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Temporal Patterns of Deer-vehicle Collisions Consistent with Deer Activity Pattern and Density Increase but not General Accident Risk

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Abstract

The increasing number of deer-vehicle collisions (DVCs) across Europe during recent decades poses a serious threat to human health and animal welfare and increasing costs for society. DVCs are triggered by both a human-related and a deer-related component. Mitigation requires an understanding of the processes driving temporal and spatial collision patterns. Separating human-related from deer-related processes is important for identifying potentially effective countermeasures, but this has rarely been done.

We analysed two time series of 341,655 DVCs involving roe deer and 854,659 non-deer-related accidents (non-DVCs) documented between 2002 and 2011. Nonparametric smoothing and temporal parametric modelling were used to estimate annual, seasonal, weekly and diurnal patterns in DVCs, non-DVCs and adjusted DVCs. As we had access to data on both DVCs and non-DVCs, we were able to disentangle the relative role of human-related and deer-related processes contributing to the overall temporal DVC pattern.

We found clear evidence that variation in DVCs was mostly driven by deer-related and not human-related activity on annual, seasonal, weekly and diurnal scales. A very clear crepuscular activity pattern with high activity after sunset and around sunrise throughout the year was identified. Early spring and the mating season between mid-July and mid-August are typically periods of high roe deer activity, and as expected we found a high number of DVC during these periods, although these patterns differed tremendously during different phases of a day. The role of human activity was mainly reflected in fewer DVCs on weekends than on weekdays. Over the ten-year study period, we estimated that DVCs increased by 25%, whereas the number of non-DVCs decreased by 10%. Increasing deer densities are the most likely driver behind this rise in DVCs.

Precise estimates of DVC patterns and their relationship to deer and human activity patterns allow implementation of specific mitigation measures, such as tailored driver

warning systems or temporary speed limits. To prevent a further increase in DVCs, state-wide measures to decrease roe deer density are required.

Keywords: Deer-vehicle accident, ungulate-vehicle collision, traffic mortality, seasonality, deer density

1. Introduction

Deer-vehicle collisions (DVCs) are a serious road safety issue and currently arguably the largest deer management problem in Europe (Groot Bruinderink and Hazebroek, 1996; Langbein et al., 2011). Estimates on the annual number of DVCs are well above 0.5 million in Europe and 1.5 million in the USA (Langbein et al., 2011). It is estimated that this leads to some 30,000 injured people and several mortalities, in addition to economic costs and animal suffering, and it is the major cause of deer mortality apart from harvesting. This increase in DVCs is thought to arise mainly from two processes related to traffic intensity and deer density. The separation of the human component from the deer component in the analysis of the frequency of DVCs has proven difficult (Mysterud, 2004), in particular because published studies on DVCs involving roe deer lack information about human activity patterns (Steiner et al., 2014). However, effective mitigation of DVCs requires a better understanding of the underlying human-related and deer-related processes.

The temporal patterns observable in DVCs can be split into annual, seasonal, weekly and diurnal patterns (Sullivan, 2011; Rodríguez-Morales et al., 2013). A meta-analytic approach (Steiner et al., 2014) highlighted diurnal bouts and seasonal activity peaks of roe deer, most prominently in early spring and during the mating or rutting season. This temporal pattern is typical for Central Europe (Groot Bruinderink and Hazebroek, 1996; Pokorny, 2006; Lagos et al., 2012; Rodríguez-Morales et al., 2013), while under more extreme climate conditions, the DVC risk shifts towards colder months (Madsen et al., 2002; Compare et al., 2007).

Diurnal and seasonal patterns in the number of DVCs are thought to reflect animal activity patterns (Steiner et al., 2014), but may also reflect human activity, such as periods of higher traffic volume during rush hours and the start and end of holidays. On annual scales, weather affects deer behaviour, but DVC increases over time are mainly assumed to be linked to deer densities (Mysterud, 2004; Apollonio et al., 2010; Gkritza et al., 2010). Weekly patterns are clearly caused by human activity but have been mostly neglected in roe deer DVC literature (Steiner et al., 2014). Rodríguez-Morales et al. (2013) investigated weekly patterns of DVCs involving roe deer but did not report clear links between DVCs and human activity.

Here we aimed at separating the human-related and deer-related processes that cause variation in DVCs involving roe deer by adjusting the observed number of DVCs to the overall number of traffic collisions. The number of accidents that did not involve an animal was used to indirectly assess DVC patterns in a quasi-induced exposure analysis

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(Haight, 1970) where deers ‘cause’ deer-vehicle collisions. Our investigation is based on a time series of 341,655 DVCs (almost exclusively involving roe deer) and 854,659 other collisions (non-DVCs) documented by police officers over a period of ten years in Bavaria, Germany. As far as we know, this is by far the largest data set on DVCs (44 times larger than that of the largest study on temporal activity reviewed by Steiner et al., 2014). We studied annual, seasonal, weekly and diurnal patterns in the number of DVCs, the number of non-DVCs and the proportion of DVCs among all collisions in this highly industrialised study area. The data were used to assess the following human-related (H1) and deer-related (H2) hypotheses: (H1a) Increased traffic on weekdays increases the risk of collisions in general, and reduced human traffic on weekends and holidays corresponds to a lower number of non-DVCs. (H1b) A peak in traffic before and after office hours irrespective of day length leads to a higher number of non-DVCs. (H1c) Deer are more difficult to spot in the dark, which leads to an increased proportion of DVCs among all collisions during the night. (H2a) Higher deer density increases the chance of deer crossing roads and thus DVCs (Vincent et al., 1988; Gkritza et al., 2010). (H2b) Roe deer are more active at dusk and dawn (crepuscular activity pattern, Cederlund, 1981; Jeppesen, 1989; Groot Bruinderink and Hazebroek, 1996), which leads to more DVCs in twilight and dark hours (for white-tailed deer see Beier and McCullough, 1990; Sullivan, 2011). (H2c) Male roe deer move more during the rutting season (Liberg et al., 1998), which leads to a higher risk of DVC (for white-tailed deer see Allen and McCullough, 1976).

2. Methods

2.1. Study Area

Bavaria is located in south-eastern Germany (48°46′N 11°25′E, see Supplementary Material). With an area of 70,500 km², it covers almost 20% of the land area of Germany; 36% of this area, i.e. 25,000 km², is covered by forests. Roe deer are abundant throughout Bavaria, with an annual harvest of approximately 280,000 animals (Deutscher Jagdschutzverband, 2010). In contrast, red deer *Cervus elaphus* occurs only in specific management districts, with an annual harvest of around 10,700 animals (Deutscher Jagdschutzverband, 2010). A very small population of fallow deer *Dama dama* lives in Bavaria, with an annual harvest of 400 animals.

2.2. Collisions Data

All DVCs (involving roe deer, red deer or fallow deer) records filed by the police in the whole study area between 2002-01-01 00:00 UTC+1 and 2011-31-12 24:00 UTC+1 were obtained from the Bavarian State Home Office (file access number IC4-3607.12-28). In addition, information about all other collisions that involved at least one car and were not classified as a minor accident by the police (non-DVCs) were obtained from the same source. The day and time of day accurate up to ±15 min was available for each collision. Under-reporting is a minor issue for both DVCs and non-DVCs as a police record is mandatory for any car insurance claim in Germany. There was no reason to assume differential reporting between DVCs and non-DVCs. The quality of non-DVCs as a surrogate for traffic intensity was evaluated on an independent set of hourly vehicle

counts obtained in 2006 and 2009 at 296 permanent traffic intensity monitoring devices (see Supplementary Material).

In principle, we were only interested in DVCs involving roe deer, and we therefore excluded all collisions that took place in a red deer management area (11% of the study area). Also, because human activity in larger cities without roe deer presence can be expected to differ from activity in suburban and rural areas, we excluded all collisions that took place in cities with more than 100,000 inhabitants.

The observational units of all subsequent analyses are based on 48×3652 half-hour intervals between 2002-01-01 00:00 UTC+1 and 2011-12-31 24:00 UTC+1. For each of these 175,296 intervals, we computed the number of DVCs and the number of non-DVCs based on the information in the police records.

2.3. Harvest Numbers

Annual harvest numbers for the years 2002 to 2011 were obtained from the Bavarian State Forest Administration. The administration manages 720,000 hectare of state-owned forests, roughly one-third of the forest area in Bavaria. Unlike state-wide harvest numbers reported by sport hunters, the harvest numbers filed by the Bavarian State Forest Administration are quality-controlled through internal and external accounting. Roe deer harvest numbers were planned in advance for each three year period based on a local assessment of roe deer browsing (Hothorn and Müller, 2010).

2.4. Statistical Analysis

Statistical models were used to infer annual, seasonal, weekly and diurnal patterns in the number of DVCs, the number of non-DVCs and the proportion of DVCs among all collisions. Nonparametric regression was used to visualise these three entities as smooth surfaces over the study period and time of day. The hypotheses specified in the Introduction were assessed by parametric models that allowed a decomposition of the overall expected number of non-DVCs and the proportion of DVCs among all collisions into annual, seasonal, weekly and diurnal effects. For both nonparametric and parametric models, the number of deer vehicle collisions DVC_{dm} and the number of other collisions non- DVC_{dm} not involving animals that were reported for each of the 48 half-hour intervals m at each of the 3652 days d were modelled by independent Poisson distributions with rates δ_{dm} and λ_{dm} , respectively.

2.4.1. Nonparametric Smoothing

In the two nonparametric models $\delta_{dm} = \exp(f_{DVC}(d, m))$ for DVCs and $\lambda_{dm} = \exp(f_{\text{non-DVC}}(d, m))$ for non-DVCs, the expected number of collisions on day d at time m was described by the two-dimensional interaction surfaces $\exp(f_{DVC}(d, m))$ and $\exp(f_{\text{non-DVC}}(d, m))$. These surfaces are functions of study day d and time of day m , where

$$d \in \{2002-01-01, \dots, 2011-12-31\} \text{ and} \\ m \in \{[00:00, 00:30), [00:30, 01:00), \dots, [23:30, 24:00)\}.$$

The two surface functions $f_{DVC}(d, m)$ and $f_{\text{non-DVC}}(d, m)$ were estimated nonparametrically under smoothness constraints using a generalised linear array boosting approach (Currie et al., 2006; Bühlmann and Hothorn, 2007; Hothorn et al., 2011); technical details

are given in the Supplementary Material. Visualisations of the fitted surfaces $\hat{\lambda}_{dm}$ and $\hat{\delta}_{dm}$ were used to identify the main temporal patterns in DVCs and non-DVCs without relying on strict model assumptions.

The main parameter we were interested in the quasi-induced exposure analysis (see [Stamatiadis and Deacon, 1997](#), for an overview) was the probability

$$\pi_{dm} = \delta_{dm}/(\delta_{dm} + \lambda_{dm})$$

of a collision taking place within half-hour interval m on day d being a DVC, i.e. the fraction of the expected number of DVCs and the total expected number of collisions in each of the 175,296 half-hour intervals. Since we can attribute the ‘cause’ of a DVC to deers, the problem of attributing cause to accidents doesn’t play a role here ([Chandraratna and Stamatiadis, 2009](#); [Jiang and Lyles, 2010](#)). Conditional on the total number of collisions ($\text{DVC}_{dm} + \text{non-DVC}_{dm}$), the number of DVCs for each half-hour interval m on day d follows a binomial distribution with size parameter equal to the total number of collisions and probability parameter π_{dm} (this is a standard result in probability theory, see for example [Lindsey, 1996](#)). The smooth interaction surface π_{dm} as a function of day d and time of day m was fitted by the same generalised linear array boosting procedure. The analysis of the DVC probability by means of a logistic regression allowed to formulate risks in terms of odds-ratios [Lardelli-Claret \(2005\)](#).

2.4.2. Parametric Modelling

For a formal statistical assessment of our six human-related and deer-related hypotheses, we modelled the expected number of non-DVCs and the DVC probability using a negative-binomial (with log link) and a quasi-binomial (with logistic link) generalised linear model, respectively. The models described the expected number of non-DVC λ_{dm} and the DVC probability π_{dm} as a function of a global intercept and the following effects:

annual effect: the difference between each year and the first year, 2002;

weekly effect: the difference between each day of the week (Sundays and bank holidays are treated the same) and Mondays;

diurnal effect: the difference between time of day in the intervals

“**Night (am)**”: [00:00, sunrise – 2h),

“**Pre-sunrise**”: [sunrise – 2h, sunrise),

“**Post-sunrise**”: [sunrise, sunrise + 2h),

“**Day (am)**”: [sunrise + 2h, 12:00),

“**Day (pm)**”: [12:00, sunset – 2h),

“**Pre-sunset**”: [sunset – 2h, sunset),

“**Post-sunset**”: [sunset, sunset + 2h) and

“**Night (pm)**”: [sunset + 2h, 24:00)

and the baseline category “Day (am)”;

weekly/diurnal effect: an interaction of the weekly and diurnal effects;

seasonal effect: an interaction of the diurnal effect with a smooth seasonal component $s(d)$.

The time of day-specific seasonal components $s(d)$ were modelled as a superposition of sinusoidal waves of different frequencies

$$s(d) = \sum_{k=1}^{10} \alpha_k \sin(k \times 2\pi \times d/365) + \beta_k \cos(k \times 2\pi \times d/365)$$

with unknown parameters α_k and β_k for $k = 1, \dots, 10$ (Diggle, 1990; Held and Paul, 2012). One such function was fitted for each time of day. Since by definition the integral of $s(d)$ over one year is zero, the seasonal effect $s(d)$ was interpreted as a seasonal deviation from the average effect of time of day. The multiplicative negative-binomial model for the number of non-DVCs addressed possible overdispersion, and we interpreted all estimated effects as multiplicative change from baseline after applying the exponential transformation to the estimated regression coefficients. The quasi-binomial model for DVC probability also dealt with possible overdispersion, and we interpreted the exponentiated estimated effects as odds-ratios to baseline. Simultaneous 95% confidence intervals for the annual and weekly effects as well as 95% confidence bands for the seasonal components for each time of day were obtained by simultaneous inference procedures described by Hothorn et al. (2008). In order to deal with potential autocorrelation remaining after modelling the temporal patterns of the DVC probability, we used a heteroskedasticity and autocorrelation consistent (HAC) sandwich estimators of the covariance matrices in both models (Zeileis, 2004). Model fit of the parametric models was assessed by comparing their fitted values $\hat{\delta}_{dm}$ and $\hat{\lambda}_{dm}$ to the respective fitted values obtained from the nonparametric smoothing method (see Supplementary Material).

2.4.3. Computational Details

All computations were performed in the R system for statistical computing (version 3.1.3, R Core Team, 2014) using the add-on packages **MASS** (Venables and Ripley, 2002; Ripley, 2015), **mboost** (Hothorn et al., 2010, 2015b), **multcomp** (Hothorn et al., 2008, 2015a), **coin** (Hothorn et al., 2006, 2014) and **sandwich** (Zeileis, 2004; Lumley and Zeileis, 2015). Data and source code are available for reproducibility (see Supplementary Material).

3. Results

[Figure 1 about here.]

The fine-scale temporal pattern of non-DVCs (Figure 1 A) was stable across the ten-year study period. Most collisions took place between 06:00 and 19:00 irrespective of season. Collisions clearly peaked during afternoon hours (14:00 to 17:00) throughout every year. Two seasonal peaks were identified in December and January, one in the morning (07:00-08:00) and one in the early evening (17:00-19:00); the latter peak was remarkably stable and prominent. Overall, the expected number of non-DVCs in 30 min was constantly between 2 and 14 throughout the study period. Non-DVCs served as a surrogate for traffic intensity. The number of vehicles passing 296 permanent traffic

intensity monitoring devices in 2006 and 2009 revealed the same pattern of increased traffic in the second half of the day (Supplementary Figure S 4). This indicates that the non-DVCs described traffic intensity relatively closely.

The fine-scale temporal pattern of DVCs (Figure 1 B) very clearly showed that DVCs occurred shortly after sunset and shortly before sunrise and in general during the dark hours. Almost no DVCs occurred during the day, except for two intervals around the beginning of May and the beginning of August. These seasonal patterns were extremely stable throughout the study period. The expected number of DVCs increased between 2002 and 2011. It is interesting to note that the expected number of DVCs in 30 min was as high as 16 and thus higher than the maximal expected number of non-DVCs, especially during the night.

The DVC probability (Figure 1 C) corrected the number of DVCs for other collisions. The overall temporal pattern was exactly the same as for the uncorrected DVCs (Figure 1 B). There seemed to be a relatively high DVC probability during the daylight morning hours in summer up to 10:00; an increase at the beginning of May and beginning of August was also clearly visible.

The absence of a strong seasonal pattern in non-DVCs and the presence of a very strong and annually stable seasonal pattern in DVCs justified application of relatively parsimonious parametric models that decomposed the annual, seasonal, weekly and diurnal effects describing human-related and deer-related processes. The fitted DVC probabilities from the nonparametric and parametric models were in good agreement (Figure 1 A and C and Supplementary Figure S 6), which indicated an adequate fit of the simpler parametric models.

3.1. Human-related Processes

Human-related processes were inferred from the non-DVC data. The multiplicative annual change in the expected number of non-DVCs for each year compared to that of 2002 (Figure 2 A) showed a decrease in the expected number of non-DVCs between 2002 and 2008 by about 10%. In the following years, there was a relatively stable plateau between 90 and 94% of the number of non-DVCs reported in 2002.

[Figure 2 about here.]

The variation in the expected number of non-DVCs over one week (Figure 3 A) identified a relatively stable risk on weekdays but showed a lower risk on weekends, especially on Sundays. More accidents occurred during Friday and Saturday nights than on nights during the week.

[Figure 3 about here.]

The seasonal pattern for each of the times of day (Figure 4 A) varied little during daytime and early dark hours. The risk was clearly higher towards the end and beginning of each year, in the morning and during the first hours of the night. During the summer months with early sunrise and late sunset, the risk around dusk and dawn was relatively low.

[Figure 4 about here.]

3.2. Deer-related Processes

Deer-related processes could be identified from the adjusted DVC probability by removing the human-processes discussed above. The annual change in the corrected DVCs measured by the odds-ratio for each year relative to 2002 (Figure 2 B) was significantly larger than one since 2004 and steadily increased up to 2008. From 2008 onwards, we observed a plateau at about 1.25 corresponding to a 25% higher DVC odds at the end of the study period compared to 2002.

The diurnal pattern of DVCs (Figure 3 B) showed a very low risk of a DVC during the day and before sunset. The odds-ratio increased with sunset and stayed very high during the whole night. Also before and after sunrise, the DVC odds was roughly ten times higher than that two hours after sunrise. The pattern was stable for all days of the week, except for a lower odds in the early hours on the weekend. The odds of a DVC during daytime on Sundays and holidays slightly increased.

The seasonal DVC odds (Figure 4 B) was high in the warm months during the night and early morning, with a steep increase during April and May. The odds sharply peaked during the day around the rutting period in late July and early August. The higher odds starting around March/April were only visible during the night and until midday but not in the afternoon.

The seasonal patterns in the morning (day am), afternoon (day pm) and pre-sunset were used to identify the average beginning (local minimum before the maximum), peak (all-year maximum) and ending (local minimum after the maximum) of the rut. The morning estimates indicated a beginning of the rut on July 23, its peak on August 3 and its ending on August 16. The afternoon estimates led to estimated ruts between July 23 and August 16, with a peak on August 4. The estimates shortly before sunset indicate a rut between July 22 and August 17, with a peak at August 3.

3.3. Annual DVC Probability and Harvest Numbers

[Figure 5 about here.]

The fraction of the annual harvest numbers (relative to 2002) for the state-owned forests in the study area showed a positive relationship to the annual odds-ratio of the DVC probability (Figure 5, Spearman's rank correlation coefficient $\rho = 0.631$, exact conditional p -value = 0.013). The simultaneous confidence intervals for the estimated odds-ratios of DVC and multiplicative change in annual harvest numbers relative to 2002 indicated a clear temporal increase in both parameters. In all years, the increase in harvest was lower than the increase in DVCs; for 2007-2009 and 2011, the corresponding confidence intervals did not overlap. In 2006, the forest administration underwent a major structural reorganisation, which explains the outlier in that year. After excluding the 2006 observation, the slope of a linear regression of DVC odds-ratio on the multiplicative change in harvest numbers was 1.096 (95% confidence interval 1.056–1.135), which also indicated that the number of DVCs increased at a higher rate than the harvest numbers.

4. Discussion

During the last decades car traffic and DVCs have increased across much of Europe (Groot Bruinderink and Hazebroek, 1996; Langbein et al., 2011; Steiner et al., 2014). Due

to the parallel increasing trends in both deer and car numbers and the decreasing number of car accidents (Shen et al., 2013, the effect is also present in our non-DVC data), it has proven difficult to tease apart the extent to which the two processes determine the number of DVCs: human-related activity, especially traffic intensity, and deer-related activity and numbers. It is important to account for human activity in the analysis of DVCs but the analysis of the proportion of fatal animal-vehicle collisions and other fatal collisions by Sullivan (2011) is the only paper implementing such an adjustment we are aware of. Precise large-scale information about traffic intensity is hard to obtain, especially in the rural areas where most of the DVCs studied here took place. We therefore used the number of non-DVCs as a surrogate measure. The advantage of adjusting DVCs by non-DVCs is that both numbers were recorded by the same local police posts with equal precision. However, road safety mitigation measures successfully lowered the number of non-DVCs in the study period and area (Shen et al., 2013), while traffic intensity (measured by the numbers of registered cars and passenger kilometers) increased slightly. For the study area, evidence for a good agreement between traffic intensity and the number of non-DVCs patterns is presented in the Supplementary Material. Thus, non-DVC accidents arguably reflect human-related activity that causes variation in traffic intensity rather closely. The residual pattern in DVCs after accounting for non-DVC accidents is thus expected to reflect deer-related activity and numbers. Overall, we found a pattern in diurnal, weekly, seasonal and annual variation in DVCs highly consistent with the hypothesis that mainly deer-related activity drives the DVC risk pattern. Some residual human activity remained, with fewer DVCs on weekends than on weekdays. This relatively minor human component in the temporal DVC patterns reported here also suggests that a spatio-temporal analysis will possibly reveal a large spatial heterogeneity (see Hothorn et al., 2012, for Bavaria) but the temporal pattern can be expected to be rather stable (as reported by Rodríguez-Morales et al., 2013).

4.1. DVC and Deer Density—A Density-Dependent Relationship?

The clear link between deer abundance and DVCs is rather intuitive, but its quantification is challenging because both human and deer activity influence DVCs (Mysterud, 2004). In our analysis, we were able to control for such human activity by means of the number of non-DVCs. During the study period, the number of non-DVCs did not increase; indeed, the annual number of non-DVCs decreased by 5 – 10% over ten years. At the same time, the proportion of DVCs among all collisions increased by 25%. The traffic-adjusted increase in the annual DVC odds-ratios thus cannot be explained by increased traffic intensity. Therefore, the reason for this increase must be endogenous, and an overall increase in deer density is the most likely cause. For the study area and period, there is a lack of information about roe deer densities because state-wide roe deer population counts were not available (in contrast to white-tailed deer counts analysed by Gkritza et al., 2010). Therefore, hypothesis H2a (higher deer density increases the chance of deer crossing roads and thus DVCs) is only indirectly supported by our data. However, an additional corresponding increase, although slightly lower, in harvest numbers was found. This adds further evidence for hypothesis H2a. Roe deer densities and thus DVCs can be expected to increase further because of an underproportional increase in harvest numbers. Consistent with this role of roe deer density for DVCs, also the spatial analysis of Hothorn et al. (2012) in the same study area showed that the DVC risk is highest in suburban areas (median population density) with both high human activity

and high deer densities and is lowest in urban (high population density) and extremely rural areas (low population density) corresponding to either low human or deer activity.

Although a monotone impact of density on DVCs is a good interpretation of our results, the interesting question of whether the relationship is linear or rather increases with deer density, i.e. positively density dependent, remains difficult to assess. In general, habitat selection (Mobaek et al., 2009; Blix et al., 2014; van Beest et al., 2014), activity (Mobaek et al., 2012) and home range size (Kjellander et al., 2004) of large herbivores are density dependent. In particular, at high density, more habitats are used, which also forces deer into more urban environments, and one might therefore expect a more than proportional increase in DVCs with increasing density of deer. An analysis of the relationship of DVCs (with red deer involved) over time in Norway suggests that DVCs increase more than expected considering deer density levels (harvest numbers), but it was not possible to determine whether this was due to positive density dependence or to a parallel increase in car traffic (Mysterud, 2004). For roe deer in France, the reason reported was more deer occupying forested areas at high deer density (Hewison et al., 1998). Vincent et al. (1988) report that increased roe deer density has a nonlinear impact on the number of DVCs. Our scatterplot of DVC odds-ratios and multiplicative change in harvest numbers suggests a linear relationship, but with a slope larger than one. The harvest number is in itself influenced by human activity and thus is an uncertain surrogate for deer density, but we have no indication of positive density dependence.

4.2. Deer and Human Daily Activity Pattern: Both are Drivers of DVC

The deer activity pattern in general (e.g., Beier and McCullough, 1990) and specifically for roe deer (Cederlund, 1981, 1989; Jeppesen, 1989) is well documented in studies of marked animals, and provides clear predictions for peaks in DVCs on diurnal and seasonal scales (see Introduction). Similarly, we can expect more car traffic before and after office hours irrespective of season and daylight, but only on weekdays. We found clear evidence that both processes affected the pattern of DVCs. The patterns were strongly diurnal in both the expected number of non-DVCs and the DVC probability. Most non-DVCs take place during the day, with a very high-risk period during the afternoon. The lack of a corresponding peak in the morning contradicts hypothesis H1b (a peak in traffic before and after office hours irrespective of day length leads to a higher number of non-DVCs). Additional information about traffic intensity revealed that direct measurements of traffic intensity exhibit the same intraday patterns. The crepuscular activity pattern typical for roe deer and many deer species is very clear in the DVC probability (Figure 1 C), i.e. the risk of a DVC post-sunset is ten times higher than before sunset; the reverse effect can be seen in the morning (H2b; roe deer are more active at dusk and dawn). In addition, the DVC probability is very high during the whole night. This effect is not only explained by a high deer activity during the night, but likely also by the deer being less visible at night (H1c; deer are more difficult to spot during dark hours, which leads to an increased proportion of DVCs among all collisions during the night). During night, roe deer also use more open areas, including agricultural fields (Mysterud et al., 1999b,a). It is thus likely that also the diurnal pattern of habitat selection by roe deer might play a further role, with more frequent crossing of roads during darkness. Further indication for a role of human activity was clear evidence that the assumed higher human activity on weekdays than on weekends (H1a; increased traffic on weekdays increases the

risk of collisions in general, and reduced human traffic on weekends and holidays corresponds to a lower number of non-DVCs) is clearly visible in the expected number of non-DVCs, whereas there were no strong weekly patterns in the DVC probability. The slightly decreased DVC odds-ratios during the early Saturday and Sunday hours may be explained by the increased high-risk night traffic of party-goers heading home, also observable in the number of non-DVCs (compared to weekdays). Thus, overall human activity has the same impact on the number of non-DVCs and the number of DVCs as the DVC probability remains constant. With the hypothesis of constant roe deer density, and thus constant risk of deer crossing roads, we would have expected the annual DVC odds-ratio would be close to one for all years. The DVC odds-ratios exceeding one found in the data analysed here is in agreement with the most likely scenario of a 25% increase in roe deer densities between 2002 and 2011.

4.3. Seasonal Patterns in Deer Activity, But Not Human Activity

We found no clear seasonal pattern in the number of non-DVCs, except the increased numbers of non-DVCs in the morning hours between December and January; the effect is presumably due to commuter traffic during dark hours under typical winter road conditions. The lack of strong seasonal patterns in human activity allows us to attribute the prominent seasonal effects in the DVC probability to deer activity. We found well-known activity peaks during summer and especially during the rut (H2c, [Cederlund, 1981](#); [Jeppesen, 1989](#); [Rodríguez-Morales et al., 2013](#)). Thus, the DVC probability is likely to reflect the seasonal roe deer activity patterns. Roe deer is the only cervid with summer rutting, and the social organisation of roe deer is very similar across Europe. We identified an increase in DVCs around July 22-23, a peak on August 3-4 and a decrease again on August 16-17, which is highly consistent with the reported period of roe deer rutting ([Sempéré et al., 1998](#)). Our data lack information about the sex of animals involved in DVCs; therefore, an assessment of increased mobility of males during this period (as reported by [Liberg et al., 1998](#)) was not possible. Further evidence that the increased DVC risk between mid-July and mid-August is linked to rutting activity pattern comes from a study in France. [Vincent et al. \(1988\)](#) report that male roe deer are more often killed than female roe deer during the rutting period. Although also females make excursions outside their usual range during the rut ([Debeffe et al., 2014](#)), this is apparently less important than the increase in male movements ([Liberg et al., 1998](#)). Other cervid species rut later, typically in September-October, depending on latitude ([Loe et al., 2005](#)). Consistent with this, peaks in DVCs with moose ([Lavsund and Sandegren, 1991](#)) and white-tailed deer ([Allen and McCullough, 1976](#)) during fall have been found. In some areas, hunting and rutting periods coincide ([Sudharsan et al., 2006](#); [Rodríguez-Morales et al., 2013](#)), which makes it difficult to tease their effects apart. In Bavaria, roe deer hunting starts May 1 and ends January 15; therefore, an additional hunting effect contributing to the rut peak is unlikely. More specifically, a direct hunting effect leading to more DVCs during intensive hunting periods (buck hunting season at the beginning of May and driven hunts in late autumn) was not observed in the DVC probability ([Rodríguez-Morales et al., 2013](#), report a similar result for Spain). The steep increase in DVC probability started earlier than May 1, in late March (Figure 4 B), and the DVC probability was extremely low during the daytime between October and December, when driven hunts typically take place.

5. Conclusion

Road managers, wildlife managers and authorities in general can benefit from the results reported here. The high-resolution temporal pattern of roe deer activity derived from DVC data, potentially combined with existing spatial patterns (Hothorn et al., 2012; Rodríguez-Morales et al., 2013), allows implementation of tailored driver warning systems, e.g. in car navigation systems, and temporary reductions of speed limits. The strong habituation effects of permanent deer crossing traffic signs can be avoided by the implementation of a spatially and temporally targeted warning system based on the data-driven risk assessment reported here. The implementation of state-wide measures to decrease roe deer density considerably is mandatory to prevent a further increase in DVC numbers. The quantification of increasing deer densities is the first evidence-based report on this phenomenon in the study area, awaiting appropriate response from both road and wildlife managers. A joint monitoring system for DVCs and non-DVCs is a powerful yet inexpensive approach to detect changes in the spatio-temporal distribution of deer and other ungulates, taking changes in human activity patterns into account.

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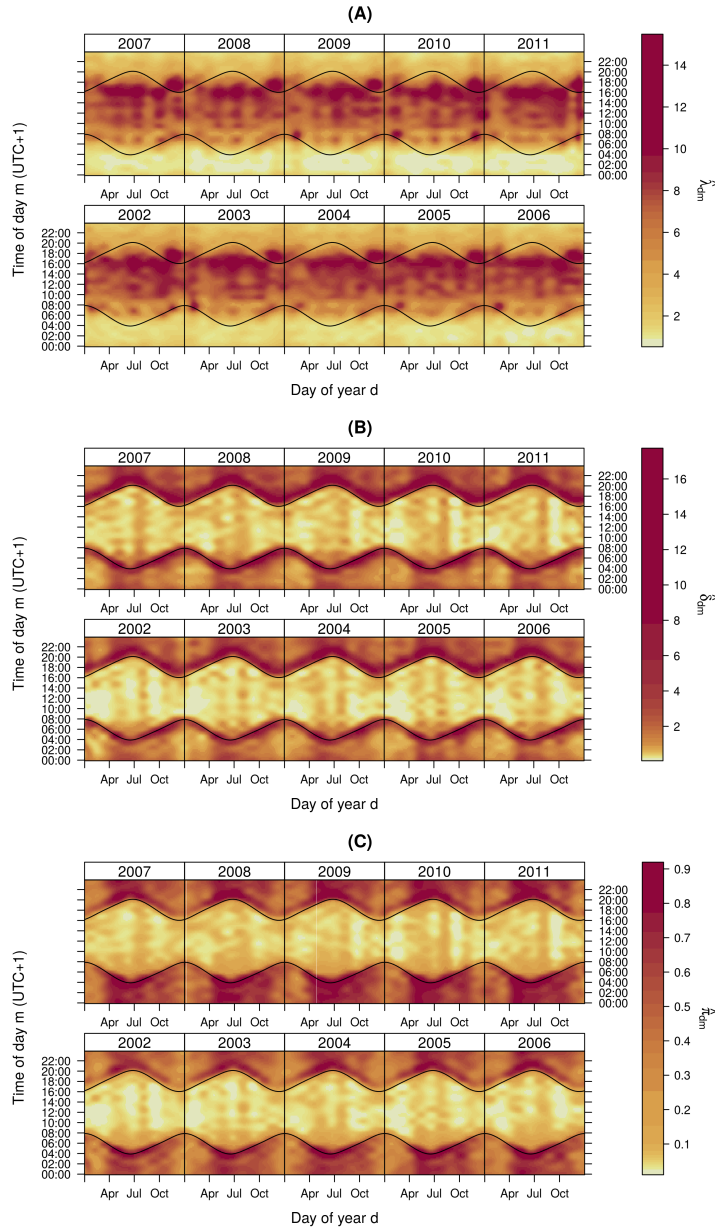


Figure 1: Smoothed expected numbers of non-deer-vehicle collisions (non-DVCs) $\hat{\lambda}_{dm}$ (A), expected number of deer-vehicle collisions (DVCs) $\hat{\delta}_{dm}$ (B) and DVC probability $\hat{\pi}_{dm}$ (C) for each of the 48×3652 half-hour intervals between 2002-01-01 00:00 UTC+1 and 2011-12-31 24:00 UTC+1. Solid black lines indicate sunrise and sunset; the colour palette is quantile based. Supplementary Figure S 5 contains animated versions of (A) and (B).

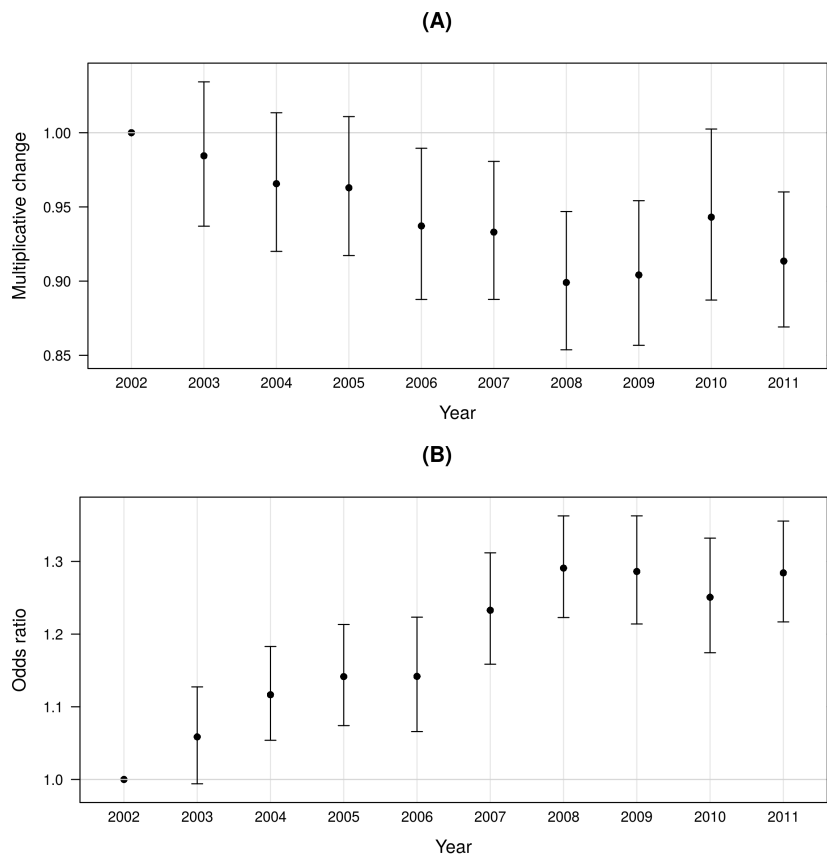


Figure 2: Multiplicative change for each year (reference: 2002) with simultaneous 95% confidence intervals for the expected number of non-deer-vehicle collisions (non-DVCs, A) and the odds-ratio of deer-vehicle collisions (DVCs, B).

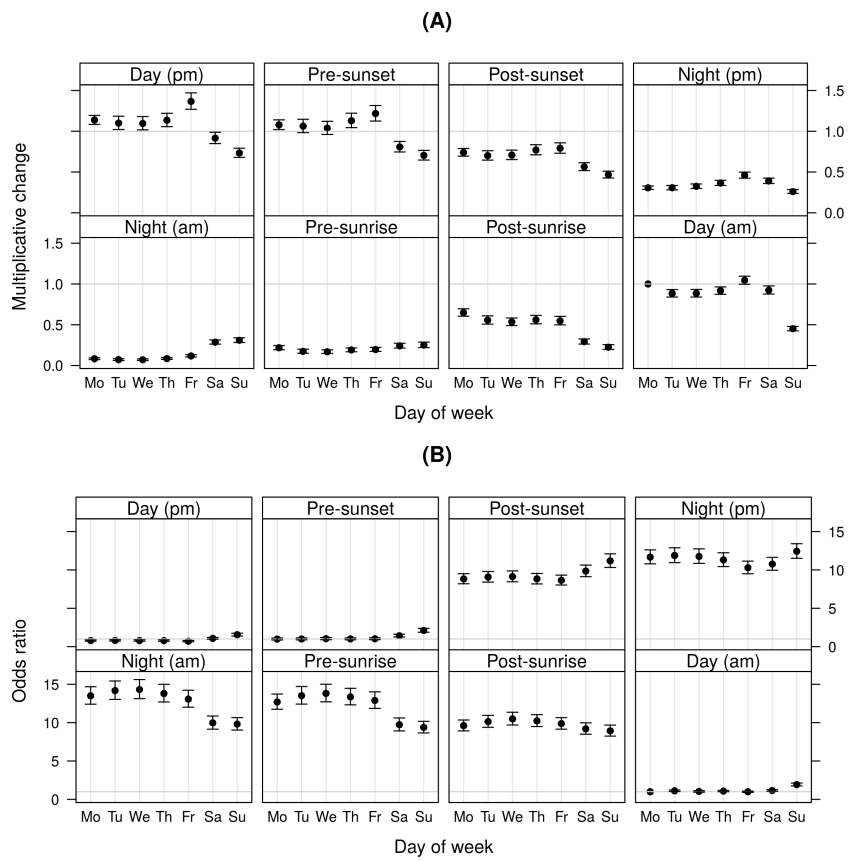


Figure 3: Multiplicative weekly and diurnal change (reference: Monday day (am)) with simultaneous 95% confidence intervals for the expected number of non-deer-vehicle collisions (non-DVCs, A) and the odds-ratio of deer-vehicle collisions (DVCs, B).

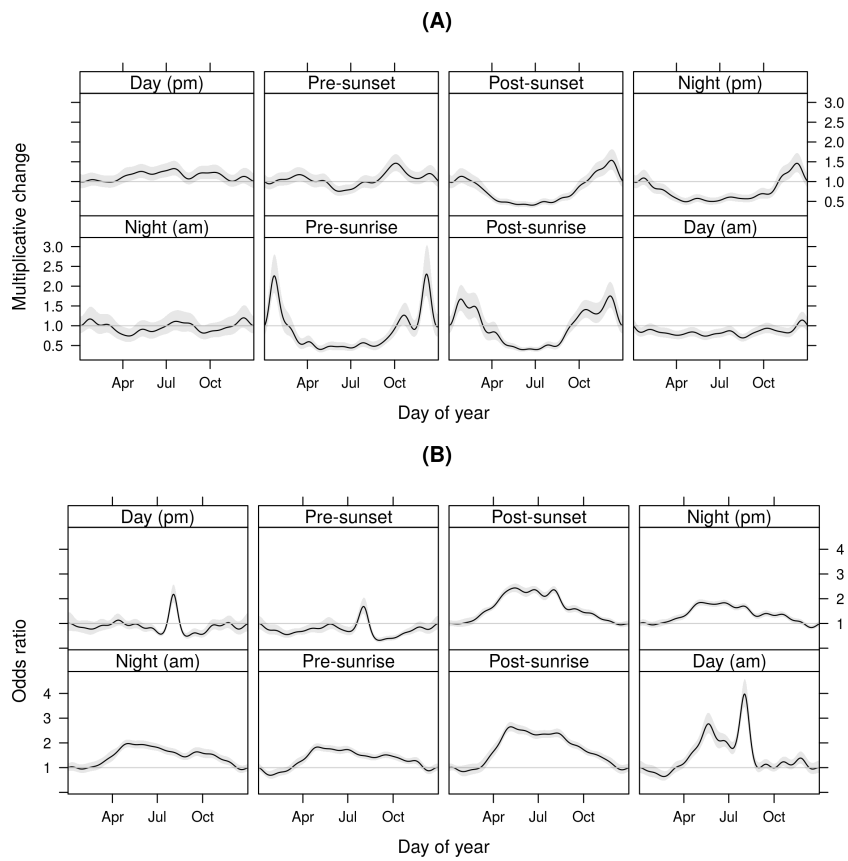


Figure 4: Multiplicative seasonal change (reference: January 1 with corresponding time of day) with simultaneous 95% confidence bands for the expected number of non-deer-vehicle collisions (non-DVCs, A) and the odds-ratio of deer-vehicle collisions (DVCs, B).

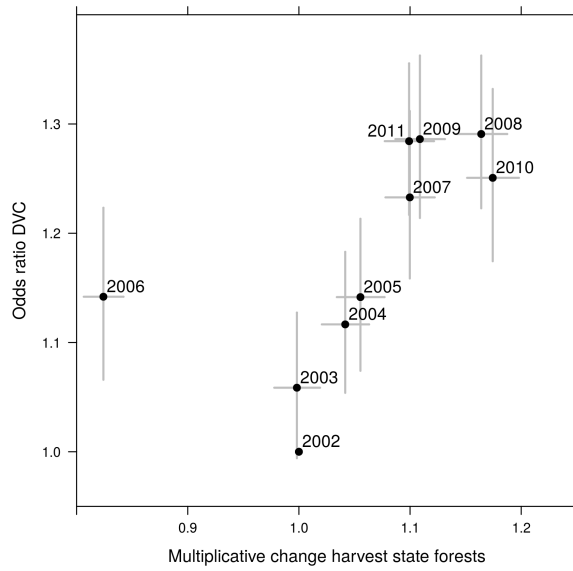


Figure 5: Scatterplot of odds ratios of deer-vehicle collisions (DVCs) versus multiplicative change in annual harvest numbers (both relative to 2002). Vertical grey lines indicate simultaneous confidence intervals for the odds ratios of DVCs (same as in Figure 2 B) and horizontal grey lines indicate simultaneous confidence intervals for the multiplicative change in annual harvest numbers.