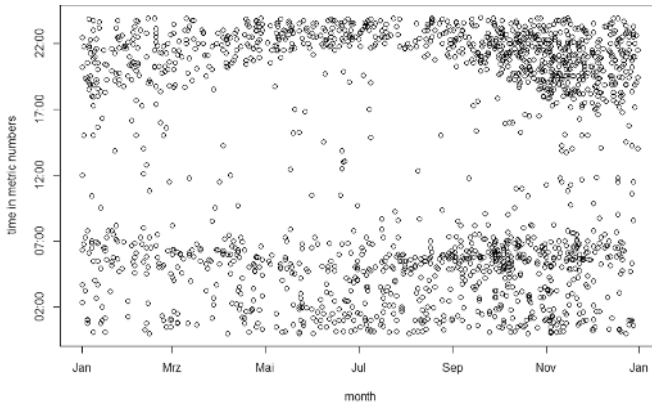


Appendix 1. Relative proportions of species killed in WVCs in the BFNatP and BFNP*.

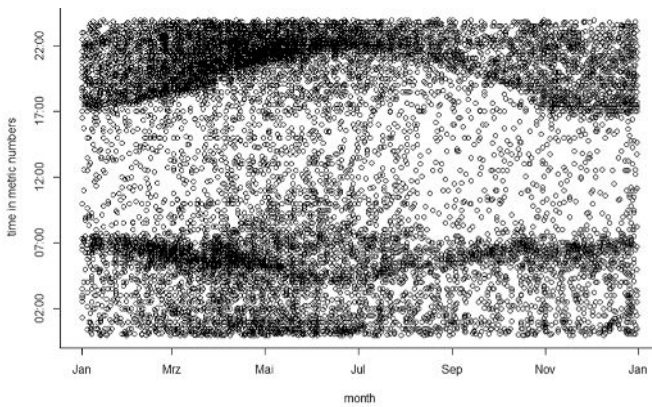
The following graphs show the temporal patterns of badger, hare, wild boar, and red fox (over 10 years) in Lower Bavaria, emphasizing the regularity of clusters/hotspots. WVCs involving European hare (Appendix 2.3), which has a strong crepuscular activity pattern, are especially frequent in March, April, and May. In contrast to roe deer, WVCs involving European hare had only a single pronounced annual peak, as the collision rate from June until February was relatively low. WVCs involving badger (Appendix 2.5) mostly occurred at night but also included a few outliers during the day. As badgers hibernate in winter, they are rarely involved in WVCs in January and February. The WVC pattern for red fox (Appendix 2.4) was well comparable to that of badgers but without a gap in winter. Red fox KDE-hotspots could often be found close to human infrastructure. For wild boar (Appendix 2.2), WVC clusters peaked during night, with higher numbers from September to December. Collisions involving birds (Appendix 2.1) had a single pronounced peak during spring. Birds are the only species with more accidents during the day. An extraction of the georeferenced data with known coordinates revealed 24 823 and 263 WVCs throughout the BFNatP and BFNP, respectively.



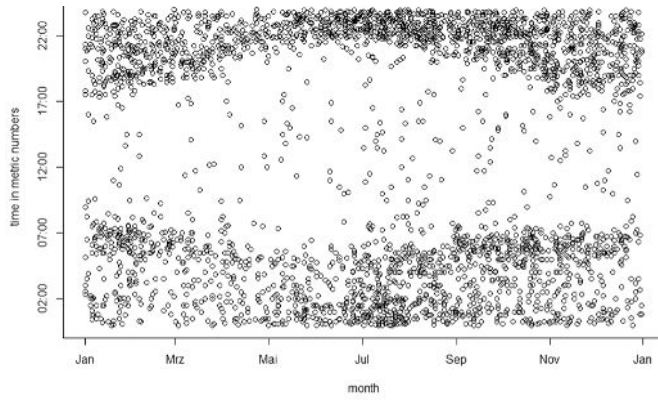
Appendix 2.1. Cumulative ultradian point pattern of birds.



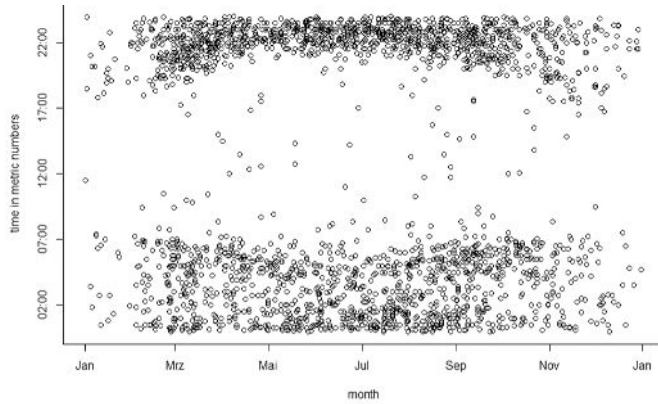
Appendix 2.2. Cumulative ultradian point pattern of wild boars.



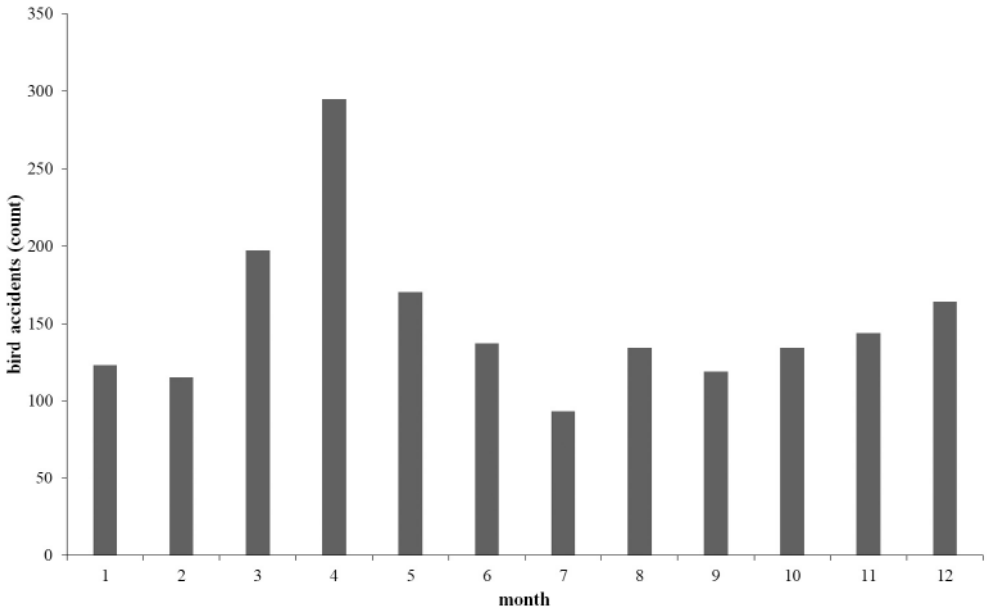
Appendix 2.3. Cumulative ultradian point pattern of European hare.



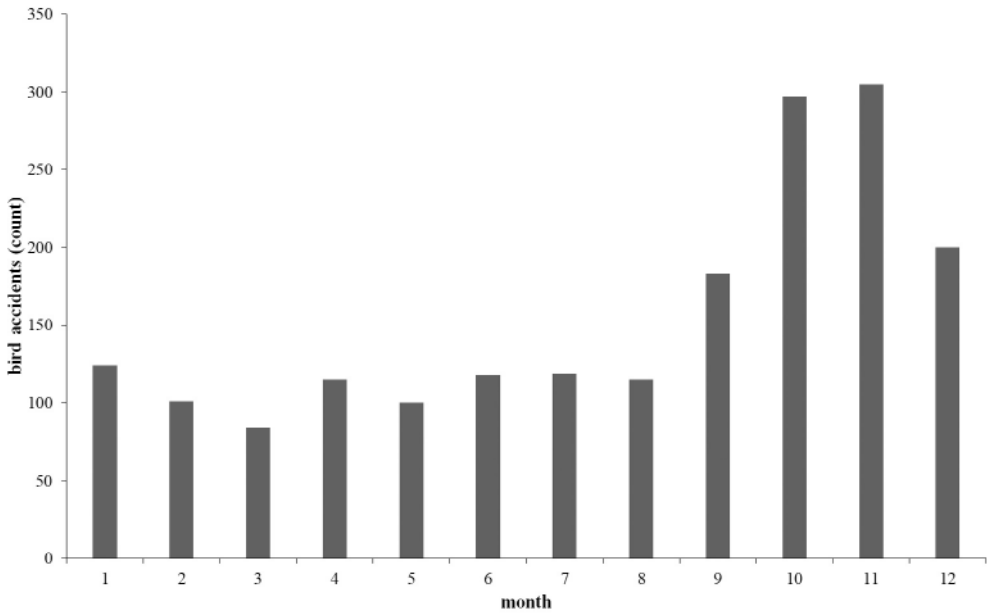
Appendix 2.4. Cumulative ultradian point pattern of red fox.



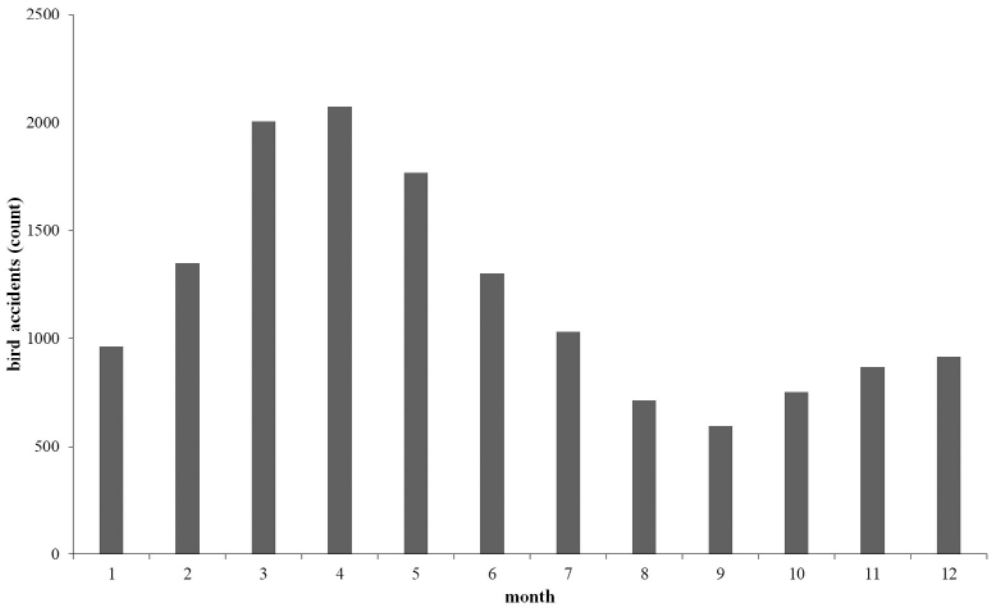
Appendix 2.5. Cumulative ultradian point pattern of badgers.



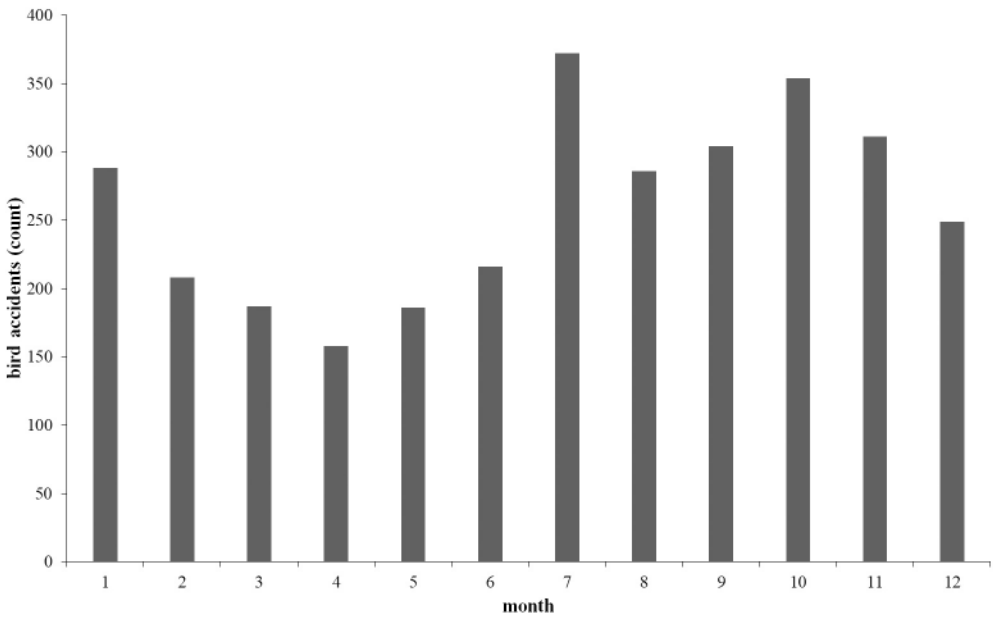
Appendix 3.1. Cumulative (10 years) bird vehicle-collisions.



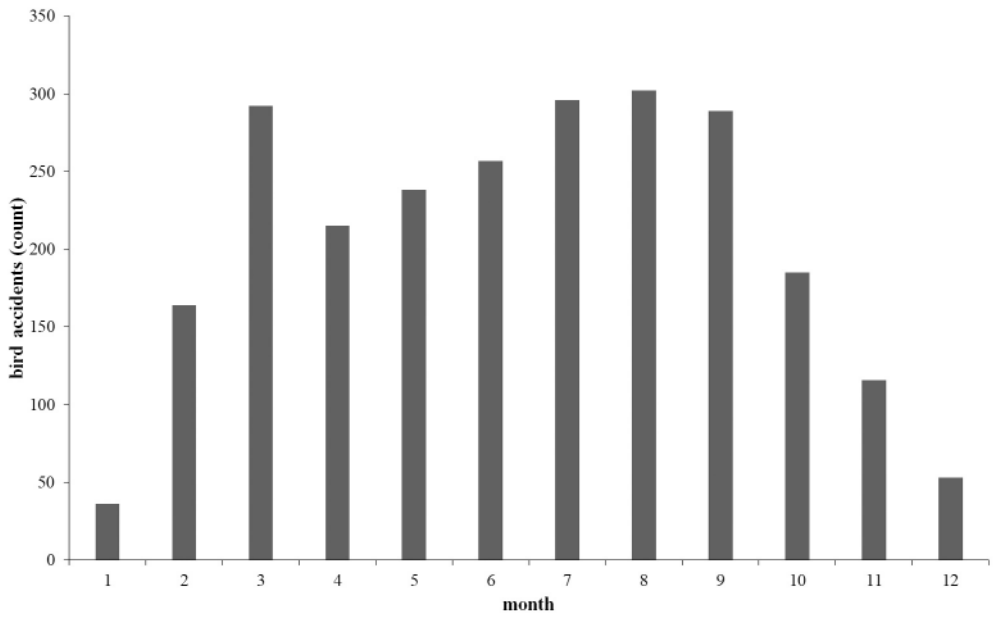
Appendix 3.2. Cumulative (10 years) wild boar vehicle-collisions.



Appendix 3.3. Cumulative (10 years) hare vehicle-collisions.



Appendix 3.4. Cumulative (10 years) red fox vehicle-collisions.



Appendix 3.5. Cumulative (10 years) badger vehicle-collisions.