Comparison of ecological, biological and anthropogenic causes of vehicle–wildlife collisions among three large herbivore species

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Abstract Vehicle–wildlife collisions are of increasing concern in modern societies caracterized by a continous and accelerating anthropogenic development. Preventing and mitigating collisions with wildlife will require a better understanding of the environmental and biological drivers of collision risks. Because species of large mammals differ in terms of food requirements, habitat selection and movement, and activity patterns we tested whether vehicle collisions with red deer, roe deer and wild boar, the most abundant large herbivores in Europe, differed in terms of spatial distribution and explanatory factors, using a Bayesian statistical framework. From 20,275 documented collisions in 9 departments of France between years 1990 and 2006, we found marked differences in magnitude and in the most influential environmental factors accounting for the density of collisions among the three species, in agreement with their biology and habitat preferences. The effect of road density was higher for the red deer than for the two other species for which it was similar, and did not level off at our large spatial-scale of observation. As expected from particle collision models, the annual hunting harvest – interpreted as a proxy of population abundance – was positively associated with the density of collisions for all species, being the strongest for red deer. Overall, the effect of landscape structure on the density of collisions was weak but while the collision density did decrease

with the proportion of forest in a management unit for wild boar, it increased with the fragmentation of forests for red deer that commute among forest patches between day and night. To reduce the number of vehicle–wildlife collisions actively, our results suggest to generalise road fencing for highways and motorways or a reduction of abundance of large herbivore populations as efficient action means. Overall, we call for of a greater consideration of the species' biology in information campaigns or by using specific road signs.

Keywords abundance, Bayesian modelling, car accidents, habitat fragmentation, mitigation measures, red deer, roe deer, ungulates, wild boar

Introduction

Over the last decades, heavier traffic loads and continuous expansion of road networks paralleled the increasing number and distribution of most large herbivore populations (Milner et al. 2006, Massei et al. 2015), resulting in a dramatic increase of vehicle–wildlife collision frequency in many European and North American countries (Langbein et al. 2010). For large mammals between one to two millions vehicle–wildlife collisions are recorded annually in the United States (Huijser et al. 2015), and about a million in Europe (Langbein et al. 2010), leading to acute ecological consequences on animal populations (Forman et al. 2003, Rytwinski and Fahrig 2015). Because of the increased risk of human injuries and fatalities, vehicle–wildlife collisions are now an important socio-economic issue and a stake in the road safety policies (Groot Bruinderink and Hazebroek 1996). The economic bulk of vehicle–wildlife collisions is substantial and the mitigation of risks raised intensive and active areas of research (Schwabe et al. 2002, Malo et al. 2004, Huijser et al. 2015, Elmeros et al. 2011, Gunson et al. 2011, Hothorn et al. 2015). Understanding and identifying hazardous areas and the ecological and biological factors that are associated with the occurrence of collisions at a given location is of prime importance to predict vehicle–wildlife collisions in space and time, and to implement appropriate and efficient mitigation measures.

First and foremost, road infrastructure and use by drivers are anthropogenic explanatory factors potentially driving the occurrence of vehicle–wildlife collisions. The density of roads and the speed of the vehicle are recognized since long to increase the frequency of vehicle–wildlife collisions

(Pojar et al. 1975, Case 1978, Hartwig 1993, Groot Bruinderink and Hazebroek 1996, Seiler 2005). For instance, the number of moose-vehicle collisions in Sweden was positively correlated with density of roads with a speed limit of 90 kph, but was negatively correlated with the density roads limited to 70 kph where motorists have more time to react and to anticipate collisions with wildlife (Seiler 2005). Road class also influences the risk of collisions markedly. Collisions are recorded on secondary roads mainly, because they represent the greater cumulative length within most national road networks. Per unit of length, however, collisions frequency is higher on primary roads where traffic volume and vehicle speed are greater (Pojar et al. 1975, Bashore et al. 1985, Désiré 1992, Hartwig 1993, Hubbard et al. 2000, Langbein et al. 2010, Roedenbeck 2007, McShea et al. 2008), except in countries where most highways are fenced like France (Vignon and Barbarreau 2008). While the number of collisions increase broadly with traffic load, the collision frequency may level off above a traffic density threshold, from which animals avoid crossing roads (Müller and Berthoud 1997, Skölving 1985, Clarke et al. 1998, Seiler 2004, 2005). In Switzerland, collision frequency increases with traffic volume up to 4 000 vehicles / day, from which the risk of accident decreases and becomes a rare event once the traffic reaches 10 000 vehicles / day (Müller and Berthoud 1997). Such a barrier effect might emerge or not depending on the considered spatial scales (see Material and Methods).

From an ecological point of view, space use and habitat selection by animals are key processes for the understanding of the spatio-temporal patterns of vehicle–wildlife collisions. Most large herbivores involved in vehicle–wildlife collisions in Europe and North America are forest-dwelling species that are strongly attracted to roadsides (Bellis and Graves 1971, Carbaugh et al. 1975, Allen and McCullough 1976, Case 1978, Bashore et al. 1985, Groot Bruinderink and Hazebroek 1996). Previous studies proposed that large herbivores would find minerals such as salts (Fraser et al. 1982, Jolicœur and Crête 1994, Bechtold 1996, Hesse et al. 2010) or a proficiency of highly palatable plant species (Bédard et al. 1978, Groot Bruinderink and Hazebroek 1996, Child 1998, Finder et al. 1999, de Bellefeuille and Poulin 2003) on roadsides. Moreover, roadsides plant communities are also often maintained at a young and attractive ecological stage to herbivores by regular cuttings for visibility maintenance. By feeding regularly on roadsides animals put themselves at a greater risk of collisions with vehicles (Puglisi et al. 1974, Bashore et al. 1985, Finder et al. 1999, Roedenbeck 2007). The

attractiveness of roadsides will therefore depends on the food requirements and preferences of herbivores which differ greatly among species.

Another important factor influencing vehicle–wildlife collisions is the habitat characteristics at different scales, from landscape to the vicinity of the road (de Bellefeuille and Poulin 2003). At large spatial scale, where landscape appears generally patchy, collisions are more likely to happen on road sections located between woods and open fields because animals move frequently between resting (covered forest) and foraging areas such as meadows or agricultural crops (Puglisi et al. 1974, Bashore et al. 1985, Hubbard et al. 2000). For instance wild boars (*Sus scrofa*) commute on a daily basis from forested patches to open fields for feeding (Carbaugh et al. 1975, Waring et al. 1991). Similarly, high collision rates with white-tailed deer (*Odocoileus virginianus*) are associated with the proportion of woodland cover in the landscape (Finder et al. 1999, Hubbard et al. 2000, Roedenbeck 2007). Consequently, when roads cross more homogeneous landscapes, vehicle–wildlife collisions are more uniformly distributed in space than in more fragmented landscapes (Bellis and Graves 1971, Bashore et al. 1985, Hubbard et al. 2000).

Most studies investigating vehicle–wildlife collisions focused on one single species (moose *Alces sp.* : Seiler (2005), Dussault et al. (2007); white-tailed deer: Bashore et al. (1985), Finder et al. (1999), Hubbard et al. (2000); roe deer: Mysterud (2004), or did not differentiate among species (Malo et al. (2004), for red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*, Gunson et al. (2009) and Nielsen et al. (2003), for white tailed deer and mule deer *Odocoileus hemionus*). In spite of many large hervivores live sympatrically, comparative analyses of vehicle–wildlife collisions in mammals have rarely been conducted. Because of marked differences in diet and body size, large herbivores show a remarkable variability of space use behaviours, sensitivity to human presence and disturbance, and levels of grouping patterns (Sáenz-de Santa-María and Tellería 2015). Such contrasting biologies and behaviours among large herbivore species could account for the different spatio-temporal distribution of collisions reported between wild boar and roe deer in Spain (Rodríguez-Morales et al. 2013). Our ability to predict where and when vehicle–wildlife collisions are the most likely to occur may actually be hampered by specific habitat choice behaviours and its ecological correlates in the landscape. If such differences are supported by observations, the plannning of mitigation measures should be species– and

context–specific.

Based on vehicle–wildlife collision data recorded between 1994 to 2006 over 9 counties in France, we first describe here the species spatial collision patterns on the sympatric red deer, roe deer and wild boar to quantify the relative effects of the ecological, biological and anthropic drivers of vehicles wildlife collisions. Using a Bayesian framework, we then tested the following predictions (see Table 1):

1. The ideal gas model is the theoretical basis of most biological studies focusing on encounter rate between moving animals (Hutchinson and Waser 2007). Applying the ideal gas model to encounters between cars and animals, collision probability becomes a positive function of animal and car densities, and of mean car speed given that animal speed is negligeable with regards to cars. Accordingly, we predicted a positive and linear relationship between the number of vehicle–wildlife collisions and abundance of species (Schwabe et al. 2002, Seiler 2005, Sudharsan et al. 2006), and between the number of vehicle–wildlife collisions and the density of roads (Romin and Bissonette 1996, Pokorny 2006, Vignon and Barbarreau 2008). (i) Vehicle–wildlife collisions should increase in number with average car speed, hence from local roads to highways. (ii) Vehicle–wildlife collisions should rank according to species average abundance, increasing from red deer, roe deer to wild boar.

2. We predicted a positive effect of habitat fragmentation on the number of collisions (Bashore et al. 1985, Romin and Bissonette 1996, Hubbard et al. 2000, Madsen et al. 2002) because animals commute daily from resting to foraging areas in patchy environments. We expected the effect of habitat fragmentation on the number of collisions to decrease from roe deer, wild boar and red deer (see Table 1) because roe deer strongly favour ecotones for foraging (Saïd et al. 2009), wild boar makes extensive use of agricultural crops (Thurfjell et al. 2009) while red deer in France is mostly restricted to forests by human disturbance and hunting.

3. Although red deer, roe deer and wild boar are forest-dwelling species mostly, the extent to which their distributions are associated to forests differ strongly (Hewison et al. 2001, Patthey 2003, Saïd et al. 2005, Keuling et al. 2009, Thurfjell et al. 2009). Consequently, we expected the recorded number of collisions to increase with the proportion of forest in the landscape

(Carbaugh et al. 1975, Waring et al. 1991), but expected stronger effects for red deer and wild boar than for roe deer (see Table 1). This is because in France red deer is confined to forests or in mountain areas, while wild boar is expending in all habitats and roe deer is ubiquitous and found virtually everywhere (Maillard et al. 2010).

4. We predicted a positive association of the proportion of the agricultural areas and the number of collisions because crops are highly attractive food resources for ungulates which frequently commute between forests and agricultural areas (Keuling et al. 2009). We expected a stronger effect of proportion of agricultural lands on collisions for wild boar and roe deer than for the red deer (see Table 1) because wild-boar use agricultural crop to a greater extent than red deer (87% of the total amount paid for big game damage are done by wild boar, Maillard et al. 2010) and roe deer exhibits behavioural plasticity, recently colonising the agricultural plain (Hewison et al. 2009).

Material and methods

Study sites and spatial working scale

The local hunting associations of 9 French departments (Cher, Jura, Loire, Loiret, Moselle, Oise, Rhône, Haute-Savoie,Vendée; see supplementary Table 1 for a detailed description) collected and centralized the collision data. Despite our choice of the departments was primarily motivated by data availability, the 9 locations are representative of most mainland French ecosystems. Vehicle–wildlife collision cases were reported by the car driver or by direct observations of carcasses on the roads by officials (game wardens, police. . .)– we did not contribute to data collection ourselves –. The monitoring spanned between 1990 and 2006 but varied among departments. Each department is divided into management units (MUs) defining administrative subdivisions of departments where game management is comprehensive and homogeneous. MUs border may differ for red deer, roe deer and wild boar. Overall, we had 266 MUs in the 9 departments for roe deer, 247 MUs for wild boar in 8 departments (no wild boar in Rhône), and 110 MUs for red deer in 7 departments (no red deer in Loire and Rhône). On average the surface of a single MU was 208 km^2 (SD = 167 km^2). Because the exact location of the collision was unknown (no GPS fixes), we assigned each collision

event to the closest MU. Therefore potential location inaccuracies were of limited consequences on the presented results.

Our statistical unit was the MU making the spatial scale of investigation of wilflife-vehicle collision pattern rather large. Because of this particular sampling design, we did not attempt to explain the location of collisions at a very fine scale *e.g.*, by comparing local conditions where the collisions took place and a couple of meters away (case-control design). Instead, we explain the collision number of each MU with the mean value of the different environmental variables measured across the corresponding MU to test their statistical association (number of MUs and descriptor measurements were of the same dimension). Predictors of vehicle–wildlife collisions change with the spatial scales (Johnson 1980, Dupke et al. 2017). At large spatial scale, habitat selection is related to landscape spatial structure, such as topography or habitat fragmentation. For example several authors have shown that vehicle collisions with red deer, roe deer and wild boar were more likely in forested environments at large spatial scale while at a smaller spatial scale, road sections with the highest collision risks were located in the open areas or at the forest border (Désiré 1992), or had roadsides with dense vegetation for roe deer (Madsen et al. 2002). In addition, the previously described barrier effect on road traffic and density on the number of collisions are not expected at large spatial scale of investigation. Being averaged over $> 100\text{km}^2$, the range of road density values across MUs is limited. It is unlikely that the road density would be so large over a whole MU that the number of collisions would plateau in this MU.

Explanatory variables of collisions

Three types of explanatory variables were used to describe the road characteristics (anthropogenic variables), the landscape patchiness based on habitat composition (ecological variables), and the large herbivore populations (biological variables).

Anthropogenic variables: We described the road network using the Routes 500 database from the Institut Géographique National (IGN 2001) to derive the road density of MUs. We classified roads in four categories based on the importance of road sections for the traffic (`http://professionnels.ign.fr/`): local roads, regional roads, national roads and motorways. For each road type, we assigned one of the three possible roads density classes (small,

average and large) to the MU to explore non-linearity in the effect of traffic on vehicle–wildlife collisions. Because the statistical distribution of the road density is strongly asymmetrical, we had to find a statistical transformation to ensure the numerical stability of our results and avoid strong leverage effects. We set the limits of density classes so that MU sample sizes were balanced in each class by computing the 1/3 and 2/3 quantiles of road density distributions. The limits defining the density classes differed according to road type. These limits were equal to 0.37 and 0.52 km per 100 ha for local roads (small, average and large categories corresponded to road densities of <0.37, between 0.37 and 0.52, and > 0.52 km per 100 ha respectively), 0.16 and 0.24 km per 100 hectares for regional roads, 0.09 and 0.16 km per 100 hectares for national roads, and 0.01 and 0.03 km per 100 hectares for motor-roads. The squared correlation between pairs of variables measuring the density of roads never exceeded 0.12, so that we did not considered these variables as redundant. We also characterized roads sinuosity for each MU by calculating the ratio between the curvilinear length of the road segments and the distance in a straight line between the extreme points of the road. A straight road would have a sinuosity index of 1. We calculated the sinuosity only for local and regional roads because national roads and motorways were mostly straight. Fencing is an efficient way to reduce vehicle–wildlife collision risk (Clevenger et al. 2001, McCollister and Van Manen 2010), accounting for its confounding effects on collision density would be relevant. However, because the information about road fencing is not available nor centralized in France, we could not assess the effect of road fencing on collision density in our study.

Ecological variables: We extracted landscape variables with a GIS by mapping all MUs and calculating 10 descriptors of the environment. We used the CORINE Land cover (2006) database to derive a categorical variable “Habitat type” (HT) describing the land cover type in the MUs. For each MU, HT returns the proportion of the area covered by forest, agricultural crops, natural open areas, and urban and anthropogenic habitats (4 habitat types). Moreover, we indexed the fragmentation of the forested habitat with the number F_f of connected forest patches in the MU. To account for the larger number of forested patches in larger MUs we scaled F_f by the area of the corresponding MU, yielding a density of connected forest patches Df. However, because the relationship between D_f and the proportion of forest in the MU was non-linear (i.e. D was redundant with the land cover variable “Forest”), we used a nonparametric loess regression (degree =

2, span = 75%, Cleveland, 1993) to predict the logarithm of D as a function of the proportion of forest in a MU. Ultimately, we used the residuals of this regression as an index of the forest fragmentation (R_f), whereby a positive values meant more forest patches in the MU for a given forest cover, and conversely for negative values. Following the same procedure, we calculated a fragmentation index of urban patches (R_u), using the density of urban patches F_u instead of the density of forest patches. Finally, we used the IGN geographic database to calculate a 3-classes categorical variable of elevation defined as the proportion of the MU area found <600 m, between 600 m and 1500 m, and > 1500 m a.s.l.

Biological variables: For the three species of large herbivores, we assessed population abundance with the number of harvested animals per km^2 for each MU (referred to "hunting bag"; see Seiler (2005), Morelle et al. (2013) for a similar approach). These data were provided by the local hunting associations in the 9 departments, for every hunting season for which we had collisions data. We used the number of harvested animals per km^2 during the previous hunting season, spanning from september of year $t-1$ to the end of february of year t,to characterise the abundance of a species during year t and to use it as a predictor of the density of vehicle–wildlife collisions.

Bayesian model fit and variable selection

For each species, we first modelled the logarithm of the mean number of collisions in a MU as a linear combination of the characteristics described in the previous section, with a Bayesian mixed model. We assumed a Poisson distribution for the number of collisions. We accounted for the overdispersion in the response variable by including gaussian residuals in our linear predictor, following the approach of Hadfield (2010). We entered the department (9 level factor) as a random effect on the intercept. We fitted this model in a bayesian context with the JAGS software (Plummer 2016).

We used a Bayesian variable selection approach to identify the variables affecting the density of vehicle-wildlife collisions in a MU. More precisely, we used the approach described by Kuo and Mallick (1998) to estimate the probability that each variable influenced the mean number of collisions. The Kuo-Mallik's approach also allowed to identify the best models predicting the number of collisions: we could estimate the probability of each possible model to be the best one

describing our data (*i.e.* every possible combination of the variables describing the management unit), and select the most likely one. We checked MCMC convergence and good mixing, and we could check that the goodness of fit of the models was excellent for all species. Technical details and a formal description of this approach are available as *Supplementary material 2*.

Note that we could not use these models to compare the influence of a given predictive variable on the collisions across species. Indeed, the slope associated to a given variable in a regression model cannot be compared across models containing different variables and different sampling units (Becker and Wu 2007). We needed to fit a more general Bayesian model to allow for this comparison. We first focused on the MUs containing all three species. Then, we identified the set D of variables belonging to the best model identified by the Kuo and Mallick (1998)'s approach for at least one of the three species. Then, for a given species, we predicted the average number of collisions per unit area and per year not only as a function of the variables identified as important for this species, but also as a function of the variables identified as influential for the other species. We also fitted these models by MCMC, using the same approach as for the fit of the previous models (more formally, we replaced the set B by the set D in equation (1) of *Supplementary material 2*), but focused on the interaction term coefficient to make inference on among species differences.

Results

For all years and departments pooled, we recorded 20,275 collisions for all species among which 69.9% were roe deer, 3.1% red deer and 27% wild-boar. The collision number averaged 6.37$\pm$ 8.62 per 100km^2 for roe deer, reaching up to 80 collisions per 100km^2 for some MUs (see Fig. 1). For red deer and wild boar, the density of collisions was lower, with on average 0.93 ± 1.89 and 4.12 ± 8.09 per 100km^2, following the same order as their respective relative densities.

Red deer

The forest fragmentation and the hunting bag had the strongest effect on the density of collisions with the red deer (Table 2). Note that the model with the largest probability was characterized by slightly more than one chance out of two to be the true model (58%, see Table 3), indicating a significant uncertainty in the model selection process. Alternative models often included a measure

of the density of humans (e.g. density of local roads – second best model, density of national roads – fourth best model, fragmentation of urban areas – 5th best model). However, none of these alternative models was characterized by a large probability to be the best model, suggesting that the frequency of collisions between red deer and vehicles are essentially determined by the density of red deer, as well as the forest fragmentation as we expected from its behaviour. This best model indicated that the number of collisions was larger when the hunting bag was high and the forest strongly fragmented (Fig. 1).

Roe deer

Roe deer relative abundance and, to a lesser extent, the density of national roads were the main variables influencing the density of collisions with the roe deer (Table 2). Note that there was also a large uncertainty in the model selection for this species (Table 3). Although the best model was the model containing the two aforementioned variables, nearly all the other models with some statistical support included both roe deer relative abundance and one or several measures of road density (whether local roads, national roads or motorways). We fit the best model to describe the relationship between these two best variables and the density of collisions for the roe deer. This model indicated that the density of collisions was larger when both roe deer abundance and the density of national roads were high (Fig. 2). The effect of national road density was, however, small in comparison to the effect of the relative abundance (Fig. 2).

Wild Boar

Three variables strongly influenced the number of collisions between vehicles and wild boars: the habitat type, the hunting bag and density of national roads (Table 2). Note that there was only a small uncertainty on the model selection process as very large probability is associated to this model (Table 3). We therefore fitted this best model (Fig. 3). To interpret the effect of HT, we had to account for the difference in average landcover between habitat types. For instance, while a MU with 80% of its area covered by agriculture is frequent in our data, a MU with 80% of urban area never occured in our data, so that we could not readily interpret the raw estimates of the coefficients to identify clearly the differences between these habitat types. To interpret these results, we

predicted the average density of collisions between vehicles and wild boars as a function of the hunting bag and the density of national roads in four types of management units (see figure 3) in four contrasting ecological conditions: (i) a MU (labeled "Forest"), characterized by 91% of forest and 3% of the three other habitat types, (ii) a MU with a high land-cover of agricultural areas (labeled "Agri"), characterized by 91% of agricultural areas and 3% of the three other habitat types, (iii) a MU (labeled "Open"), characterized by 37% of open areas, 30% of forests, 30% of agricultural areas, and 3% of urban areas, and (iv) an urbanized MU (labelled "Urban") characterized by 16% of urban area, 14% of open area, 35% of forests and 35% of agricultural areas. After a deep exploration of our dataset, we consider that these particular sets of ecological conditions are typical of those encountered in France: thus, the habitat composition in the "Forest" MU is typical of the more forested management units observed in our dataset; the habitat composition in the "Urban" MU is typical of the highly urbanized management units, etc. According to the best model, the density of collisions increased with the hunting bag and the density of national roads (Fig. 3). On the other hand, the density of collisions was much lower in forested management units than in other types of management units.

Comparison of patterns among species

Finally, we compared across species the effect of the variables identified by the Kuo and Mallik's approach as important for at least one species. The coefficients of the variables for each species are given in table 4. These models indicated that the effect of the forest fragmentation on the density of collisions was stronger for the red deer than for the two other species (for which it was roughly equal to zero). The effect of national roads was on average higher for the red deer than for the two other species, but this coefficient was characterized by a larger variance: the 90% credible interval included 0 for this species, explaining why this variable was not initally selected as part of the best model for red deer. The effect of the national road on the density of collisions was similar for the wild boar and the roe deer. The credible interval on the coefficients of the various habitat types (forest, urban, open, agriculture) included zero for all species except the wild boar. The density of collisions between vehicles-wild boar was negatively affected by the density of forest. Finally, relative abundance was positively related to the density of collisions for all species.

Discussion

In spite of its substantial economic burden (Bissonette et al. 2008) and ecological consequences (Forman et al. 2003), vehicle–wildlife collisions with large mammals are most often considered as a general, non-specific problem. Improving the efficiency of mitigation measures likely requires a better and finer knowledge about the causes of collision risks, including inter-specific variations. For instance in Spain, collisions with vehicles did not occur at the same time of the year or of the day, and at different geographical locations for roe deer and wild boar (Rodríguez-Morales et al. 2013). By comparing vehicle collisions with red deer, roe deer and wild boar we emphasize the differences in the most important environmental and ecological factors accounting for the spatio-temporal variation in the density of collisions reported in the management units of 9 departments in France. Common to all species, hunting bag, a proxy of population abundance, was the most influential variable, confirming that the species abundance in an area is strongly and positively associated to collision risks. As expected from the contrasting ecology and behaviour of the three species we focused on, environmental explanatory variables of the vehicle–wildlife collisions differed among species (Fig. 3). While vehicle collisions with red deer were associated with the fragmentation of the forest habitat, collisions with roe deer appeared more uniformly distributed in the landscape, and collisions with wild boars depended on the landscape composition (Table 3; Fig. 3). Overall, our results call for the consideration of species-specific mitigation policies with regards to vehicle–wildlife collision risks.

Population abundance and collisions with vehicles

It has been repeatedly shown that local densities of large herbivores strongly influence collision risks (Puglisi et al. 1974, Farrell et al. 1996, Seiler 2004). Similarly, we find that population abundance is the only common predictor of vehicle–wildlife collisions for the three large herbivore species. The effect is always positive but small as for a given MU, collision density increased by approx. 1% (range 0.5 – 1.5) for each additional thousands of animals shot per year. The relationship between population abundance and frequency of collisions however differed among the three species, the largest effect being observed for red deer and the smallest for roe deer (Table 4). Accordingly, the annual number of vehicle–wildlife collisions increased 6-fold between 1986 and 2006 at the national

scale in France, while at the same time the hunting bag, a large-scale proxy of animal abundance, was 4 times larger for red deer, 5 times for roe deer and 6 times for wild boar (Vignon and Barbarreau 2008). This, however, does not necessarily indicate a stronger effect of the animal density on the density of collisions for the red deer: this difference in slopes for red deer, roe deer and wild boar may arise from a combination of different ecology and hunting policies among species.

In France, annual quotas set how many roe deer and red deer may be harvested during the hunting season, while wild boar hunting is either unlimited or with quotas, which could also explain the different relationships between population abundance and collision density we find. Because red deer face high hunting pressure to control its colonisation to new areas and its associated damages on crops and forests, any increase in hunting bags likely reflects an increase in abundance (Saint-Andrieux et al. 2004). Conversely roe deer is ubiquitous in France, over a much longer period of time than red deer, and its population dynamics is currently levelling off (Maillard et al. 2010). Consequently, hunting bag may not capture variation in roe deer abundance as for the red deer, so that the relationship between hunting bag and collision frequency is weaker for the roe deer. Similarly, wild boar reproduction is strongly influenced by oak masting events (Gamelon et al. 2013), which leads to delayed effects on abundance not immediately reflected into hunting bags, and hence on its relationship with the number of collisions. We contend, like previous studies (Iverson and Iverson 1999, Morelle et al. 2013), that we used hunting bag as a proxy of population abundance to account for wildlife vehicle collision. Because hunting bag may be be affected by hunting effort, the relative effect of relative abundance of herbivores on the number of collisions should be confirmed with more accurate estimates of population densities.

Importance of inter-specific differences

Related to their body size and specific food requirements, the ranging behaviour of the three species differ markedly. At the individual level, a larger home range size increases the probability of road inclusion within and individual's area of use. At the population level, species with the larger home range put more individuals at risk of collision than species with smaller home range. Having more individuals at risk of collision could in turn lead to a stronger association between population

abundance and the density of vehicle–wildlife collisions. In mammals, home range size is associated with species' body size (Lindstedt et al. 1986, Mysterud et al. 2001) and should decrease from red deer to wild boar and roe deer. Although limited to three species, the effect of hunting bag on collision frequency decreases from red deer, to wild boar and roe deer (Table 4), as expected from their respective average body size. The lower collision density we observe for red deer could result from a greater sensitivity to anthropic activities and avoidance behaviour of roads as well. We currently have no direct observation from animal relocations to support this hypothesis and empirical evidence for road avoidance behaviour in large herbivores are equivocal. For instance, no road avoidance was found for red deer in Norway where traffic and road density are comparatively lower than in France (Meisingset et al. 2013). Conversely, D'Amico et al. (2016) reported road avoidance for red deer and wild boar although to a similar extent for the two species (see also Rowland et al. (2000) on elk in North America).

We found that the risk of collision exists in all kind of environment, but differed in magnitude according to the species. Collisions with wild boars were more likely to occur in MU with agricultural, urban and open areas and less in forested areas, which differentiates this species from red deer and roe deer (Table 3; Fig. 3). The concomitant growth of urban areas and wild boar populations in recent years has increased the presence of this species around cities and in suburbans areas (Cahill et al. 2012). These last years have seen wild boar colonizing new areas such as industrial wastelands and urban forests where hunting is difficult and rather limited. If motorists are aware of collision risks with wildlife in non-urbanized landscapes, their vigilance toward this hazard is likely reduced when entering cities or suburbs. As urbanization encroaches more and more on the agricultural and forested lands, we expect an increasing number of collisions in urbanized areas, and particularly so with the wild boar. Conversely, red deer is a typical forest dwelling-species which occasionally feeds on of agricultural and mixed habitats in the vicinity of forest patches. Males make large movements over the year to commute between foraging and rutting areas (Hamann et al. 1997), which put them at risk of collision with vehicles. In lowland forests, females have limited seasonal migration movements, but can travel long distances to reach foraging areas at night (Klein and Hamann 1999). Accordingly, we found that collisions with red deer were more numerous as the fragmentation of forest patches increases (Table 4; Fig. 3). The role of landscape structure had no

influence on roe deer collisions contrary to our predictions. The reason is probably because roe deer is present in all habitat types, so population abundance may have a more important effect than environment.

Influence of road network on collisions

The road network configuration in the landscape is a key structuring factor of the collision risks with wildlife. A review of the vehicle–wildlife collisions with mammals showed that 39% of studies (7 out of 18) reported a positive effect of traffic, road width or speed limit on collisions number (Gunson et al. 2011). The "national" roads are the only type of roads affecting collision numbers with wild boars and roe deer in France (Fig. 3). Similarly in Slovenia, among a set of 40 tested variables describing landscape features, density of roads has an overwhelming effect on the number of collisions with roe deer (Pokorny 2006). These "national" roads connecting the main urban centres in France combines a heavy traffic load with a low level of protection such as fences or wildlife crossing. Unexpectedly though, the density of roads has no detectable effects on collision number with red deer that was more related to landscape structure. Red deer behaviour in habitat selection could account for this relatively low the risk of collision. For instance, red deer select mostly for forested habitats with only a marginal use of agricultural crops (Hamann et al. 1997), hence restricting the area at risk of collision. In addition red deer forage on food patches close to roads at a time of low traffic burden mostly (Meisingset et al. 2013) or select habitat away from roads with the greatest vehicle use such as primary roads (Montgomery et al. 2012).

The density of other road types seems to have little influence on the density of collisions, whatever the species (Table 2). In France, highways and motorways are fenced most of the time. According to our results, road fencing proves to be an efficient method to limit collision risks despite a high speed limit (>110 km.h-1). Accordingly, in France in 2008 and 2009, 86 777 vehicles collisions with red deer, roe deer and wild boar have been recorded by insurance companies, of which only 1% occurred on highways and in spite of highways represent 97% of the daily traffic (40 400 versus 1 030 vehicles/day/km for highways vs other roads in 2010 respectively). Conversely, lower speed and narrower lane width likely limit traffic load on this secondary road network both factors being known to reduce vehicle–wildlife collision risks substantially (Hubbard et al. 2000).

We found more collisions with roe deer and wild boar in MUs with a higher road density and with a traffic ranging between 2500 and 10 000 vehicles per day. More surprisingly collisions frequency kept on increasing with traffic over than 10 000 vehicles per day and we could not detect any barrier effect. Previous studies indeed suggested that traffic volume could prevent animals to cross the road Skölving (1985), Clarke et al. (1998), with varying thresholds (approx. 4000-5000 vehicle per day in Sweden: Seiler (2005); >10 000 vehicles per day in Germany: Müller and Berthoud (1997)), which is consistent with behavioural observation of habitat selection of red deer patterns according to traffic volume in red deer for instance (Meisingset et al. 2013). In our study, the traffic load of roads is likely confounded with road type and road fences, which may have hampered our ability to test for the effect of traffic volume per se, or to detect any threshold effect of traffic load on collision risk.

Management implications and conclusion

Our results suggest two lines of actions to mitigate vehicle–wildlife collisions. A first mitigation measures would be road fencing as most – but not all – highways and motorways, that are fenced in France, had lower collision density despite their high traffic load (between 1 and 2% of ungulates were killed on motorways). This would be an effective measure for all species (Clevenger et al. 2001, McCollister and Van Manen 2010) but, in addition to be expensive, road fencing would come at the costs of a reduced connectivity for wildlife (Forman and Alexander 1998). Green bridges, overpasses and underpasses are potential compensatory measures, maintaining connectivity for large herbivores, while also contributing to a reduction in collision number locally. Alternatively, reducing population densities of large herbivores could limit the number of collisions per MU. Previous studies showed a reduction in the frequency of deer-vehicle collisions with lower deer densities (Rondeau and Conrad 2003, Sudharsan et al. 2006). Nevertheless, for population size reduction to lead to a substantial reduction in the collision frequency with wildlife would require a massive hunting effort, given the rather weak relationship we report here for the three species.

Awareness and prevention campaign could also be a way to mitigate vehicle–wildlife collision. Warning signs are often used in France to reduce wildlife vehicle collisions by warning drivers about the potential presence of wildlife on the road, although only the one sign pictures a jumping deer.

Warning signs are posted at road sections with high number of vehicle–wildlife collisions but are now so frequent in France that drivers do not pay attention. The efficiency of the warning signs would be improved if adapted to the local risks with the appropriate species. For exemple in departments with no red deer presence but with a lot of wild boar collisions, a warning sign with a wild boar would definitely be more relevant. Similarly warning signs for red deer crossing in agrosystems is not relevant according to our results. An efficient way of reducing the number of collisions may be a better information of the motorists for whom collision risk mainly occurs on roads driving through forests. Information campaigns are needed for a general awareness that the collisions can take place everywhere, even around cities and on highways. Finally, motorists would benefit from a better knowledge about large herbivore behaviour. For example, if one roe deer crosses the road, a second animal or a third one is likely to come out.

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Data and code accessibility

We have bundled the code used for the analysis as well as the complete data set in a R package named “ungulateCollisions”. This package contains a vignette named “modelfit” which describes how the analyses carried out in this paper were performed. To install it, the reader should first install the software JAGS on their computer (see `http://mcmc-jags.sourceforge.net/` for instructions). The reader can easily install the package and access the vignette by copying the following R code in the R console:

```
library(devtools)
install_github("ClementCalenge/ungulateCollisions")
vignette("modelfit")
```

Compliance with ethical standards

Conflict of interest

We declare no potential conflicts of interest.

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Figure captions

Fig. 1 (a) Location of the nine departments (administrative subdivision of the country) from France used in our study, where $n = 20\,275$ vehicle–wildlife collisions were recorded between 1990 and 2006. (b))Average spatial distributions of vehicle-wildlife collisions with with red deer, roe deer and wild board in each of the management units of the nine departments.

Fig. 2 Model predictions of the average density of collisions between red deer and vehicles per year and per squared kilometre in a management unit, as a function of the hunting bag and the forest fragmentation. To enable a graphical display of the fit, we considered here three values of forest fragmentation: (i) low fragmentation (value = -1; only 2% of the management units present a value lower than -1), (ii) medium fragmentation (value = 0, corresponding to the mean fragmentation observed in a management unit), and (iii) high fragmentation (value = 1; 4% of the management units present a value larger than 1). The central curve corresponds to the point prediction of the model. The four shades of grey indicate (from darker to lighter shades): 20%, 40%, 60% and 80% credible intervals.

Fig. 3 Model predicting the average density of collisions between the roe deer and vehicles per year and per squared kilometre in a management unit, as a function of the hunting bag and the density of national roads (this variable was already discrete, so that we did not have to discretize this variable, as for figure 1). The central curve corresponds to the point prediction of the model. The four shades of grey indicate (frow darker to lighter shades): The four shades of grey indicate (from darker to lighter shades): 20%, 40%, 60% and 80% credible intervals.

Fig. 4 Model predicting the average density of collisions between the wild boar and vehicles per year and per squared kilometre in a management unit, as a function of the hunting bag, the density of national roads (this variable was already discrete, so that we did not have to discretize this variable, as for figure 1), and the landcover by three habitat types. We have defined 4 types of management units here (see text for details): (i) a forested management unit ("Forest"), (ii) an agricultural management unit ("Agri"), (iii) a management unit with an important landcover by open natural areas ("Open"), and (iv) an urbanized management unit. The central curve corresponds to the point

prediction of the model. The four shades of grey indicate (from darker to lighter shades): 20%, 40%, 60% and 80% credible intervals.

Table 1 Rationale for the different predictions we test under the hypotheses that environmental explanatory variables of the spatial distribution of wildlife-vehicle collisions differ according the species' habitat selection behaviour. Symbols within brackets stand for the direction and relative magnitude of the effects for relatively to each of the three species of large herbivore consider in the study.

Hypothesis	Red deer	Roe deer
Abundance	(++)	(++)
Habitat fragmentation	(0), present in forested areas mostly, excluded by hunters in other habitats	(+++), favourable environment
Proportion of forested area in the management unit	(+++), use forested area mostly to minimize disturbance and is highly mobile	(++), roe deer favor fragmented
Proportion of agricultural land in the management unit	(+), red deer uses agricultural crops close to forested areas	(+), roe deer favor fragmented h

Table 2 Description of the variables and their associated probability of inclusion in the best model predicting the average density of vehicle-wildlife collisions ($n = 20\ 275$) for red deer, roe deer, wild boar recorded in 9 departments (administrative boundaries) of France between years 1990 730 and 2006. These probabilities (corresponding to $P(\alpha_j = 1)$, using the notation introduced in the text) were calculated using the Bayesian approach suggested by Kuo and Mallick (1998), introduced in *Supplementary Material 2*). We fitted statistical models separately for each species.

Variable	Code	Red deer	Roe deer	Wild boar
Elevation	elev	0	0	0
Urban areas fragmentation	urbFrag	0.05	0.01	0.01
Forest fragmentation	forFrag	0.87	0.04	0.01
Habitat type	hab	0	0	1
Hunting bag hunt	1	1	1	
Roads sinuosity	sinus	0.03	0.01	0.01
Density of local roads	locr	0.13	0.14	0.01
Density of regional roads	regr	0.02	0.01	0.01
Density of national roads	natr	0.12	0.66	1
Density of motorways	motr	0.03	0.24	0.03

Table 3 Probability (p) that the model is true, for the five best models predicting the average density of vehicle-wildlife collisions ($n = 20\,275$) for red deer, roe deer, wild boar recorded in 9 departments (administrative boundaries) of France between years 1990 and 2006. These probabilities were calculated using the Bayesian approach suggested by Kuo and Mallick (1998), see *Supplementary Material 2*. The probability of a given model correspond to the proportion of Markov Chain Monte Carlo (MCMC) iterations for which $\alpha_j = 1$ for the variables j of the model, and $\alpha_j = 0$ for the other variables j' (see *Supplementary Material 2* for a description of the parameters α_j). See Table 2 for a description of the variable codes.

Species	Model	p
Red deer	hunt + forFrag	0.58
	hunt + forFrag + locr	0.10
	hunt	0.10
	hunt + forFrag + natr	0.06
	hunt + forFrag + urbFrag	0.04
Roe deer	hunt + natr	0.5
	hunt + motr	0.17
	hunt	0.1
	hunt + locr + natr	0.09
	hunt + motr + natr	0.03
Wild boar	hab + natr + hunt	0.93
	hab + natr + hunt + motr	0.03
	hab + natr + hunt + sinus	0.01
	hab + natr + hunt + urbFrag	0.01
	hab + natr + hunt + forFrag	0.01

Table 4 Coefficients of the environmental variables in the final model predicting the average density of vehicle-wildlife collisions (n = 20 275) for red deer, roe deer, wild boar. These collisions were recorded in 9 departments (administrative boundaries) of France between years 1990 and 2006. All fitted models include all the variables belonging to the best model for at least one species (identified by the Kuo and Mallik's approach, see *Supplementary Material 2*). We present the 90% credible intervals in parentheses (intervals with a probability equal to 0.9). See Table 2 for a description of the variable codes.

Variable	Red deer	Roe deer	Wild boar
Forest	-2.44 (-9.64 – 4.76)	-1.1 (-7.21 – 4.53)	-6.17 (-12.31 – -0.33)
Agriculture	-6.81 (-14 – 0.31)	-0.69 (-6.87 – 4.98)	-4.48 (-10.71 – 1.57)
Open	-4.32 (-11.54 – 2.85)	-1.43 (-7.69 – 4.34)	-3.95 (-10.22 – 2.17)
Urban	-0.32 (-9.08 – 8.45)	-1.09 (-7.28 – 4.81)	1.62 (-5.24 – 8.33)
natr	0.38 (-0.02 – 0.78)	0.21 (0.04 – 0.38)	0.29 (0.04 – 0.53)
hunt	0.015 (0.009 – 0.022)	0.005 (0.003 – 0.006)	0.007 (0.006 – 0.009)
forFrag	0.83 (0.52 – 1.18)	0.1 (-0.03 – 0.23)	0.03 (-0.15 – 0.2)

Fig. 1a

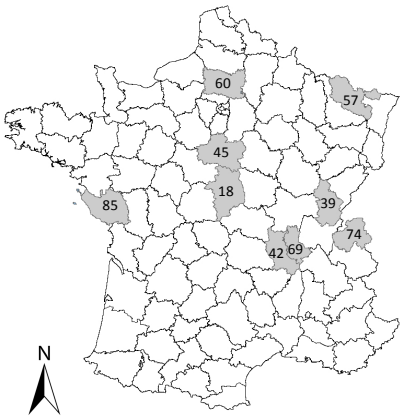


Fig. 1b

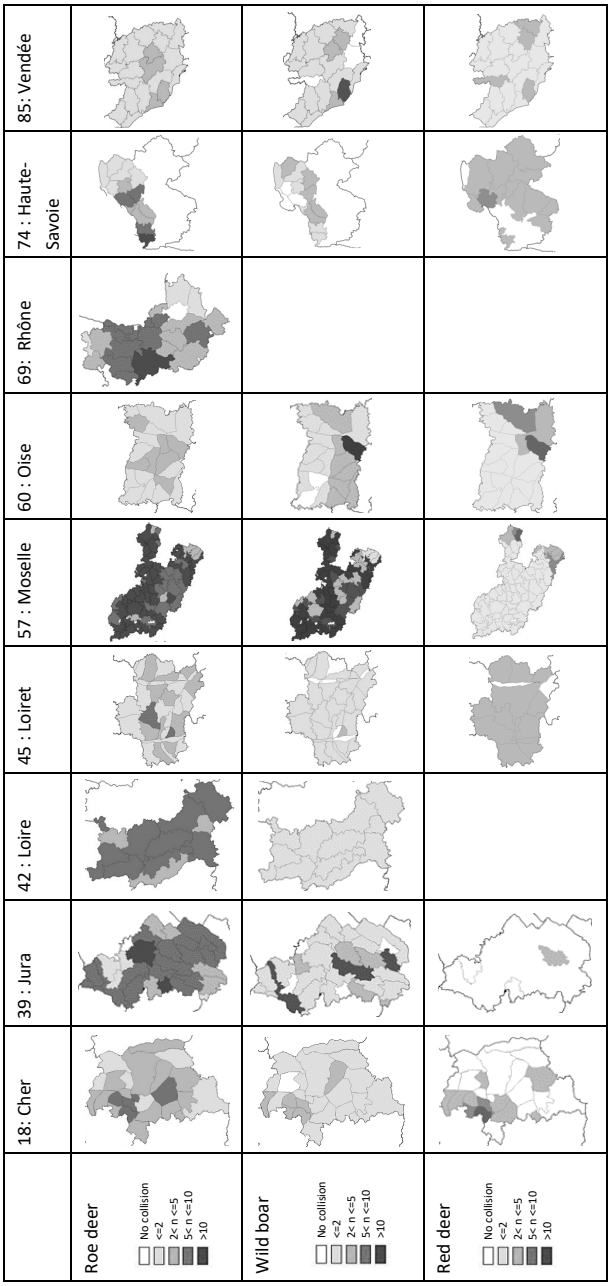

18: Cher
39 : Jura
42 : Loire
45 : Loiret
57 : Moselle
60 : Oise
69: Rhône
74 : Haute-Savoie
85: Vendée
Roe deer
No collision
<=2
2< n <=5
5< n <=10
>10
Wild boar
No collision
<=2
2< n <=5
5< n <=10
>10
Red deer
No collision
<=2
2< n <=5
5< n <=10
>10

Fig. 2

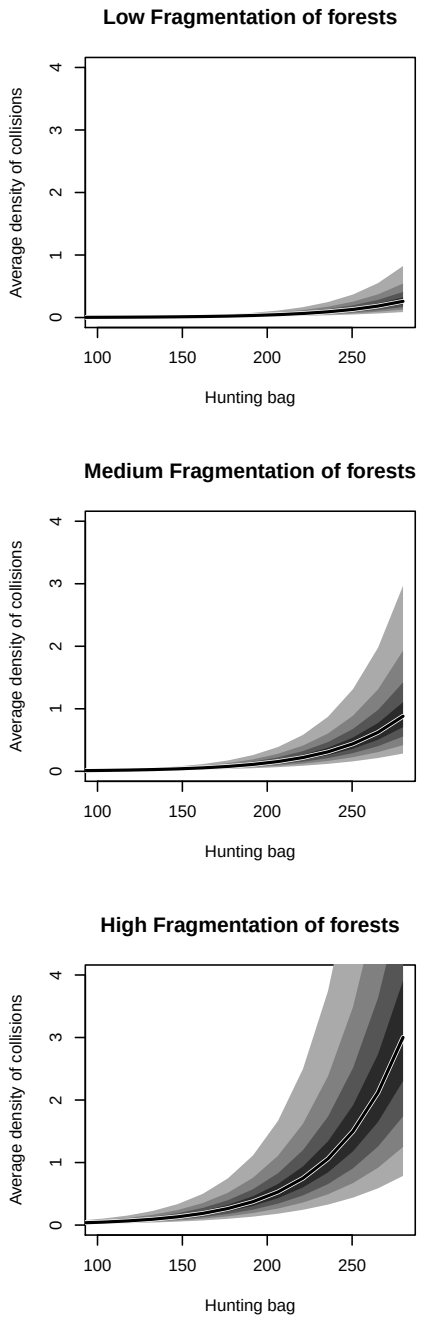
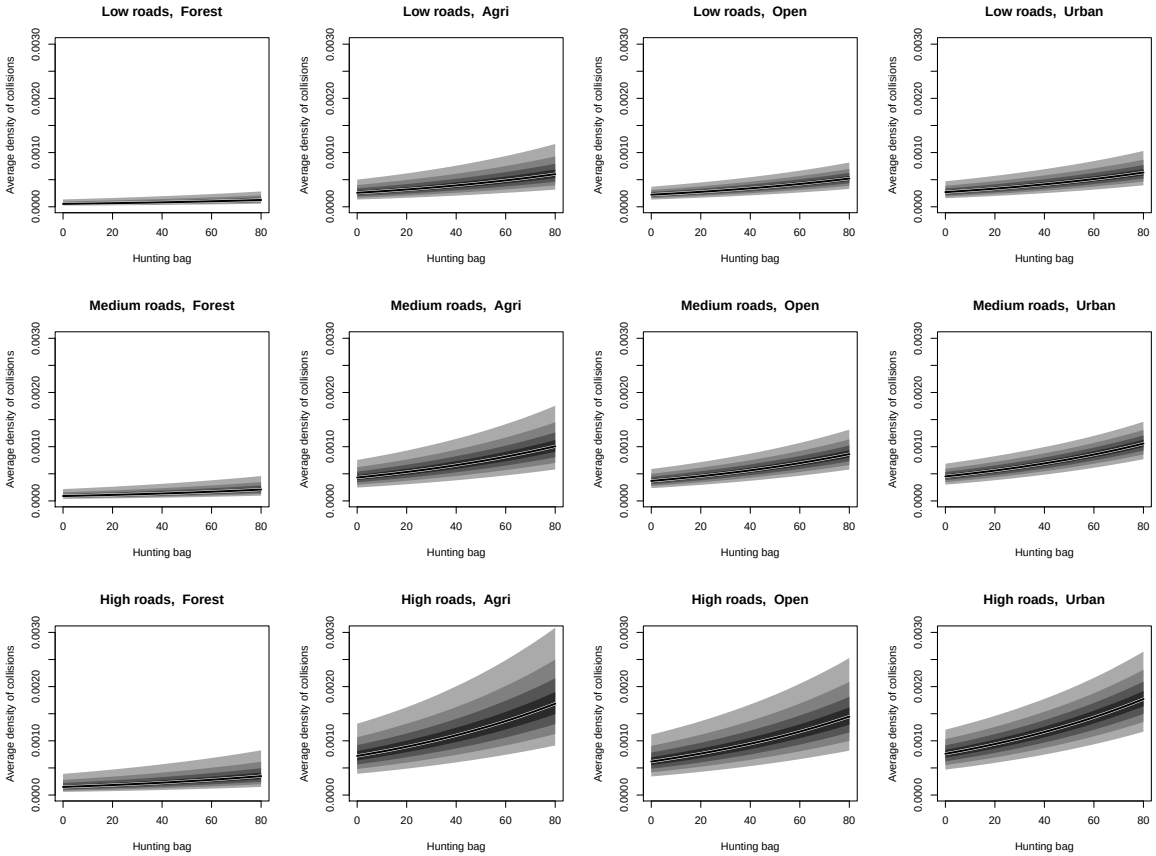

Low Fragmentation of forests
Average density of collisions
0
1
2
3
4
100
150
200
250
Hunting bag
Medium Fragmentation of forests
Average density of collisions
0
1
2
3
4
100
150
200
250
Hunting bag
High Fragmentation of forests
Average density of collisions
0
1
2
3
4
100
150
200
250
Hunting bag

Fig. 3

Low density of roads
80%
60%
40%
20%
Average density of collisions
0.0
0.1
0.2
0.3
0.4
0
50
100
150
200
250
Hunting bag
Medium density of roads
Average density of collisions
0.0
0.1
0.2
0.3
0.4
0
50
100
150
200
250
Hunting bag
High density of roads
Average density of collisions
0.0
0.1
0.2
0.3
0.4
0
50
100
150
200
250
Hunting bag

Fig. 4


Low roads, Forest
Low roads, Agri
Low roads, Open
Low roads, Urban
Medium roads, Forest
Medium roads, Agri
Medium roads, Open
Medium roads, Urban
High roads, Forest
High roads, Agri
High roads, Open
High roads, Urban
Average density of collisions
0.0000
0.0010
0.0020
0.0030
Hunting bag
0
20
40
60
80

Supplementary material 1: Detailed description of the 9 departments of France

Table 1 Description of the 9 departments of France where the collisions between vehicles and wildlife have been recorded from 1990 to 2006. Column headings mean population density for 'pop', average elevation a.s.l. for 'elev', and minimum and maximum elevation a.s.l. for 'elev. min' and 'elev. max', the percentage area of forest for '% for.', the road network density for 'rd. dens.', the percentage of motorways for '% Mways', the percentage of national roads for '% nat.', the percentage of regional roads for '% reg.' and the percentage of local roads for '% loc.'. The last column describes the main land use and habitat types of each department.

Department	area (km^2)	pop. ind/km^2	elev. (m)	elev. min. (m)	% for. max. (m)	rd dens.	% Mways	% nat.	% reg.	% loc	Land use and main habitats
Cher	7 235	43	87	502	24	1.4	1	1	47	51	Extensive crops, vineyard, deciducous forest, multiple cropping and grove
Jura	4 999	52	177	1 495	44	2.1	1	1	33	65	Lowland forest <200-300m a.s.l.; grassland plateau from 400 to 700 m a.s.l.; mountains and coniferous forest >1000 m a.s.l.
Loire	4 781	159	130	1 631	26	2.6	1	1	30	68	Continuous mixed forests of beech and fir tree, vineyards, moorlands
Loiret	6 775	99	67	281	26	1.7	2	0	32	66	Large agricultural lands, deciduous forest and typical peat swamp forest from Sologne
Moselle	6 200	168	145	986	28	1.8	2	1	39	58	50% area is used for agricultural crops, mixed forest surrounds the Vosges mountain foothills
Oise	5 860	140	22	236	21	2.1	1	1	33	65	Vast cultivated lowlands, deciduous forests
Rhône	2 715	166	140	1 008	22	2.1	2	1	27	70	Vineyards, small crops, mid-elevation mountains covered with mixed forests
Haute-savoie	4 388	181	250	4 809	39	2.1	2	0	33	65	Grasslands, beech forest at low elevation and Alpine grasslands
Vendée	6720	99	0	290	5	2.4	1	0	29	70	Grove and coastal pine forests

Supplementary material 2: Bayesian modelling fit and variable selection

We used a Bayesian variable selection approach to identify the variables affecting the most the density of vehicle–wildlife collisions in a MU. As a first step, we replicated the same approach for each species. For a given species, let N_i be the number of collisions with a vehicle in the MU i. We assumed that this variable could be described by the following over-dispersed Poisson distribution:

$$N_i \sim P(\epsilon_i \times \lambda_i \times Y_i \times S_i)$$

$$\log \epsilon_i \sim \mathcal{N}(0, \sigma)$$

where Y_i is the number of years of data available in the MU i, S_i is the area of the MU i, λ_i is the average number of collisions per unit area and per year expected under our model (see below) and ϵ_i is a normal over-dispersion residual with zero mean and a standard deviation equals to σ.

The average number of collisions per unit area and per year in a management unit i was modeled as a function of the P=10 variables described in the last section (see Table 1), according to the following log-linear model:

$$\log \lambda_i = \beta_0 + \sum_{j=1}^{P} \alpha_j \times \beta_j \times X_{ij} + \eta_{d(i)}$$

$$\eta_{d(i)} \sim \mathcal{N}(0, \sigma_d)$$

where X_{ij} is the value of the jth variable describing the management unit i, η_d is a random effect describing the effect of the department d, $d(i)$ is the department corresponding to the management unit i, and α_j and β_j are two coefficients characterizing the role of the jth variable in this linear combination: (i) the coefficient α_j can only take values 0 and 1. When this coefficient is equal to 1, the jth variable belongs to the model; when this coefficient is equal to 0, the jth variable does not belong to the model. In a Bayesian context, the value of this coefficient is therefore considered as the realization of a Bernoulli variable characterized by a probability p_j, which is the probability that this

variable belongs to the model; (ii) the coefficients β_j can take any real value, and determines the importance of the jth variable on the average number of collisions when this variable belongs to the model, as in a classical regression model. This approach consists in separating the presence of a variable in a model from its importance, and then to estimate the probability of presence of each variable in the model from the data, as suggested by Kuo and Mallick (1998). In the rest of this paper, we refer to this approach as the Kuo and Mallick (1998)'s approach.

We set the following vague priors on the coefficients of the model:

$$\beta_0 \sim \mathcal{N}(0, 100)$$

$$\sigma \sim \mathcal{T}(0.01, 0.01)$$

$$\sigma_g \sim \mathcal{T}(0.01, 0.01)$$

$$\alpha_j \sim \mathcal{B}(0.5)$$

$$\beta_j \sim \mathcal{N}(0, 100)$$

Posterior distributions of parameters were deduced from prior information about parameters and likelihood functions of the data by Monte Carlo Markov Chain (MCMC) simulations, i.e, inferences are made empirically by collecting many realizations from the posterior distribution using a variant of Metropolis method called Gibbs sampling (Gilks and Richardson 1996). We ran one chain for an initial period of 1,000 cycles (burn-in period) and then collected information for the next 500,000 iterations. We implemented the MCMC simulations with the JAGS software (Plummer 2010). From our analyses, we could (i) identify those variables with the largest influence on the number of vehicle–wildlife collisions and calculate the probability P $(\alpha_j = 1)$ that each variable j belong to the best model; (ii) identify the best models predicting the number of collisions and calculate the probability P$(\alpha_1, \alpha_2, \ldots, \alpha_J)$, for each possible combination of the coefficients $\{\alpha_1, \alpha_2, \ldots, \alpha_J\}$, that the corresponding model is the best model. Then, for each species, we fitted and interpreted the best regression model predicting the average number of collisions per unit area and per year, *i.e.*:

$$\log \lambda_i = \beta_0 + \sum_{j \in B} \beta_j \times X_{ij} + \eta_{d(i)}$$

$$\eta_{d(i)} \sim \mathcal{N}(0, \sigma_d)$$

where B is the set of variables corresponding to the best model identified by the Kuo & Mallik's approach. We checked the convergence of the MCMC chains both visually and by using the diagnostic of Raftery and Lewis (1992). None of these diagnostics showed any evidence of nonconvergence of the MCMC. We then examined the fit of the model using the approach recommended by Gelman and Meng (1996). For every iteration of the MCMC, i.e. for every value $\theta^r = \beta_0 \ldots$ of the vector of parameters of this second model sampled by MCMC, we simulated a hypothetical replication of the dataset using equation (1), i.e. we simulated a number of collisions in each management unit. We then compared the observed number of collisions with the statistical distribution of simulated numbers of collisions. We calculated that 99% (red deer), 100% (roe deer) and 100% (wild boar) of the 90% of the credible intervals contained the observed number of collisions, which indicates that the fit was correct for the three species.

Note that it is difficult to compare coefficients β_j of a variable j across models containing different variables and different sampling units (Becker and Wu 2007), which precluded the comparison of the models across species. We needed to fit another general Bayesian model to allow for this comparison. We first focused on the MUs containing all three species. Then, we identified the set D of variables belonging to the best model identified by the Kuo and Mallick (1998)'s approach for at least one of the three species. Then, for a given species, we predicted the average number of collisions per unit area and per year not only as a function of the variables identified as important for this species, but also as a function of the variables identified as influential for the other species (more formally, we replaced the set B by the set D in equation (1)). We also fitted these models by MCMC, using the same approach as for the fit of the previous models. Note the collision data can be downloaded and the analyses replicated or compared with other approaches (see section

Data and code accessibility).

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