

1 Comparison of environmental, biological and 2 anthropogenic causes of wildlife–vehicle collisions 3 among three large herbivore species

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5 **Abstract** Wildlife–vehicle collisions are of increasing concern with regards to the continuous and
6 accelerating anthropogenic development. Preventing and mitigating collisions with wildlife will
7 require a better understanding of the environmental and biological drivers of collision risks. Because
8 species of large mammals differ in terms of food requirements, habitat selection and movement
9 behaviours we tested at the management unit level if the density of collisions with red deer, roe deer
10 and wild boar differed in terms of spatial distribution and explanatory factors. From 20,275
11 documented collisions in France between years 1990 and 2006, we found marked differences in the
12 most influential environmental factors accounting for the density of collisions among the three
13 species. The effect of road density was higher for the red deer than for the two other species and did
14 not level off at our spatial-scale of observation. As expected, the annual hunting harvest – interpreted
15 as a proxy of population abundance – was positively associated with the density of collisions for all
16 species, being the strongest for red deer. While the collision density decreased with the proportion of
17 forest in a management unit for wild boar, it increased with the fragmentation of forests for red deer
18 that commute among forest patches between day and night. To reduce the number of wildlife–

19 vehicle collisions, our results suggest to generalise road fencing and/or a control of abundance of
20 large herbivore populations. Mitigation measures should target units where the collision risk is the
21 highest for the most problematic species.

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

24 **Introduction**

25 Over the last decades, heavier traffic loads and continuous expansion of road networks paralleled the
26 increasing number and distribution of most large herbivore populations (Milner et al. 2006, Massei
27 et al. 2015), resulting in a dramatic increase of wildlife–vehicle collision frequency in many
28 European and North American countries (Langbein et al. 2010). For large mammals between one to
29 two millions wildlife–vehicle collisions are recorded annually in the United States (Huijser et al.
30 2015), and about a million in Europe (Langbein et al. 2010), generating acute ecological
31 consequences on animal populations (Forman et al. 2003, Rytwinski and Fahrig 2015). The risk for
32 human safety make wildlife–vehicle collisions an important socio-economic issue and a major issue
33 in the road safety policies (Groot Bruinderink and Hazebroek 1996). The substantial economic bulk
34 of wildlife–vehicle collisions and the need for mitigation of risks raised active areas of research
35 (Schwabe et al. 2002, Malo et al. 2004, Huijser et al. 2015, Elmeros et al. 2011, Gunson et al. 2011,
36 Hothorn et al. 2015). Understanding and identifying high collision risk areas and its ecological and
37 biological drivers is of prime importance to predict wildlife–vehicle collisions in space and time, and
38 to implement appropriate and efficient mitigation measures.

39 First and foremost, road infrastructure and use by drivers are anthropogenic explanatory factors
40 potentially driving the occurrence of wildlife–vehicle collisions. The vehicle speed and the density
41 of roads are since long recognized to increase the frequency of wildlife–vehicle collisions (Pojar
42 et al. 1975, Case 1978, Hartwig 1993, Groot Bruinderink and Hazebroek 1996, Seiler 2005). For
43 instance, the number of moose-vehicle collisions in Sweden was positively correlated with density
44 of roads with a speed limit of 90 kph (Seiler 2005). Road class also influences the risk of collisions
45 and mosts are recorded on secondary roads, mainly because they represent the greater cumulative
46 length within most national road networks. Per unit of length, however, collisions frequency is
47 higher on primary roads where traffic volume and vehicle speed are greater (Pojar et al. 1975,
48 Bashore et al. 1985, Désiré 1992, Hartwig 1993, Hubbard et al. 2000, Langbein et al. 2010,
49 Roedenbeck 2007, McShea et al. 2008). While the number of collisions increases broadly with
50 traffic load, collision frequency can level off above a traffic density threshold, from which animals
51 avoid crossing roads (Müller and Berthoud 1997, Skölving 1985, Clarke et al. 1998, Seiler 2004,
52 2005).

53 From an ecological point of view, space use and habitat selection by animals are key processes
54 for the understanding of the spatio-temporal distribution of wildlife–vehicle collisions. Habitat
55 selection by animals is a hierarchical process whereby choices observed at small scales are
56 constrained by previous choices made at larger spatio-temporal scales (Johnson1980; Levin1992).
57 Hence habitat characteristics, from landscape to the vicinity of the road, should influence
58 wildlife–vehicle collisions at different spatial scales (de Bellefeuille and Poulin 2003). Most
59 previous studies investigating collision patterns did so either at very large, state-wise or continental
60 scales (Brockie et al. 2009, Červinka et al. 2015, Seiler et al. 2004), or at a very fine scale (Taylor
61 and Goldingay 2004, Grilo et al. 2009). However, intermediate spatial scales are also relevant
62 because in a patchy landscape collisions are more likely to happen on road sections located between
63 woods and open fields because animals move frequently between protected resting areas and
64 meadows or agricultural crops to forage (Puglisi et al. 1974, Bashore et al. 1985, Hubbard et al.
65 2000). This is the case for wild boars (*Sus scrofa*) commuting on a daily basis from forested patches
66 to open fields (Carbaugh et al. 1975, Waring et al. 1991, Keuling et al. 2009). Consequently, when
67 roads run through homogeneous landscapes, wildlife–vehicle collisions are more uniformly
68 distributed in space than in fragmented and heterogeneous landscapes (Bellis and Graves 1971,
69 Bashore et al. 1985, Hubbard et al. 2000). A study on white-tailed deer (*Odocoileus virginianus*)
70 illustrates how landscape affect collision risks, being higher with the proportion of woodland cover
71 level (Finder et al. 1999, Hubbard et al. 2000, Roedenbeck 2007). Matching observation with
72 management scales of species is also way to provide managers with efficient policies they can act
73 on, particularly because our ability to predict collision location increases with the spatial scale (*e.g.*
74 Orrock et al. 2000).

75 Most large herbivores in Europe and North America are forest-dwelling species that are strongly
76 attracted to roadsides (Bellis and Graves 1971, Carbaugh et al. 1975, Bashore et al. 1985,
77 Groot Bruinderink and Hazebroek 1996). By regularly feeding on roadsides animals put themselves
78 at a greater risk of collisions with vehicles (Puglisi et al. 1974, Bashore et al. 1985, Finder et al.
79 1999, Roedenbeck 2007), previous works searched for causal factors of wildlife–vehicle collisions,
80 but focused on one single species (moose *Alces sp.* : Seiler (2005), Dussault et al. (2007);
81 white-tailed deer: Bashore et al. (1985), Finder et al. (1999), Hubbard et al. (2000); roe deer:

82 Mysterud (2004)), or did not differentiate among species (Malo et al. (2004), for red deer *Cervus*
83 *elaphus*, roe deer *Capreolus capreolus* and wild boar, Gunson et al. (2009) and Nielsen et al. (2003),
84 for white tailed deer and mule deer *Odocoileus hemionus*). In spite of many large herbivore species
85 live sympatrically, comparative analyses of wildlife–vehicle collisions in mammals have rarely been
86 conducted. Differences in diet and body size, space use behaviours, sensitivity to human presence
87 and disturbance, or levels of grouping patterns (Sáenz-de Santa-María and Tellería 2015) could
88 generate contrasting spatio-temporal distribution of collisions (as documented by
89 Rodríguez-Morales et al. 2013). Our ability to predict where and when wildlife–vehicle collisions
90 most likely occur may actually be hampered by specific habitat choice behaviours and its ecological
91 correlates in the landscape.

92 Based on data recorded at the management unit (MU) scale over 9 departments between 1990 to
93 2006 in France, we first describe the spatial distribution of vehicle-wildlife collisions of the
94 sympatric red deer, roe deer and wild boar. At this scale of observation, we aim at explicating what
95 factors affect the number of roadkills in a given MU. To do so, we compare the relative effects of a
96 set of environmental, biological and anthropogenic variables on the number of wildlife–vehicle
97 collisions among species, using a Bayesian statistical framework to test the following predictions
98 (Table 1):

- 99 1. We predict a positive relationship between the number of wildlife–vehicle collisions and the
100 density of roads (Romin and Bissonette 1996, Pokorny 2006, Vignon and Barbarreau 2008), and
101 between collision number and average car speed, hence leading to an increasing risk from local
102 roads to highways. Also, the average number of wildlife–vehicle collisions should increase with
103 population abundance, both across species and increasing from red deer, roe deer to wild boar,
104 and in time with the annual variation of each species abundance (Schwabe et al. 2002, Seiler
105 2005, Sudharsan et al. 2006).
- 106 2. We expect more collisions with the proportion of forest in the landscape (Carbaugh et al. 1975,
107 Waring et al. 1991) because red deer, roe deer and wild boar are all forest-dwelling species and
108 found at highest densities in this habitat type (*e.g.* Telleria and Virgós 1997, Virgós 2002).
109 However, the association between herbivore abundance and forest densities differs among the

110 three species (Hewison et al. 2001, Patthey 2003, Saïd et al. 2005, Keuling et al. 2009, Thurfjell
111 et al. 2009). In France red deer is confined by hunters to forests or to mountain areas, wild boar is
112 also a forest species, but is currently expanding in all in all ecosystems thanks to its flexible
113 behaviour, and roe deer is more ubiquitous and present in all departments (Maillard et al. 2010).
114 Consequently, we predict a decreasing effect of the proportion of forest on the number of
115 collisions from red deer, to roe deer and wild boar (Table 1).

116 3. Large herbivore move between different habitat patches so we expect landscape fragmentation to
117 increase these movements and, as a consequence, the number of collisions too (Bashore et al.
118 1985, Romin and Bissonette 1996, Hubbard et al. 2000, Madsen et al. 2002). Moreover, with
119 smaller home ranges, landscape fragmentation is less likely to increase an individual home range
120 heterogeneity and among-patch movements. We hence expect the effect of habitat fragmentation
121 on the number of collisions to decrease in magnitude from roe deer, wild boar and red deer
122 following their respective average home range size (Table 1).

123 4. For large herbivores, crops are highly attractive food resources and individuals frequently
124 commute between forests and agricultural areas on a daily basis (Keuling et al. 2009). We predict
125 a positive association between the proportion of agricultural areas and the number of collisions
126 but expect different responses for the three species with a stronger effect for wild boar and roe
127 deer than for the red deer (Table 1). Wild-boar indeed use agricultural crop intensively (87% of
128 the total amount paid for big game damage are done by wild boar, Maillard et al. 2010) and roe
129 deer has colonised the agricultural plain (Hewison et al. 2009). Conversely red deer spatial
130 distribution is restricted and strongly associated with forest (Milner et al. 2006), while being less
131 attracted to crops than wild boar (Schley and Ropper 2003, Gebert and Verheyden-Tixier 2001).

132 **Material and methods**

133 **Study sites**

134 The local hunting associations of 9 French departments (Cher, Jura, Loire, Loiret, Moselle, Oise,
135 Rhône, Haute-Savoie, Vendée; see Fig. 1 and Table S1 for a detailed description) collected and
136 centralized the collision data. Despite our choice of the departments being primarily motivated by

137 data availability, the 9 locations are representative of most mainland French ecosystems. We did not
138 contribute to data collection ourselves and wildlife–vehicle collision cases were reported by the car
139 driver or by direct observations of carcasses on the roads by officials (game wardens, police. . .). The
140 monitoring spanned between 1990 and 2006 but varied among departments. Each department is
141 divided into management units (MUs) defining administrative subdivisions of departments where
142 game management is comprehensive and homogeneous. MU border may differ for red deer, roe deer
143 and wild boar. Overall, we had 266 MUs in the 9 departments for roe deer, 247 MUs for wild boar in
144 8 departments (no wild boar data in Rhône), and 110 MUs for red deer in 7 departments (no red deer
145 in Loire and Rhône). On average the surface of a single MU was 208 km² (SD = 167 km²). Because
146 the exact location of the collision was unknown (no GPS fixes), we assigned each collision event to
147 the closest MU. Therefore potential location inaccuracies were of limited consequences on the
148 presented results.

149 **Spatial scale of observation**

150 Our statistical unit was the MU making the spatial scale of investigation of wildlife-vehicle collision
151 pattern rather large. Because of this particular sampling design, we did not attempt to explain the
152 location of collisions at a very fine scale *e.g.*, by comparing local conditions where the collisions
153 took place and a couple of meters away (case-control design, *e.g.* Eberhardt and Thomas 1991).
154 Instead, we explain the collision number of each MU with the mean value of the different
155 environmental variables measured across the corresponding MU to test their statistical association
156 and to guaranty that number of MUs and environmental descriptors were of the same dimension. As
157 for all processes of habitat use (Johnson 1980, Dupke et al. 2017), predictors of wildlife–vehicle
158 collisions likely change with the spatial scales. At large spatial scale, habitat selection is related to
159 landscape spatial structure, such as topography or habitat fragmentation. For example several
160 authors have shown that vehicle collisions with red deer, roe deer and wild boar were more likely in
161 forested environments at large spatial scale while at a smaller spatial scale, road sections with the
162 highest collision risks were located in the open areas or at the forest border (Désiré 1992), or had
163 roadsides with dense vegetation for roe deer (Madsen et al. 2002). In addition, the previously
164 described barrier effect on road traffic and density on the number of collisions are not expected at

165 large spatial scale of investigation because the range of road density is limited in each MU (see
166 discussion).

167 **Explanatory variables of observation**

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

171 *Anthropogenic variables:* We described the road network using the Routes 500 database from the
172 Institut Géographique National (IGN 2001) to derive the road density of MUs. We classified roads in
173 four categories based on the importance of road sections for the traffic (see Supporting information
174 1): local roads, regional roads, national roads and motorways. For each road type, we assigned one
175 of the three possible road density classes (low, medium and high) to the MU to explore non-linearity
176 in the effect of traffic on wildlife–vehicle collisions. Because the statistical distribution of the road
177 density is strongly asymmetrical, we had to find a statistical transformation to ensure the numerical
178 stability of our results and avoid strong leverage effects. We set the limits of road density classes so
179 that MU sample sizes were balanced in each class by computing the 1/3 and 2/3 quantiles of road
180 density distributions. The limits defining the density classes differed according to road type. These
181 limits were equal to 0.37 and 0.52 km per 100 ha for local roads (low, medium and high categories
182 corresponded to road densities of <0.37, between 0.37 and 0.52, and > 0.52 km per 100 ha
183 respectively), 0.16 and 0.24 km per 100 hectares for regional roads, 0.09 and 0.16 km per 100
184 hectares for national roads, and 0.01 and 0.03 km per 100 hectares for motor-roads. The Pearson's
185 correlation (ρ) between pairs of variables measuring the density of roads never exceeded 0.36, so
186 that we did not consider these variables as redundant. Note, however, that most roads in a MU are
187 local roads, so that the overall road density is strongly correlated with the local road density
188 ($\rho = 0.72$), and we did not try to test the effect of the overall road density alone, in addition to other
189 road effects.

190 We also characterized roads sinuosity for each MU by calculating the ratio between the
191 curvilinear length of the road segments and the distance in a straight line between the extreme points
192 of the road. A straight road would have a sinuosity index of 1. We calculated the sinuosity only for

193 local and regional roads because national roads and motorways were mostly straight. Fencing is an
194 efficient way to reduce wildlife–vehicle collision risk (Clevenger et al. 2001, McCollister and
195 Van Manen 2010), accounting for its confounding effects on collision density would be relevant.
196 However, because the information about road fencing is not available nor centralized in France, we
197 could not assess the effect of road fencing on collision density in our study.

198 *Environmental variables:* We extracted landscape variables with a GIS by mapping all MUs and
199 calculating 10 descriptors of the environment. We used the CORINE Land cover (2006) database to
200 derive a categorical variable “Habitat type” (HT) describing the land cover type in the MUs. For
201 each MU, HT returns the proportion of the area covered by forest, agricultural crops, natural open
202 areas, and urban and anthropogenic habitats (4 habitat types).

203 Moreover, we indexed the fragmentation of the forested habitat with the number of connected
204 forest patches in the MU. Let F_f be the number of connected forest patches. To account for the
205 larger number of forested patches in larger MUs we scaled F_f by the area of the corresponding MU,
206 yielding a density of connected forest patches D_f . However, because the relationship between D_f
207 and the proportion of forest in the MU was non-linear (*i.e.* D was redundant with the land cover
208 variable “Forest”), we used a nonparametric loess regression (degree = 2, span = 75%, Cleveland,
209 1993) to predict the logarithm of D as a function of the proportion of forest in a MU. Ultimately, we
210 used the residuals of this regression as an index of the forest fragmentation (noted R_f), whereby a
211 positive values meant more forest patches in the MU for a given forest cover, and conversely for
212 negative values. Following the same procedure, we calculated a fragmentation index of urban
213 patches (R_u), using the density of urban patches F_u instead of the density of forest patches. Finally,
214 we used the IGN geographic database to calculate a 3-classes categorical variable of elevation
215 defined as the proportion of the MU area found <600 m, between 600 m and 1 500 m, and > 1 500 m
216 a.s.l.

217 *Biological variables:* For the three species of large herbivores, we assessed population
218 abundance with the number of harvested animals per km² for each MU (referred to “hunting bag”;
219 see Seiler (2005), Morelle et al. (2013) for a similar approach). We used the number of harvested
220 animals per km² during the previous hunting season, spanning from September of year $t - 1$ to the
221 end of February of year t , to characterise the abundance of a species during year t and to use it as a

222 predictor of the density of wildlife–vehicle collisions. We hence make the assumption that annual
223 hunting bag is positively associated with the population abundance of large herbivores. These data
224 were provided by the local hunting associations in the 9 departments, for every hunting season for
225 which we had collisions data.

226 **Bayesian model fit and variable selection**

227 For each species, we first modelled the number of collisions in a MU with a log-linear model with
228 mixed effects. We assumed a Poisson distribution for the number of collisions, and we classically
229 modelled the logarithm of the mean of this distribution as a linear combination of the characteristics
230 described in the previous section (the usual log-link was used to ensure a positive predicted mean
231 number of collisions). We accounted for the overdispersion in the response variable by including
232 Gaussian residuals in our linear predictor, following the approach of Hadfield (2010). We entered the
233 department (9 levels factor) as a random effect on the intercept. We fitted this model in a Bayesian
234 context with the JAGS software (Plummer 2016).

235 We used a Bayesian variable selection approach to identify the variables affecting the density of
236 vehicle-wildlife collisions in a MU, that is the number of collisions per surface unit. More precisely,
237 we implemented Kuo and Mallick (1998)'s method to estimate the probability that each variable
238 influenced the mean number of collisions. The Kuo-Mallick's approach also allowed to identify the
239 best models predicting the number of collisions: we could estimate the probability of each possible
240 model to be the best one describing our data (*i.e.* every possible combination of the variables
241 describing the management unit), and select the most likely one. We checked MCMC convergence
242 and good mixing of MCMC chains graphically. We also checked the convergence of the chain with
243 the criterion of Raftery and Lewis (1992). This criterion indicated no lack of convergence for any
244 parameter of any model (the minimum number of iterations required to allow the calculation of 95%
245 credible intervals with an accuracy of 0.02 and a probability of 0.9 was much smaller than the 500
246 000 iterations of the chains for all models and all parameters). Overall, the goodness of fit of the
247 models was excellent for all species. Technical details and a formal description of this approach are
248 available as *Supporting information 2*.

249 Note that we could not use these models to compare the influence of a given predictive variable

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

261 **Results**

262 For all years and departments, we recorded 20,275 collisions for all species among which 69.9%
263 were roe deer, 3.1% red deer and 27% wild-boar. The collision number averaged 6.37 ± 8.62 per
264 100km^2 for roe deer, reaching up to 80 collisions per 100km^2 for some MUs (see Fig. 2). For red
265 deer and wild boar, the density of collisions was lower, with on average 0.93 ± 1.89 and 4.12 ± 8.09
266 per 100km^2 , following the same order as their respective relative densities.

267 **Red deer**

268 The forest fragmentation and the hunting bag had the strongest effect on the density of collisions
269 with the red deer (Table 2). Note that the model with the largest probability was characterized by
270 slightly more than one chance out of two to be the true model (58%, see Table 3), indicating a
271 significant uncertainty in the model selection process. Alternative models often included a measure
272 of human density (*e.g.* density of local roads – second best model, density of national roads – fourth
273 best model, fragmentation of urban areas – 5th best model). However, none of these alternative
274 models was characterized by a large probability to be the best model, suggesting that the frequency
275 of collisions between red deer and vehicles are essentially determined by the density of red deer, as
276 well as the forest fragmentation as we expected from its behaviour. This best model indicated that

277 the number of collisions was larger when the hunting bag was high and the forest was strongly
278 fragmented (Fig. 3).

279 **Roe deer**

280 Roe deer relative abundance and, to a lesser extent, the density of national roads were the main
281 variables influencing the density of collisions with the roe deer (Table 2). Note that there was also a
282 large uncertainty in the model selection for this species (Table 3). Although the best model was the
283 model containing the two aforementioned variables, nearly all the other models with some statistical
284 support included both roe deer relative abundance and one or several measures of road density
285 (whether local roads, national roads or motorways). We fit the best model to describe the
286 relationship between these two best variables and the density of collisions for the roe deer. This
287 model indicated that the density of collisions was larger when both roe deer hunting bag and the
288 density of national roads were high (Fig. 4). The effect of national road density was, however, small
289 in comparison to the effect of the relative abundance of roe deer (Fig. 4).

290 **Wild Boar**

291 Three variables strongly influenced the number of collisions between vehicles and wild boars: the
292 habitat type, the hunting bag and density of national roads (Table 2). Note that there was only a
293 small uncertainty on the model selection process as a very large probability is associated to this
294 model (Table 3). We therefore fitted this best model (Fig. 5). To interpret the effect of habitat type,
295 we had to account for the difference in average landcover between habitat types. For instance, while
296 a MU with 80% of its area covered by agriculture is frequent in our data, a MU with 80% of urban
297 area never occurred in our data, so that we could not readily interpret the raw estimates of the
298 coefficients to identify the differences between these habitat types clearly. To interpret these results,
299 we predicted the average density of collisions between vehicles and wild boars as a function of the
300 hunting bag and the density of national roads in four types of management units (see Fig. 5) in four
301 contrasting environments: (*i*) a MU (labeled “Forest”), characterized by 91% of forest and 3% of the
302 three other habitat types, (*ii*) a MU with a high land-cover of agricultural areas (labeled “Agri”),
303 characterized by 91% of agricultural areas and 3% of the three other habitat types, (*iii*) a MU

304 (labeled “Open”), characterized by 37% of open areas, 30% of forests, 30% of agricultural areas,
305 and 3% of urban areas, and (*iv*) an urbanized MU (labelled “Urban”) characterized by 16% of urban
306 area, 14% of open area, 35% of forests and 35% of agricultural areas. A careful examination of our
307 dataset revealed that these particular sets of environmental conditions are typical of those
308 encountered in France: thus, the habitat composition in the “Forest” MU is typical of the more
309 forested management units observed in our dataset; the habitat composition in the “Urban” MU is
310 typical of the highly urbanized management units, etc. According to the best model, the density of
311 collisions increased with the hunting bag and the density of national roads (Fig. 5). On the other
312 hand, the density of collisions was much lower in densely forested management units than in other
313 types of management units.

314 **Comparison of patterns among species**

315 We compared across species the effect of the variables identified by the Kuo and Mallik (1998)’s
316 approach as important for at least one species. The coefficients of the variables for each species are
317 given in Table 4. These models indicated that the effect of the forest fragmentation on the density of
318 collisions was stronger for the red deer than for the two other species for which it was not different
319 from zero. The effect of national roads was on average higher for the red deer than for the two other
320 species, but this coefficient was characterized by a larger variance: the 90% credible interval
321 included 0 for this species, explaining why this variable was not initially selected as part of the best
322 model for red deer. The effect of the national road on the density of collisions was similar for the
323 wild boar and the roe deer. The credible interval on the coefficients of the various habitat types
324 (forest, urban, open, agriculture) included zero for all species except the wild boar. The density of
325 collisions between vehicles-wild boar was negatively affected by the density of forest. Finally,
326 relative abundance was positively related to the density of collisions for all species but was three
327 times larger for the red deer than for the roe deer and wild boar.

328 **Discussion**

329 By comparing the spatio-temporal pattern of vehicle collisions with red deer, roe deer and wild boar
330 we found that population density and movement behaviour of animals govern collision density

331 differently for the three species. Hunting bag, used as a proxy of population density, was the most
332 influential variable, confirming that the species abundance in an area is positively associated to
333 collision risks (Puglisi et al. 1974, Farrell et al. 1996, Seiler 2004) but this effect was, for instance, 3
334 times larger for the red deer than roe deer and wild boar. Similarly, for red deer and wild boar
335 collisions with vehicles likely increase with movements between patches of favored habitats in
336 response to habitat selection for foraging and disturbance. Conversely, collisions between roe deer
337 and vehicles appeared more uniformly distributed in the landscape.

338 **Population abundance and collisions with vehicles**

339 It has been repeatedly shown that local densities of large herbivores strongly influence collision risks
340 (Puglisi et al. 1974, Farrell et al. 1996, Seiler 2004). Accordingly, we found that hunting bag, a
341 proxy population abundance, is the only common predictor of wildlife–vehicle collisions for the
342 three large herbivore species in agreement with our predictions. The effect is always positive but
343 small as for a given MU, collision density increased by approx. 1% (range 0.5 – 1.5) for each
344 additional thousands of animals shot per year. The relationship between population abundance and
345 frequency of collisions differed among the three species, the largest effect being observed for red
346 deer and the smallest for roe deer (Table 4). Accordingly, the annual number of wildlife–vehicle
347 collisions increased 6-fold between 1986 and 2006 at the national level in France, while at the same
348 time the hunting bag, a large-scale proxy of animal abundance, was 4 times larger for red deer, 5
349 times for roe deer and 6 times for wild boar (Vignon and Barbarreau 2008).

350 We contend, like previous studies (Iverson and Iverson 1999, Morelle et al. 2013), that we used
351 hunting bag as a proxy of population abundance to account for wildlife vehicle collision. In France,
352 annual quotas set how many roe deer and red deer may be harvested during the hunting season,
353 while wild boar hunting is either unlimited or with quotas, which could also explain the different
354 relationships between population abundance and collision density we find. Because red deer face
355 high hunting pressure to control its colonisation to new areas and its associated damages on crops
356 and forests, any increase in hunting bags likely reflects an increase in abundance (Saint-Andrieux
357 et al. 2004). Conversely roe deer is ubiquitous in France, over a much longer period of time than red
358 deer, and its population dynamics is currently levelling off (Maillard et al. 2010). Consequently,

359 hunting bag may not capture variation in roe deer abundance as for the red deer, so that the
360 relationship between hunting bag and collision frequency is weaker for the roe deer. Similarly, wild
361 boar reproduction is strongly influenced by oak masting events (Gamelon et al. 2013), which leads
362 to delayed effects on abundance not immediately reflected into hunting bags, and hence on its
363 relationship with the number of collisions.

364 Clearly, hunting bag may be affected by hunting effort (Iijima 2017), the relative effect of
365 relative abundance of herbivores on the number of collisions should be confirmed with more
366 accurate estimates of population densities. Our results do not necessarily indicate a stronger effect of
367 the animal population abundance on the density of collisions for the red deer. Alternatively, this
368 difference could arise from a combination of different ecology, behavioural responses to hunting,
369 and hunting practices among species.

370 **Importance of inter-specific differences**

371 Related to their body size and specific food requirements, the ranging behaviour and abundance of
372 the three species differ markedly. At the individual level, a large home range size increases the
373 probability of road inclusion within and individual's area of use. At the population level, species
374 with the larger home range put more individuals at risk of collision than species with smaller home
375 range. Having more individuals at risk of collision could in turn lead to a stronger association
376 between population abundance and the density of wildlife–vehicle collisions. In mammals, home
377 range size is associated with species' body size (Lindstedt et al. 1986, Mysterud et al. 2001) and
378 should decrease from red deer to wild boar and roe deer. Similarly in large herbivores population
379 abundance is lower for large than small sized species (Silva and Downing 1995). Although limited
380 to three species, the effect of hunting bag on collision frequency decreases from red deer, to wild
381 boar and roe deer (Table 4), as expected from their respective average body size. The lower collision
382 density we observe for red deer could result from a greater sensitivity to anthropogenic activities and
383 avoidance behaviour of roads (Frid and Dill 2002). We currently have no direct observation from
384 animal relocations to support this hypothesis and empirical evidence for road avoidance behaviour in
385 large herbivores are equivocal. For instance, no road avoidance was found for red deer in Norway
386 where traffic and road density are comparatively lower than in France (Meisingset et al. 2013).

387 Conversely, D'Amico et al. (2016) reported road avoidance for red deer and wild boar although to a
388 similar extent for the two species (see also Rowland et al. (2000) on elk in North America).

389 Our results show that although the risk of collision exists in all kinds of environment, it differed
390 in magnitude according to the species and the landscape structure. Collisions with wild boars were
391 more likely to occur in MU with agricultural, urban and open areas and less in forested areas, which
392 differentiates this species from red deer and roe deer (Table 3; Fig. 3 & 4). The concomitant growth
393 of urban areas and wild boar populations in recent years has increased the presence of this highly
394 plastic species around cities and in suburbans areas (Cahill et al. 2012) where hunting is difficult and
395 rather limited. As urban encroachment expands on the agricultural and forested lands, we expected
396 more collisions with the wild boar in urbanized areas. Wild boar frequently move from one habitat
397 to another and does not preferentially seek forest patches, explaining why habitat type rather than
398 forest fragmentation accounts for collisions number for this species. Opposed to wild boar is the
399 typical forest dwelling red deer which occasionally feeds on of agricultural and mixed habitats in the
400 vicinity of forest patches. Males make large movements across seasons to commute between
401 foraging and rutting areas (Hamann et al. 1997), which put them at risk of collision with vehicles. In
402 lowland forests, females have limited seasonal migration movements, but can travel relatively long
403 distances to reach foraging areas at night (Klein and Hamann 1999). In agreement with the
404 hypothesis that animal movement put them at risk of encounter with vehicles, we found that
405 collisions with red deer were more numerous when the number of forest patches increases in the
406 landscape (Table 4; Fig. 2). Conversely, the role of landscape structure had no detectable influence
407 on roe deer collisions contrary to our predictions. Since roe deer is found in all habitats, population
408 abundance could reflect habitat selection at the population scale better than our environmental
409 variables. Moreover, habitat selection of ecotones by roe deer likely occurs at a small spatial scale
410 and because they live on a small home range, forest fragmentation is less likely to increase home
411 range heterogeneity and inter-patch movements. Consequently our environmental variables,
412 measured at the management unit level, may not capture spatial heterogeneity relevantly for roe deer.

413 **Influence of road network on collisions**

414 The road network configuration in the landscape is a key structuring factor of the collision risks with
415 wildlife. A review of the wildlife–vehicle collisions with mammals showed that 39% of studies (7
416 out of 18) reported a positive effect of traffic, road width or speed limit on collisions number
417 (Gunson et al. 2011). The “national” roads are the only type of roads affecting collision numbers
418 with wild boars and roe deer in France (Fig. 3 & 4). Similarly in Slovenia, among a set of 40 tested
419 variables describing landscape features, density of roads has an overwhelming effect on the number
420 of collisions with roe deer (Pokorny 2006). These “national” roads connecting the main urban
421 centres in France combines a heavy traffic load with a low level of protection such as fences or
422 wildlife crossing and make most of the transportation network. Unexpectedly though, the density of
423 roads has no detectable effects on collision number with red deer that was more related to landscape
424 structure. Red deer behaviour in habitat selection could account for this relatively low the risk of
425 collision. For instance, red deer select mostly for forested habitats with only a marginal use of
426 agricultural crops (Hamann et al. 1997), hence restricting the area at risk of collision. In addition red
427 deer forage on food patches close to roads at a time of low traffic burden mostly (Meisingset et al.
428 2013) or select habitat away from roads with the greatest vehicle use such as primary roads
429 (Montgomery et al. 2012).

430 The density of other road types seems to have little influence on the density of collisions,
431 whatever the species (Table 2). In France, highways and motorways are fenced most of the time.
432 According to our results, road fencing proves to be an efficient method to limit collision risks despite
433 a high speed limit (>110 km.h⁻¹). Accordingly, in France in 2008 and 2009, 86 777 vehicles
434 collisions with red deer, roe deer and wild boar have been recorded by insurance companies, of
435 which only 1% occurred on highways and in spite of highways represent 97% of the daily traffic (40
436 400 versus 1 030 vehicles/day/km for highways vs other roads in 2010 respectively). Conversely,
437 lower speed and narrower lane width likely limit traffic load on this secondary road network both
438 factors being known to reduce wildlife–vehicle collision risks substantially (Hubbard et al. 2000).

439 We found more collisions with roe deer and wild boar in MUs with a higher road density and
440 with a traffic ranging between 2 500 and 10 000 vehicles per day. More surprisingly collisions
441 frequency kept on increasing with traffic over than 10 000 vehicles per day and we could not detect

442 any barrier effect. Previous studies indeed suggested that traffic volume could prevent animals to
443 cross the road Skölving (1985), Clarke et al. (1998), with varying thresholds (approx. 4 000–5 000
444 vehicle per day in Sweden: Seiler (2005); >10 000 vehicles per day in Germany: Müller and
445 Berthoud (1997)), which is consistent with behavioural observation of habitat selection of red deer
446 patterns according to traffic volume in red deer for instance (Meisingset et al. 2013). In our study,
447 the traffic load of roads is likely confounded with road type and road fences, which may have
448 hampered our ability to test for the effect of traffic volume *per se*, or to detect any threshold effect of
449 traffic load on collision risk. Our large working spatial scale is an alternative explanation for the
450 absence of saturation effect of traffic load on collision number. Being averaged over $> 100\text{km}^2$, the
451 range of road density values across MUs is limited. It is unlikely that the road density would be so
452 large over a whole MU that the number of collisions would plateau in this MU.

453 **Management implications and conclusion**

454 In spite of its economic burden (Bissonette et al. 2008) and ecological consequences (Forman et al.
455 2003), wildlife–vehicle collisions with large mammals are most often considered as a general,
456 non-specific problem. Improving the efficiency of mitigation measures likely requires a better and
457 finer knowledge about the causes of collision risks, including inter-specific variations. For instance
458 in Spain, collisions with vehicles did not occur at the same time of the year or of the day, and at
459 different geographical locations for roe deer and wild boar (Rodríguez-Morales et al. 2013). Our
460 results suggest two lines of actions to mitigate wildlife–vehicle collisions. The species-specific
461 factors affecting the collision process can help to focus the measures on high-risk areas, depending
462 on which species is the most at risk in a management unit. For example, we have demonstrated that
463 a high forest fragmentation can increase the collision risk with the red deer in management units
464 where this species is dense. Thus, focusing the mitigation measures on roads crossing highly
465 fragmented forests could reduce this risk. If most collisions occur with the wild boar in a
466 department, the mitigation measures will be more efficient if focused on roads crossing areas where
467 both the wild boar density is large and the agricultural habitat is large.

468 An alternative measure would be road fencing as most – but not all – highways and motorways,
469 that are fenced in France, had lower collision density despite their high traffic load (between 1 and

470 2% of ungulates were killed on motorways: Clevenger et al. 2001, McCollister and Van Manen
471 2010). The number collisions with the red deer increasing with forest fragmentation, road fencing
472 should be focused on roads crossing the most fragmented forests and targeting MU with high
473 number of collisions with that species. Alternatively, fragmentation could be reduced with green
474 bridges, overpasses and underpasses, in addition to maintaining connectivity for large herbivores
475 (reduced connectivity is a major ecological consequence of road fencing, see Forman and Alexander
476 1998). Because vehicle speed increases collision density for wild boar and roe deer, speed should be
477 reduced in high collision zones with these species. Alternatively, reducing population densities of
478 large herbivores could limit the number of collisions per MU. Previous studies showed a reduction in
479 the frequency of deer-vehicle collisions with lower deer densities (Rondeau and Conrad 2003,
480 Sudharsan et al. 2006). Nevertheless, for population size reduction to lead to a substantial reduction
481 in the collision frequency with wildlife would require a massive hunting effort, given the rather weak
482 relationship we report here for the three species.

483 Awareness and prevention campaign could also be a way to mitigate wildlife–vehicle collision.
484 Warning signs are often used in France to reduce wildlife vehicle collisions by warning drivers about
485 the potential presence of wildlife on the road, although only the one sign pictures a jumping deer.
486 The efficiency of the warning signs would be improved if adapted to the local risks with the
487 appropriate species. For exemple in departments with no red deer and many wild boar, a warning
488 sign with a wild boar would definitely be more relevant. An alternative way of reducing the number
489 of collisions may be a better information of the motorists for whom collision risk mainly occurs on
490 roads driving through forests. Information campaigns are needed for a general awareness that the
491 collisions can take place everywhere, even around cities and on highways. Finally, motorists would
492 benefit from a better knowledge about large herbivore behaviour. For example, if one wild boar
493 crosses the road, a second animal or a third one is likely to come out.

494 **Acknowledgments**

495 We thank the French Fédérations départementales des chasseurs of Cher, Jura, Loire, Loiret,
496 Moselle, Oise, Rhône, Haute-Savoie et Vendée for providing us with the collisions data. We are
497 grateful to two anonymous referees who greatly helped at improving previous drafts of the

498 manuscript.

499 **Data and code accessibility**

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

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

509 **Compliance with ethical standards**

510 **Conflict of interest**

511 We declare no potential conflicts of interest.

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729 **Figure captions**

730 **Fig. 1** Location of the nine departments (administrative subdivision of the country) from France used
731 in our study, where $n = 20\ 275$ wildlife–vehicle collisions were recorded between 1990 and 2006.

732 **Fig. 2** Average spatial distributions of vehicle-wildlife collisions with with red deer, roe deer and
733 wild board in each of the management units of the nine departments where collision data have been
734 collected in France.

735 **Fig. 3** Model predictions of the average density of collisions between red deer and vehicles per year
736 and per squared kilometre in a management unit, as a function of the hunting bag (x-axis) interpreted
737 as a proxy of population abundance, and the forest fragmentation (from top to bottom).

738 Wildlife–vehicles collision data were collected in 9 departments (administrative boundaries) of
739 France from 1990 to 2006. To enable a graphical display of the fit, we considered three values of
740 forest fragmentation: (a) low fragmentation (value = -1; only 2% of the management units present a
741 value lower than -1), (b) medium fragmentation (value = 0, corresponding to the mean fragmentation
742 observed in a management unit), and (c) high fragmentation (value = 1; 4% of the management units
743 present a value larger than 1). The central curve corresponds to the point prediction of the model.
744 The four shades of grey indicate (from darker to lighter shades): 20%, 40%, 60% and 80% credible
745 intervals.

746 **Fig. 4** Model predicting the average density of collisions between the roe deer and vehicles per year
747 and per squared kilometer in a management unit, as a function of the hunting bag (x-axis) interpreted
748 as a proxy of population abundance, and the density of national roads (from top to bottom).

749 Wildlife–vehicles collision data were collected in 9 departments (administrative boundaries) of
750 France from 1990 to 2006. This latter variable was already discrete, so that we did not have to
751 discretize it, as for figure 1. Relative roe deer abundance increases from panel a to c. The central
752 curve corresponds to the point prediction of the model. The four shades of grey indicate (frow darker
753 to lighter shades): The four shades of grey indicate (from darker to lighter shades): 20%, 40%, 60%
754 and 80% credible intervals.

755 **Fig. 5** Model predicting the average density of collisions between the wild boar and vehicles per
756 year and per squared kilometre in a management unit, as a function of the hunting bag (x-axis)
757 interpreted as a proxy of population abundance, the density of national roads (increasing from top to
758 bottom, this variable was already discrete as for figure 1), and the landcover by four habitat types.
759 Wildlife–vehicles collision data were collected in 9 departments (administrative boundaries) of
760 France from 1990 to 2006. We have defined 4 types of management units here (see text for details):
761 (a, e, i) a forested management unit (“Forest”), (b, f, j) an agricultural management unit (“Agri”), (c,
762 g, k) a management unit with an important landcover by open natural areas (“Open”), and (d, h, l) an
763 urbanized management unit. The central curve corresponds to the point prediction of the model. The
764 four shades of grey indicate (from darker to lighter shades): 20%, 40%, 60% and 80% credible
765 intervals.

Table 1 Hypothesis-predictions table. Here we present the rationale for the different predictions stemming from the hypotheses that 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	Wild boar
Abundance	(++)	(++)	(++)
Habitat fragmentation	(0), present in forested areas mostly, excluded by hunters in other habitats	(+++), favourable environment	(++), Ubiquitous, wild boar use open areas to feed and forested areas for protection
Proportion of forested area in the management unit	(+++), use forested area mostly to minimize disturbance and is highly mobile	(++), roe deer favor fragmented habitats	(+), (Keuling et al. 2009)
Proportion of agricultural land in the management unit	(+), red deer uses agricultural crops close to forested areas	(+), roe deer favor fragmented habitats	(+++), (Keuling et al. 2009)

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 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 *Supporting information 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 *Supporting information 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 *Supporting information 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 *Supporting information 2*). We present the 90% credible intervals in parentheses (intervals with a probability equal to 0.9).

Variable	Red deer	Roe deer	Wild boar
Percentage of forest habitat	-2.44 (-9.64 – 4.76)	-1.1 (-7.21 – 4.53)	-6.17 (-12.31 – -0.33)
Percentage of agricultural lands	-6.81 (-14 – 0.31)	-0.69 (-6.87 – 4.98)	-4.48 (-10.71 – 1.57)
Percentage of open habitat	-4.32 (-11.54 – 2.85)	-1.43 (-7.69 – 4.34)	-3.95 (-10.22 – 2.17)
Percentage of urban habitat	-0.32 (-9.08 – 8.45)	-1.09 (-7.28 – 4.81)	1.62 (-5.24 – 8.33)
Density of national roads	0.38 (-0.02 – 0.78)	0.21 (0.04 – 0.38)	0.29 (0.04 – 0.53)
Hunting bag	0.015 (0.009 – 0.022)	0.005 (0.003 – 0.006)	0.007 (0.006 – 0.009)
Forest fragmentation	0.83 (0.52 – 1.18)	0.1 (-0.03 – 0.23)	0.03 (-0.15 – 0.2)

766 **Supporting information 1: Road classification and detailed description of the 9**
767 **departments of France**

768 Road classification in France is official and based on its function, reflecting the size and
769 administrative importance of the different urban areas it connects. The different functional types of
770 roads has been defined by a document called “l’ARP, aménagement des routes principales”,
771 available for download at <http://dtrf.setra.fr/notice.html?id=Dtrf-0001919>,
772 published in 1994 and edited by the French Ministry of the Infrastructure. An updated overview of
773 the different road types may be found in Wikipedia at [https://fr.wikipedia.org/wiki/](https://fr.wikipedia.org/wiki/Classification_fonctionnelle_des_routes_nationales_en_France)
774 [Classification_fonctionnelle_des_routes_nationales_en_France](https://fr.wikipedia.org/wiki/Classification_fonctionnelle_des_routes_nationales_en_France). Three
775 main road types are currently recognized:

- 776 • *L* type road, long distance roads connecting major urban centers, mainly highways with two
777 causeways;
- 778 • *T* type road, or transit roads, encompasses express roads with one causeway and two to three
779 lanes;
- 780 • *R* type road, are multi-function roads, making most of the French road network. Those roads
781 have various configurations ranging from two causeways for inter-city roads to one lane roads
782 in the countryside;

783 The above mentioned road classification is the basis of the road network mapping available from
784 the Institut Géographique National (IGN), the French Geographic Institution, in its ROUTE 500
785 database (<http://professionnels.ign.fr/route500>). We used the road classification
786 by IGN in our paper, which subdivises the R road type into two more homogeneous road types. The
787 road categorization by IGN strongly correlates with the average traffic density and road width. Our
788 classification is ecologically relevant because roads more and more difficult to cross for wildlife
789 from local to highway roads.

Table S1 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, deciduous 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

790 **Supporting information 2: Bayesian modelling fit and variable selection**

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

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

795

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

796 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
797 the average number of collisions per unit area and per year expected under our model (see below)
798 and ϵ_i is a normal over-dispersion residual with zero mean and a standard deviation equals to σ .

799 The average number of collisions per unit area and per year in a MU i was modeled as a function
800 of the $P = 10$ variables described in the last section (Table S1), according to the following log-linear
801 model:

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

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

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

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

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

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

816

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

817

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

818

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

819

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

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

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

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

832 where B is the set of variables corresponding to the best model identified by the Kuo & Mallik's
833 approach. We checked the convergence of the MCMC chains both visually and by using the
834 diagnostic of Raftery and Lewis (1992). None of these diagnostics showed any evidence of
835 nonconvergence of the MCMC. We then examined the fit of the model using the approach
836 recommended by Gelman and Meng (1996). For every iteration of the MCMC, i.e. for every value
837 $\theta^r = \beta_0 \dots$ of the vector of parameters of this second model sampled by MCMC, we simulated a
838 hypothetical replication of the dataset using equation (1), i.e. we simulated a number of collisions in
839 each MU. We then compared the observed number of collisions with the statistical distribution of
840 simulated numbers of collisions. We calculated that 99% (red deer), 100% (roe deer) and 100%
841 (wild boar) of the 90% of the credible intervals contained the observed number of collisions, which
842 indicates that the fit was correct for the three species.

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

854 Data and code accessibility).

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