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RESEARCH ARTICLE

Accounting for cloud cover and circannual variation puts the effect of lunar phase on deer–vehicle collisions into perspective

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Abstract

1. Although several studies have focused on the influence of moonlight on deer–vehicle collisions, findings have been inconsistent. This may be due to neglect of the effects of cloud cover, a major impediment to moon illumination and circannual variation in both deer and human activity.
2. We assessed how median cloud cover interacted with the illuminated fraction of the moon in affecting daily roe deer (*Capreolus capreolus*) roadkill in Slovenia (Central Europe). Data included nationwide roadkill ($n = 49{,}259$), collected between 2010 and 2019 by hunters, as required by law.
3. Roadkill peaked under medium to high cloud cover and decreased during nights with low or extremely high cloudiness. This pattern was more pronounced on nights with a full moon. However, the effects of moon illumination and cloud cover had a lower predictive potential than circannual variation, as collisions clearly peaked in April/May, July and August/September.
4. Our results suggest that moonlight could influence roe deer movements through compensatory foraging. However, on nights with a full moon, collisions could also be affected by weather. On bright nights, roe deer might be less active due to increased human presence and sustained vehicular traffic. Then, with medium to high cloud cover and also rainfall, human presence in the environment may be low enough to increase deer movements, but vehicular traffic can still be intermediate, maximizing the risk of collisions. Finally, with overcast skies, widespread rainfall can reduce both traffic volume and human outdoor activity, decreasing the risk of collisions.
5. Moon illumination may indeed affect wildlife–vehicle collisions and roadkill, but its effects should be quantified as a function of cloud cover. Moreover, to make studies truly comparable, research about wildlife–vehicle collisions should also account for time of the year.
6. *Policy implications*. Because collisions with roe deer peak at particular periods of the year, signs should be installed seasonally. By doing so, they would warn drivers about the risk, improve drivers' awareness and increase their safety. Moreover, as collisions also increase on nights with a full moon and overcast skies, interactive warning signs that are activated by ground illumination should also be useful.

KEYWORDS
cloudiness, MODIS Surface Reflectance, moon, road ecology, roe deer, Slovenia, thin-plate splines, wildlife–vehicle collisions

1 | INTRODUCTION

Understanding environmental and biological factors that affect wildlife roadkill is fundamental to predict their spatial and temporal occurrence, and thus mitigate their effects on human welfare (Bissonette et al., 2008; Conover, 2019) and wildlife populations (Hill et al., 2019; Schwartz et al., 2020). Although many studies have focused on which landscape features are associated with collision hotspots or the circadian patterns of collisions, less attention has been paid to which environmental or seasonal factors drive their occurrence over time (Pagany, 2020).

Among environmental factors associated with wildlife roadkill, moon illumination has received a certain attention, due to its widespread influence on ecological dynamics in terrestrial and aquatic ecosystems (Kronfeld-Schor et al., 2013). In terrestrial mammals, lunar cycles alter movement, primarily by acting on foraging and antipredatory behaviour (Prugh & Golden, 2014). For example, in cervids (deer species), probably the most studied mammals in road ecology (Steiner et al., 2014; see also Table S1), some species were found to increase their movements during full moon nights, although no universal consensus exists (Sullivan et al., 2016). Thus, by affecting the movements of wild ungulates, full moon nights are thought to promote road crossings and collisions with vehicles. In addition, there is mounting evidence that full moon may also slightly increase accident risk by affecting drivers' behaviour, through distraction (Onozuka et al., 2018; Redelmeier & Shafir, 2018) or an increase in perceptual errors (Jägerbrand & Sjöbergh, 2016; Singh & Kathuria, 2021).

However, findings from the few studies that have examined the effect of moon illumination on wildlife–vehicle collisions are quite contradictory (see Table S2). While some indeed found that vehicles and trains collide more with deer at some particular times of the lunar cycle (e.g. full moon nights; see Colino-Rabanal et al., 2018; Gundersen & Andreassen, 1998; Ignatavičius et al., 2021; Kawata, 2011; Steiner et al., 2021), others found no effect at all (Kreling et al., 2019; Vrkljan et al., 2020) or showed that lunar cycles were associated with collisions only at certain times of the year (Colino-Rabanal et al., 2018; Muller et al., 2014). Finally, studies that considered multiple species found significant species-specific differences in the effect of lunar cycles on roadkill (Mayer et al., 2021).

This heterogeneity can be caused by several factors, including behavioural differences among deer species, or different traffic volumes and patterns. Moreover, while some studies relied on time-series analysis (Steiner et al., 2021) or spatiotemporal modelling (Mayer et al., 2021), others compared pooled data through null-hypothesis testing (Colino-Rabanal et al., 2018). Another important but yet underestimated factor, that may have biased results from previous studies, is cloud cover. Although cloud cover generally increases the number of collisions due to precipitation, which makes driving far more demanding than usual (Maze et al., 2006; Qiu & Nixon, 2008) and also either increase or decrease traffic volume (Maze et al., 2006), clouds are also a major barrier to moonlight, reducing moon illuminance and irradiance up to 99.7%–99.9% (Krieg, 2021), and thus curtailing illumination on the ground. Illumination on the ground is the primary mechanism by which the moon affects ungulate nocturnal movement, as it enables the use of vision (D'Angelo et al., 2008) and thus is important for effective spatial orientation and antipredatory vigilance (Lashley et al., 2014), in turn enabling compensatory or cumulative foraging (Grignolio et al., 2018).

Thus, a failure to account for cloud cover may lead to false associations between lunar cycles and wildlife–vehicle collisions. What makes terrestrial wildlife move at night is the available illumination on the ground, not the lunar cycle per se. Although this idea has already been considered in movement ecology (Brivio et al., 2017; Grignolio et al., 2018), it has been ignored in road ecology, despite being mentioned in some studies (Colino-Rabanal et al., 2018; Ignatavičius et al., 2021; Vrkljan et al., 2020).

In this study, we provide the first quantification of the combined effects of lunar cycles and cloudiness on deer–vehicle collisions by combining: (i) daily data on roadkill of European roe deer (*Capreolus capreolus*) as a reliable indicator of the number of collisions between this species and vehicles, collected across Slovenia in a 10-year period (2010–2019) through a robust and standardized protocol (for details, see Pokorny et al., 2022), (ii) data on lunar cycles and (iii) time series of remote sensing data on cloud cover.

2 | MATERIALS AND METHODS

2.1 | Study area and data collection

The study area covered the entire land area of Slovenia, a central European country spanning over 20,273 km^2, characterized by a complex assemblage of mammals, including high densities of large carnivores and ungulates (Ražen et al., 2020; Skrbinšek et al., 2019; Stergar et al., 2009). There are no large urbanized areas in Slovenia, and environmental connectivity between undisturbed habitat patches makes wildlife prone to live alongside with humans and susceptible to collision with vehicles (Pokorny, 2006; Pokorny et al., 2022).

In our study, we considered collisions between vehicles and European roe deer, the most widespread deer species in Europe (Apollonio et al., 2010), and by far the most frequently involved in collisions with vehicles of all European ungulates (Langbein et al., 2011). Roe deer is common in anthropogenic areas, where it adapts its activity rhythms to cope with human disturbance (Bonnot et al., 2020). Roe deer is most active at dawn and at dusk, when traffic volume is also high due to daily commuting movements. Therefore, the species is very often involved in collisions with vehicles (Hothorn et al., 2015; Ignatavicius & Valskys, 2018; Langbein et al., 2011). In Slovenia alone, between 4000 and 6000 vehicles collide with roe deer each year (Pokorny, 2006; Pokorny et al., 2022).

Our data include almost all registered roadkill of roe deer in Slovenia (i.e. in all hunting grounds, managed by hunting clubs) between 2010 and 2019 ($n = 49{,}259$), recorded on paved and dirt roads (Figure 1). Data from 2020 were not included because this year was characterized by a significant change in wildlife–vehicle collisions (including roe deer) in Slovenia, caused by COVID-19 lockdowns (Bíl et al., 2021; Pokorny et al., 2022). Data on roadkill were obtained from an on-line information system, developed in 2006 by the Hunters Association of Slovenia (HAS), with the aim of collecting and archiving data on wildlife mortality, including roadkill. The information system includes a mobile application for trained data officers (i.e. assigned hunters for each hunting ground), aimed to register a roadkill in situ, and a reporting scheme for nonhunters through the regional emergency call centres. All carcasses reported to the emergency call centres are immediately associated with the hunting ground where the collision occurred and are rapidly removed by a commissioned hunter. Afterwards, data officers upload biological data relevant for the individual, date and exact location of a collision in a national database. Hunters are incentivized to register each roadkill, as harvest plans in Slovenia are based on total 'elimination quotas' (i.e. hunting bags, plus all the individuals found dead), and hunting ground managers can be fined (4200–125,000 €) when quotas are not met. On the other hand, over-reporting is prevented by the fact that hunters have to collect, prepare and hand over relevant proof of individuals that are found dead (e.g. left hemimandible for each ungulate).

We excluded data from 12 hunting grounds with special purposes (approx. 10% of Slovene surface) managed by public institutions (the Slovenia Forest Service and the Triglav National Park). We excluded them because they are quite large (25,000–60,000 ha) and are located in remote areas, so the percentage of undetected road-mortality cases might be higher. Moreover, these remote areas have low road densities, and the frequency of roadkill there is very low (Pokorny et al., 2022).

To carry out this study, we did not need neither any licence from competent authorities, nor the approval from an animal ethics committee. This because our research activity involved only the analysis of roadkill data that had already been collected by the HAS, as part of its regular professional activities, between 2010 and 2019.

2.2 | Statistical analysis

We predicted the number of daily collisions between vehicles and roe deer (based on registered roadkill data), according to a set of relevant covariates, by means of generalized additive models. We adopted a negative binomial distribution of the response variable as this distribution approximated well the distribution of the roe deer roadkill (see Figure S1).

We did not include spatially explicit covariates, such as artificial light at night (Ciach & Fröhlich, 2019; Ditmer et al., 2021) or rainfall, as these can be quite hard to measure at a good spatiotemporal resolution.

Although some previous studies argued that roe deer activity decreases (Jasińska et al., 2020) or does not change with increasing moonlight (Pagon et al., 2013), these studies did not quantify cloud cover, so we did not consider their findings.

The lunar cycle was measured as the illuminated fraction of the moon, varying between 0 (dark nights) and 1 (nights with full moon). Values were extracted for Central European Timezone with R, through the package 'suncalc' (Thieurmel et al., 2019).

Cloud cover was measured through the MODIS Surface Reflectance products, obtained from Terra and Aqua satellites. Time series, with a spatial resolution of 1 km, were processed through the Google Earth Engine platform (https://earthengine.google.com/platform/) exploiting the datasets: MODIS/061/MOD09GA and

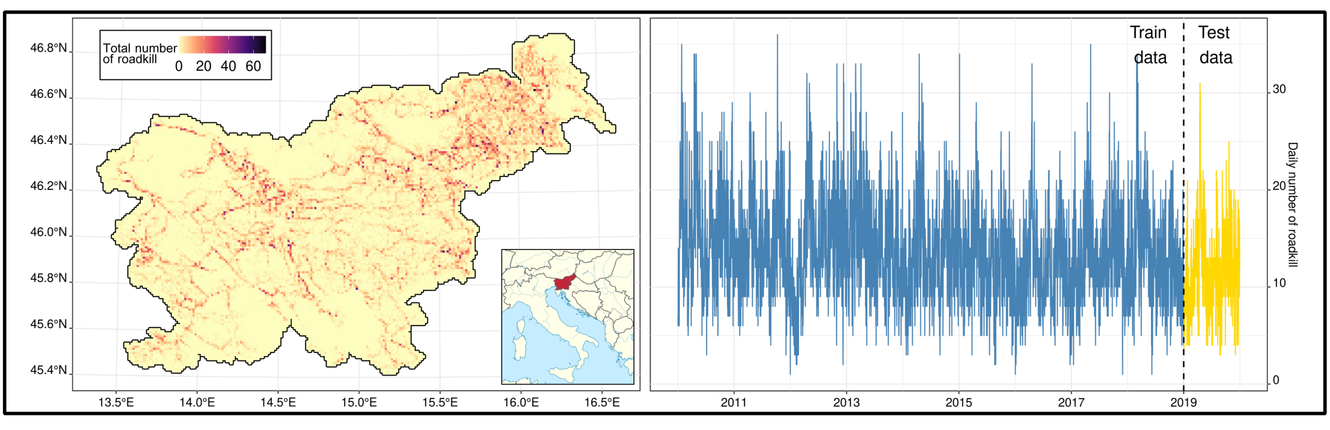

FIGURE 1 Map of the study area (on the left), depicting the total number of road-killed roe deer in Slovenia, between 2010 and 2020. Daily number of roadkill involving roe deer (on the right), between 2010 and 2019, highlighting train and test data used in the analyses.

MODIS/061/MYD09GA. These data offer a daily estimate of the surface spectral reflectance as it would be measured at ground level in the absence of atmospheric scattering or absorption. Based on the 'state_1km' band, we classified 1 km cells as covered by clouds (cloudy and mixed cloudy), or not (clear and not set, assumed clear). Values were then averaged between Terra and Aqua satellites, to merge morning (Terra) and afternoon (Aqua) MODIS data. Next, the proportion of covered cells was calculated for each day of the time series and for the entire study area (e.g. a value of 0.6 indicated that 60% of 1 km-wide cells were covered by clouds). As Slovenia covers a relatively small area, this approach was deemed to be suitable at the national scale to distinguish days on which weather conditions were generally bad from days with bright skies.

To further regularize time series, we also included three more variables that can increase wildlife–vehicle collisions. The first one was the day of the year, as it captures the duration of the day and thus the importance of moonlight on animal movements (through multiple mechanisms: Martin et al., 2018; Morellet et al., 2013; Peters et al., 2019), the volume of vehicular traffic and its overlap with activity rhythms of deer at dawn and dusk (Rodríguez-Morales et al., 2013). The second one was the day of the week, as vehicular traffic is different between work-week days and the weekend, when the consumption of alcohol and drugs can also make driving more dangerous. We also included the year of each roadkill: this variable captured long-term trends in wildlife–vehicle collisions, caused by a mixture of processes, such as simultaneous changes in the abundance of roe deer, in the volume of vehicular traffic or in road development in Slovenia, as well as long-term changes and interannual variability in vegetation characteristics, which could indirectly affect collisions by acting on roe deer behaviour (e.g. masting: Bogdziewicz et al., 2020; vegetation development: Aikens et al., 2020). We decided to use a single variable, corresponding to the year of each roadkill, as not all these processes had been adequately quantified for each year in Slovenia, at the time of the study.

The day of the week was treated as ordered factors with zero-sum contrasts, where the value of each level was compared to the average value of roadkill. The year was treated as a linear term, after we could not detect any pattern in model residuals. Continuous variables were centred and standardized.

Model selection was conducted using a forward stepwise approach. We started by fitting a null model and then added covariates, and interaction terms. The effect of lunar cycle and cloud cover was modelled by considering thin-plate splines, tensor splines and cyclic cubic splines. The effect of the day of the year, and in some cases its three-way interaction with lunar cycle and cloud cover, was modelled through a thin-plate spline, a tensor spline, a cyclic cubic spline and a Gaussian process. A complete overview of these smoothers is provided in Wood (2017). Fitted models were then compared based on the mean absolute percentage error (MAPE), when trained on test dataset containing daily roadkill in 2019, and also by using the Akaike's information criterion (AIC) and the residual deviance as a complementary criterion to evaluate the performances of nonautoregressive models. The best candidate model was the one with the lowest value of the MAPE. The MAPE expresses the mean absolute percentage errors of forecasts, expressed as the difference between observed and forecasted values of a time series. It is evaluated as a per cent value, meaning that a value of, for example, 20% indicates that the average difference between predicted and observed values is 20% (Swamidass, 2000). A complete overview of model fitting is available in Table 1.

Statistical analyses were carried out in R (R Core Team, 2022). A reproducible software code for R and Google Earth Engine, altogether with the reproducible dataset about road-killed roe deer, is available in Cerri et al. (2022).

3 | RESULTS

Model selection indicated relatively small differences among best candidate models. While model fit improved when we accounted for the effects of each year, day of the week and interplay between the lunar cycle and cloud cover, most of the predictive accuracy came from accounting for circannual variation, by using the day of the year as a covariate (Table 1). Namely, the best candidate model, which had a MAPE of about 36% when tested on 2019 roadkill data, adopted a bivariate thin-plate spline for measuring the interplay between cloud cover and the lunar cycle, and an adaptive thin-plate spline for the effect of the day of the year. Interestingly, although the autocorrelation density function of model residuals highlighted temporal dependence between observations, this was not eliminated through first-, second- or third-order autoregressive correlation structures.

The number of road-killed roe deer increased with the illuminated fraction of the moon, and peaked at full moon nights; there was also a nonlinear relationship with cloud cover. Roadkill peaked at intermediate values of cloud cover. The effect of cloud cover on roadkill had a clear interaction with the lunar cycle, being more pronounced on nights with a high moon illumination than on nights without the moon. The lowest number of collisions was observed on nights with a new moon and very low or, on the contrary, high cloudiness through Slovenia (Figure 2).

The day of the year had a much stronger marginal effect on collisions, in terms of magnitude, than lunar cycles and cloud cover. Roadkill peaked at three distinct periods of the year. The first, and the most pronounced peak was in April/May, followed by a second one in September/October, while a third, lower peak was observed in July (Figure 3).

4 | DISCUSSION

Our results indicate that road ecology studies should take a holistic approach when evaluating the effects of environmental correlates on wildlife–vehicle collisions. This is especially true in complex and cross-related variables, such as the lunar cycle, whose effects depend on other factors, such as cloud cover. Consideration of cloud cover revealed an important, yet variable, effect of the lunar cycle

TABLE 1 Comparison of selected models, the mean average percentage error (MAPE, calculated on 2019 data), the Akaike's information criterion (AIC), and model deviance. For each model, the formula mimics that of the 'mgcv' package (Wood, 2017): 'ad.cc', adaptive cyclic cubic spline; 'ad.cp', adaptive p-spline; 'ad', adaptive thin-plate spline; 'cc', cyclic cubic splines; 'gp', Gaussian process; 'te', full tensor product smooth; 'ti', tensor product interaction; 'tp', thin-plate splines. 'AR1', 'AR2' and 'AR3' indicate a first-, second- and third-order temporal correlation between residuals. Models with an autoregressive structure of residuals were fitted through penalized quasi-likelihood and thus only the MAPE was calculated. For further guidance about splines, see Wood (2017). Models are reported in the order through which they were fit in our forward stepwise approach. Readers should check the MAPE column, to understand how overall model performances varied. The 'Best model' column indicates if a certain model was retained as the best candidate model.

Model formula	MAPE	AIC	Deviance	Best model
N. roadkill ~ 1	53.37	20,029.15	3345.47	No
N. roadkill ~ day of the week	52.60	19,914.41	3337.84	No
N. roadkill ~ day of the week + year	43.70	19,820.97	3338.49	No
N. roadkill ~ day of the week + $year^2$	47.26	19,814.83	3336.95	No
N. roadkill ~ day of the week + $year^3$	52.03	19,813.78	3335.74	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon)	43.26	19,780.40	3335.49	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon) + tp(cloud cover)	43.09	19,728.96	3329.98	No
N. roadkill ~ day of the week + year + te(illuminated fraction of the moon)	43.27	19,780.24	3335.59	No
N. roadkill ~ day of the week + year + te(illuminated fraction of the moon) + te(cloud cover)	43.05	19,729.58	3330.94	No
N. roadkill ~ day of the week + year + cc(illuminated fraction of the moon)	43.37	19,799.64	3334.66	No
N. roadkill ~ day of the week + year + cc(illuminated fraction of the moon) + cc(cloud cover)	43.25	19,754.34	3330.26	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover)	43.07	19,728.76	3323.66	No
N. roadkill ~ day of the week + year + te(illuminated fraction of the moon, cloud cover)	43.04	19,728.24	3325.66	No
N. roadkill ~ day of the week + year + te(illuminated fraction of the moon) + te(cloud cover) + ti(illuminated fraction of the moon, cloud cover)	43.02	19,727.18	3327.40	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + tp(day of the year)	37.26	19,285.46	3329.91	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + gp(day of the year)	37.26	19,283.99	3329.98	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + cc(day of the year)	37.40	19,276.11	3331.52	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + te(day of the year)	39.00	19,503.95	3319.63	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + ad(day of the year)	36.55	19,181.78	3315.75	Yes
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + ad.cp(day of the year)	36.95	19,194.09	3318.71	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + ad.cc(day of the year)	36.92	19,193.32	3314.85	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover, day of the year)	39.67	19,489.13	3269.42	No
N. roadkill ~ day of the week + year + te(illuminated fraction of the moon, cloud cover, day of the year)	39.30	19,504.90	3296.54	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + ad.cp(day of the year, illuminated fraction of the moon)	38.03	19,373.80	3285.33	No
Autoregressive models				
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + tp(day of the year) + AR1	37.29	—	—	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + tp(day of the year) + AR2	37.27	—	—	No
N. roadkill ~ day of the week + year + tp(illuminated fraction of the moon, cloud cover) + tp(day of the year) + AR3	37.24	—	—	No

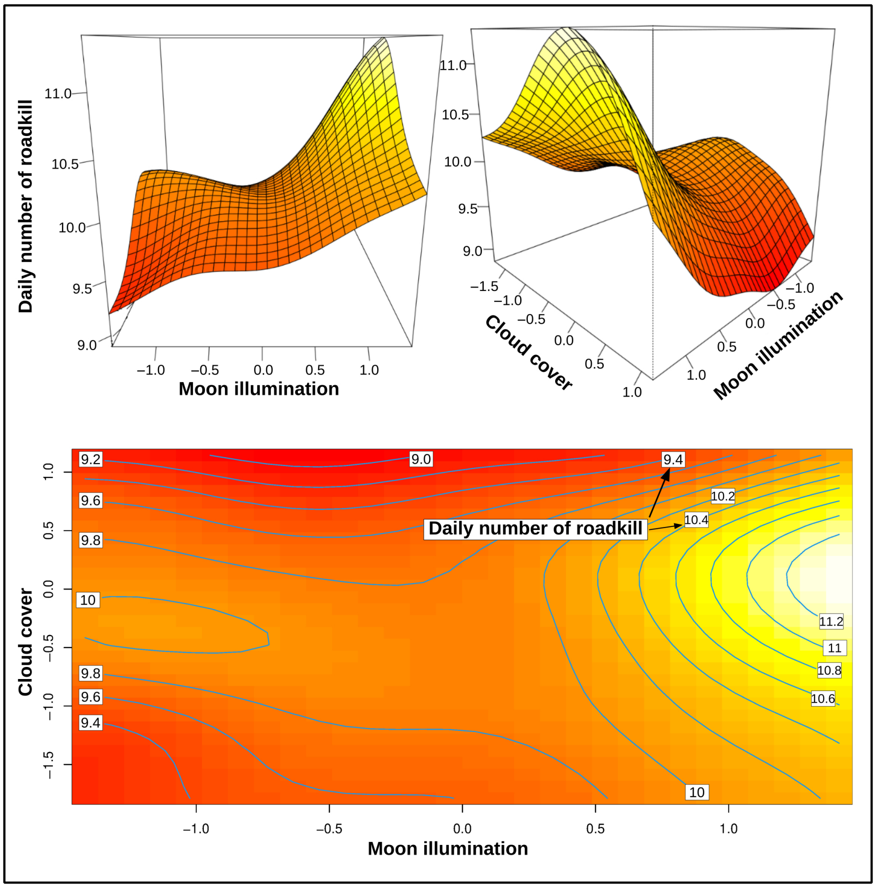

FIGURE 2 Surface plot (top left, top right) and mosaic plot (bottom) showing the interactive effect of moon illumination and cloud cover over the number of road-killed roe deer in Slovenia in the period 2010–2019. Moon illumination and cloud cover are represented as *Z*-scores, or standard deviations from the mean.

on collisions between vehicles and roe deer: the highest roadkill occurred on nights with a full moon and with medium to high values of cloud cover, whereas the interaction between the illuminated fraction and cloud cover was weaker on nights with a dim moon.

This interaction is almost certainly based on several mechanisms, and may reveal a hierarchical dynamic between the lunar cycle and cloud cover. Roe deer probably move more at full moon nights because the ground is illuminated and there are more opportunities to forage safely, which in turn leads to more road crossings. However, this may be affected by cloud cover which could—apart from having direct effects on roe deer behaviour—also affect human activity, that is, by reducing the number of people practicing outdoor activities (Tucker & Gilliland, 2007) and by altering traffic volumes (Verovšek et al., 2022), mostly through rainfall. Therefore, cloud cover exerts a nonlinear effect over collisions. At bright, low cloud nights, roe deer might be less active along roads due to increased human presence (e.g. outdoors; Wyttenbach et al., 2016) and sustained vehicular traffic (Kušta et al., 2017; Olson et al., 2015). Then, with medium to high cloud cover, and therefore with a higher amount of rainfall, human presence in the environment may be lower, that is, low enough to increase deer movements across roads, but vehicular traffic can still be intermediate, thus maximizing the risk of collisions (Mayer et al., 2021). Under such conditions, poor visibility and rainfall can further impair the ability of drivers to detect and avoid crossing deer. Finally, under high levels of cloud cover, weather conditions are likely to be characterized by widespread rainfall, that reduce traffic volume and people outdoor. This nonlinear effect of cloud cover on collisions would not occur at dark nights, perhaps due to the lower movement of animals in response to lower illumination on the ground.

Interestingly, our best candidate model did not detect any change in the effects of moon illumination during the year. This finding is surprising, as the main effect of the full moon on the behaviour of some wild ungulates is the increased opportunity to forage at night or during warm summer weather (Grignolio et al., 2018). It is possible that circannual changes in human mobility, or in roe deer behaviour other than foraging (e.g. breeding: Debeffe et al., 2014; hunting disturbance: Picardi et al., 2019), are more important than movements associated with nighttime foraging in determining the risk of roe deer–vehicle collisions. Integrating data on animal movements, vehicular traffic and outdoor activities would be essential to test these mechanisms we mentioned, and thus to obtain more robust insights in nuanced seasonally varying interplays between lunar cycles and cloud cover. This detailed information about human and animal movements would also be important to identify the potential causal mechanisms behind seasonal peaks of collisions. By testing, for example, if peaks in collisions during April/May and August/September are driven by an overlap between higher activity of roe deer at dawn/dusk and commuters moving in their vehicles (Rodríguez-Morales et al., 2013). Quantifying the relative weight of these mechanisms could be important to design widely applicable policy interventions, such as year-round daylight saving (Cunningham et al., 2022).

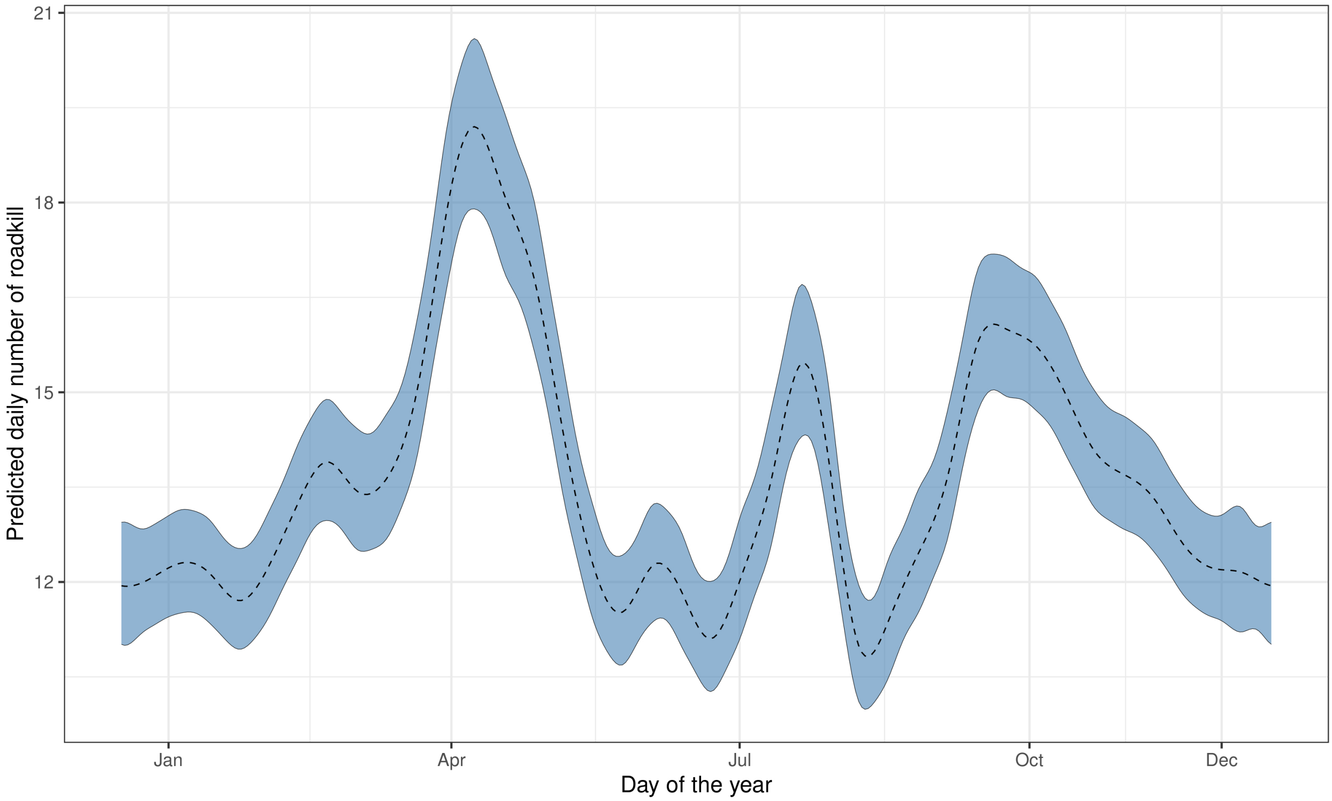

FIGURE 3 Marginal effect plot, representing changes in the volume of road-killed roe deer in Slovenia (period 2010–2019), according to the day of the year. Shaded area corresponds to 95% confidence intervals.

However, even without this information, our results already allow making two concrete recommendations for future research on wildlife–vehicle collisions.

First, rather than attempting to assess an 'average' effect of the lunar cycle (e.g. Steiner et al., 2021), future studies should focus on estimating its interaction with other environmental variables, such as cloud cover. So far, this interplay has been largely ignored in road ecology, but it would make findings from different studies truly comparable. Nowadays, open datasets allow to retrieve daily-level information on moon and atmospheric conditions effortlessly; indeed, there is no longer a need to use moon quarters, and it is possible to rather work on more refined, and comparable, temporal scales. We also believe that the results of previous studies should be reanalysed, that is, by considering cloud cover.

The second point is to avoid using simple univariate comparisons to test for the effect of moon illumination over collisions (e.g. chi-square testing: Colino-Rabanal et al., 2018). Our results suggest that other time-varying factors, such as the day of the year, have a much larger effect on roe deer–vehicle collisions, and should be accounted for through appropriate time-series analysis. Focusing on the magnitude of the effect of each covariate (Cumming, 2014) would also allow the effect of the lunar cycle itself to be considered with caution. Although model selection, in our case, did not provide evidence in favour of an interplay between the lunar cycle and the day of the year, model residuals still had strong temporal autocorrelation. This may suggest that relevant time-varying covariates are likely still missing and they could affect the estimated effect of the lunar cycles itself, once included in a statistical model. A comprehensive analysis of deer–vehicle collisions, accounting both for systematic seasonal fluctuations and the interplay between lunar cycles and weather conditions, could also be important to design risk mitigation strategies against wildlife–vehicle collisions, acting on the behaviour of drivers.

Considering that most collisions between roe deer and vehicles systematically occur during only few weeks of the year, with approx. 35% of collisions being concentrated in 15 weeks (Figure 3), local authorities could shift from permanent to temporary warning signs (Sullivan et al., 2004) or radio messages (Jägerbrand et al., 2018), deployed at these narrow time windows. This would minimize the habituation of drivers to warning signs and increase their vigilance and compliance with speed limits when it matters the most. Panel layout could also be changed, from one critical period to another, to increase the cognitive load associated with panel recognition and further decrease in vehicle speed (Hurtado & Chiasson, 2016).

Furthermore, interactive road signals (Huijser et al., 2015) could be programmed to measure illumination on the ground, traffic intensity and vehicle speed with sensors, and to activate warning signs under critical combinations of weather and lunar cycles Again, to limit the habituation of drivers, these panels should be activated only at the most critical periods. Due to their high costs, spatial analysis of deer–vehicle collisions (Pagany, 2020) could be used to prioritize their positioning at collision hotspots. Available evidence indicates that interactive panels, like speed feedback signs, are effective at reducing driver speeds (Flynn et al., 2020). Therefore, interactive panels/signs activated only when illumination on the ground is critical could be a further refinement of this tool.

Finally, as the real-time collection of fine-scale weather data and the integration of safe infotainment technologies into vehicles become wider, local authorities could develop intelligent speed advisory apps (Starkey et al., 2020), that would warn drivers at the most critical periods of the year as well as whenever combination of lunar cycle and cloud cover could increase the risk for deer–vehicle collisions.

AUTHOR CONTRIBUTIONS

Jacopo Cerri, Elena Bužan and Boštjan Pokorny conceived the ideas and designed the methodology; Boštjan Pokorny and Laura Stendardi collected the data; Jacopo Cerri and Laura Stendardi analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declared no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Open Science Framework Repository via EcoEvorxiv Digital repository https://doi.org/10.32942/X2RG6J (Cerri et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Fit of the daily number of road-killed roe deer in the dataset, with respect to a negative binomial distribution. Only 9 days out of 3660 had no reported roadkill.

Table S1. Review of the previous studies on the effect of moon over deer movements.

Table S2. Review of the previous studies on the effect of moon over ungulates-vehicle collisions.

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