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► **To cite this version:**

Annaëlle Bénard, Thierry Lengagne, Christophe Bonenfant. Integration of animal movement into wildlife-vehicle collision models. *Ecological Modelling*, 2024, 492, pp.110690. <10.1016/j.ecolmodel.2024.110690>. <hal-04552796>

**HAL Id: hal-04552796**

**<https://hal.science/hal-04552796v1>**

Submitted on 19 Apr 2024

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1 **Integration of animal movement into vehicle-wildlife collision models**

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9

10 **Abstract**

11

12 Road networks have major ecological impacts on living organisms consequent to habitat loss and  
13 fragmentation, chemical and acoustic pollution, and direct mortality when wildlife-vehicle  
14 collisions are involved (WVC). The many past empirical studies revealed major variables  
15 accounting for WVC incidence (*e.g.*, population density). Similarly, spatial locations of WVC hot-  
16 spots are associated to landscape features at large spatial scales, and to road characteristics at small  
17 spatial scale. Yet, we currently lack a comprehensive theoretical framework for WVC. Animal  
18 movement in relation to habitats is likely an essential driver of encounters with roads, but this  
19 remains largely ignored in most studies. Movement ecology now provides the necessary tools to  
20 investigate the impact of animal movement on WVC. We built a general individual-based model  
21 incorporating recent knowledge in movement ecology (movement typology: roaming, migratory  
22 route crossing a road, active attraction and active repulsion of roads) to estimate WVC risks. We  
23 explored the relative effects of animal and vehicle movement parameters (speed, abundance, road  
24 sinuosity and animal movement pattern) on collision probability. We show that animal behaviour  
25 toward roads has major impacts on the number and risks of WVC, but also modulate the effects of  
26 other factors (animal traveling speed, species local abundance, road traffic volume) on WVC.  
27 Sensitivity analyses show that the movement and behaviour of the animal has more influence on  
28 WVC risks than any of the characteristics of roads and vehicles we tested. Our results suggest that  
29 empirical studies of WVC should incorporate knowledge about the behavioural habits of the focal  
30 species in relation to roads.

## 31 **1. Introduction**

32 The last century has witnessed a continuous urbanization of almost all ecosystems, with profound  
33 influences on living organisms (Corlett, 2015). A particularly important anthropogenic factor  
34 generating major ecosystem modification and disturbance is the increasing densification and  
35 encroachment of the earth-bound transportation systems, and particularly of the road network  
36 (Davenport & Davenport, 2006). The presence of roads modify the local and large-scale  
37 environment of species as a consequence of chemical and noise pollution, changes in vegetation  
38 diversity, habitat loss and fragmentation (see Forman & Alexander, 1998; Coffin, 2007, for  
39 reviews). Roads can also have profound effects on ecosystem functioning and the biology of living  
40 organisms (Holderegger & Di Giulio, 2010). For instance, road mortality is a key driver of  
41 biodiversity loss in amphibians (Hels & Buchwald, 2001), birds and mammals (Grilo et al., 2020)  
42 and has been shown to affect animal behaviour (Andrews & Gibbons, 2005; Legagneux & Ducatez,  
43 2013). In the context of the ongoing biodiversity crisis (Ceballos & Ehrlich, 2002), knowledge  
44 about the mechanisms that lead to road mortality in wildlife is therefore critical.

45 For decades, empirical studies have been accumulating, reporting on collision hot-spots (Teixeira et  
46 al., 2013; Silveira Miranda et al., 2020), animal foraging habits near roadsides (Carvalho-Roel et  
47 al., 2019), or the seasonal variation in the number of reported cases (Medinas et al., 2021). We now  
48 have a clearer picture of what factors mainly account for collision risks (Table 1). Species with life  
49 history traits such as extended home ranges or slow travel speeds, and species occurring at high  
50 abundances, are more often subjected to roadkill. Road characteristics such as high traffic volume  
51 and landscape features (*e.g.* habitats promoting high levels of animal activity and mobility) account  
52 for WVC hot-spots locations at small spatial scales, but collision distribution can also be predicted  
53 at large spatial scales from variables such as road density, hunting bags (Saint-Andrieux et al.,  
54 2020) or landscape connectivity (Girardet et al., 2015). However, the relative effects of risk factors  
55 are difficult to disentangle. For example, as traffic mortality depletes local populations, roadkill  
56 numbers will decrease and simply counting collisions in high-risk areas could lead to an  
57 underestimation of the importance of animal abundance as a key determining factor of roadkill hot-  
58 spots (Teixeira et al., 2017). So far few attempts at building a theoretical model for wildlife-vehicle  
59 collisions (WVC) have been made, and our current knowledge on the quantitative effects of traffic  
60 on encounter and mortality risks for wildlife remains essentially descriptive, with little predictive  
61 abilities.

62 The very first model dealing with collision probabilities is the ideal gas model, first coined by  
63 physicist J. C. Maxwell in the context of molecule collisions in a gas (Maxwell, 1860). The ideal  
64 gas model posits that encounter rate within a defined volume or plane is a function of molecule

65 speed, density and collision zone (Hutchinson & Waser, 2007). Despite its heuristic value in  
66 ecology, to estimate encounter rates between males and females of a given species for example  
67 (Harcourt & Greenberg, 2001), it has seldom been used to study WVC as the general application in  
68 this context is not straightforward. For example, in most wildlife-vehicle encounters, the animal is  
69 likely to die and will no longer be at risk of collision again, which is not reflected in colliding  
70 molecules. Others proposed WVC-specific mechanistic models: Hels & Buchwald (2001) modelled  
71 the probability of death for an amphibian crossing a road (see Gibbs & Shriver, 2002; van  
72 Langevelde & Jaarsma, 2005, for an application to other species), allowing the integration of road  
73 mortality into population persistence models (Gibbs & Shriver, 2002).

74 A shortcoming shared by all current WVC models is the lack of consideration for animal movement  
75 and habitat use behaviour, often limiting when one aims at describing the complexity of animal  
76 movement in a heterogeneous landscape (Siniff & Jessen, 1969). For example, not only do animals  
77 cross roads, but they can roam along roadsides to forage, hence putting them at much higher risk of  
78 being hit by a car (scavenging: Schwartz et al. 2018; Ratton et al. 2014, hunting: Gomes et al. 2009;  
79 D'Amico et al. 2013, salt licking: Fraser & Thomas 1982). More importantly, collision probabilities  
80 in a landscape are intrinsically linked to the number of encounters an animal has with roads, and  
81 peaks in activity. Mate searching, breeding, and juvenile dispersal have repeatedly been cited to  
82 explain seasonal patterns in WVC numbers (Steiner et al., 2014; Ryu & Kim, 2021; Raymond et al.,  
83 2021). Despite its expected effects, the influence of patterns of space use by animals on WVC has  
84 yet to be adequately addressed in mechanistic models.

85 Movement patterns of animals are now well described within the frameworks of movement ecology  
86 (Demšar et al., 2015). The advances of the last decades in bio-logging (*e.g.*, animal-borne GPS  
87 collars, tags or transponders) have made it increasingly easy to acquire position data characterizing  
88 these individual trajectories for a growing number of species, therefore providing a solid empirical  
89 basis to develop mathematical models of animal movement. Large-scale patterns emerge from  
90 movement at the individual level: for example, oriented movement, based on environmental cues or  
91 memory, is the basis for migratory routes and sedentary ranges (Mueller & Fagan, 2008; Van  
92 Moorter et al., 2009), which in turn affect WVC occurrences (Bonnet et al., 1999; Kantola et al.,  
93 2019). To our knowledge however, WVC studies seldom incorporate theoretical advances of  
94 movement ecology, although space use is the main driver of animal encounters with roads.  
95 Therefore, we argue that modelling wildlife-vehicle collisions from a movement ecology  
96 perspective would improve our ability to understand the main factors driving WVC (Hels &  
97 Buchwald, 2001; van Langevelde & Jaarsma, 2005).

98 We here propose an individual-based model to simulate animal trajectories using biased and  
99 unbiased correlated random walks, as a mean of exploring the effects of road characteristics, species  
100 traits and patterns of space use on the number and probability of collisions between animals and  
101 vehicles. Our two main goals are i) to quantify the relative effects of several road characteristics  
102 (road sinuosity, vehicle speed and traffic volume) and species traits (animal speed, local abundance,  
103 movement patterns, foraging and dispersal behaviours) on WVC occurrences and ii) for a set of  
104 biologically realistic scenarios of animal movement, to identify what factors have the largest impact  
105 on wildlife-vehicle collision risks. Understanding which of the biological, human and  
106 environmental factors modulate the risks of wildlife-vehicle collisions the most is key to the  
107 selection and implementation of efficient mitigation policies such as fences, over or underpasses,  
108 and traffic signage that raises drivers' attention (Davenport & Davenport, 2006). Our model should  
109 help to build qualitative predictions either for inter-specific studies or WVC mitigation.

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121 Table 1: Overview of the different factors correlated to the incidence of wildlife-vehicle collisions  
 122 in the current literature.  
 123

|                             |                                      |  |
|-----------------------------|--------------------------------------|--|
| <b>BIOLOGICAL FACTORS</b>   | <b>Animal Speed</b>                  | While crossing a road, slower-moving animals such as herpetofauna will be more impacted by roadkill. Hels & Buchwald 2001, Eigenbrod et al. 2009, Grilo & Bissonette 2010, Van Langevelde & Jaarsma 2005   |
|                             | <b>Habitat use</b>                   | Highly mobile individuals cross roads more often. When mobility levels are season, age or sex-dependant, these biases are reflected in roadkill (more mobile individuals being killed more often). Steen & Smith 2006, Aresco 2005, Coelho et al. 2008, Newell 1999  |
|                             | <b>Road-related behaviours</b>       | Some species can be attracted to roads, including but not limited to:<br>- Ungulates licking salt on or near roadsides (Rea et al. 2021)<br>- Carrion feeders foraging on roadkill (Laurance et al. 2009, Mukherjee et al. 2013)<br>- Birds using roadside perches (Grilo et al. 2011)<br>- Reptiles using road surfaces to bask (Meek 2009)<br>- Turtles laying eggs on road shoulders (Aresco 2005)<br>- Amphibians breeding in road-adjacent water retention ponds (Smith & Dodd 2003, Hamer et al. 2012) |
|                             | <b>Species local abundance</b>       | <i>"To some extent, road-kill statistics actually give a crude but useful index of wildlife occurrences in a region"</i><br>Seiler & Helldin 2006  |
|                             | <b>Car avoidance behaviours</b>      | Species-specific or individual reactions to oncoming vehicles dictate whether the animal will have a chance of avoiding a collision. Documented behaviours that increase roadkill probabilities include:<br>- not detecting oncoming vehicles,<br>- habituation and not perceiving moving vehicles as threats,<br>- freezing in front of vehicles and following conspecifics on the road.<br>Lima et al. 2015  |
|                             | <b>ANTHROPOGENIC FACTORS</b>         | <b>Traffic volume</b>  |
| <b>Traffic speed</b>        |                                      | High-speed roads generate more roadkill<br>Hobday & Minstrell 2008, Farmer & Brooks 2012   |
| <b>Road characteristics</b> |                                      | Roads on which WVC are more frequent include:<br>- wider roads with multiple lanes (Bright et al. 2015),<br>- raised roads and embankments promoting low-altitude flight in birds (Canal et al. 2019)<br>- sinuous roads (Grilo et al. 2011, Zuberogoitia et al. 2014)   |
| <b>Mitigation measures</b>  |                                      | - Warning signage is often ineffective in preventing collisions (Huijser et al. 2015)<br>- Road-crossing structures (bridges, underpasses) can counter-intuitively correspond to roadkill hotspots when looking at species they are not suitable for, e.g. by lacking proper fencing for smaller vertebrates (D'Amico et al. 2015)   |
| <b>LANDSCAPE</b>            | <b>Roadside features</b>             | <i>"The concentration of forage or cover plants, accumulation of salt, or close proximity of wetland may cause some animals to concentrate their activities near roadsides"</i><br>Livaitis & Tash 2008  |
|                             | <b>Landscape connectivity</b>        | Landscape connectivity, by influencing animal movement, is a predictor of roadkill spatial patterns: roads in high-connectivity landscapes are more dangerous.<br>Grilo et al. 2011, Fabrizio et al. 2019, Girardet et al. 2015  |
|                             | <b>Adjacent habitats suitability</b> | Roadkill occurrences in a species are higher in the presence of optimal habitats. At broad scales, habitat suitability models are used as predictors for spatial roadkill patterns.<br>Balčiauskas et al. 2020, Wright et al. 2020   |

## 125 **2. Material & Methods**

126 Following previous work on simulations for the ideal gas model (Hutchinson & Waser, 2007), we  
127 constructed a discrete-time simulation of particles movement in which all trajectories were  
128 approximated by a series of straight-line steps of constant duration. Two classes of particles were  
129 considered: vehicles and animals, each with their own speed, movement patterns and density. We  
130 conducted preliminary testing of the model by replicating the conditions under which the ideal gas  
131 model applies, and subsequently ensured that simulation results matched the model predictions.  
132 From there, we used biased and unbiased correlated random walk models to represent animal  
133 movement. Random walk parameter values were chosen to match real-life scenarios. The goal of  
134 the simulations was to keep track of the number of encounters between vehicles and animals per  
135 unit of time (fig. 1). We set a duration of 12 hours per simulation run, as a broad representation of  
136 the amount of time during which most diurnal and nocturnal terrestrial species are active (Refinetti,  
137 1999). Two types of experiments were conducted: (1) to test the quantitative and qualitative effects  
138 of the different focal parameters (animal and vehicle speed, movement and densities) independently,  
139 we replicated the simulations for different values of the parameter under study, holding everything  
140 else constant; (2) to evaluate the relative importance of each focal parameters on the number of  
141 WVC, we conducted one-at-a-time sensitivity analyses.

### **Basic simulation layout**

143 We first assumed two separate entities, thereafter designated ‘vehicles’ and ‘animals’, moving on a  
144  $30 \times 30 \text{ km}^2$  plane mapped by  $x$  and  $y$  axes. We treated the plane like a torus, meaning that an animal  
145 or a vehicle crossing the edge reappeared at the same location, but on the opposite edge of the plane  
146 (see fig. 2). The vehicle movement followed a road defined as  $0 \leq x \leq 30$  and  $y = \cos(\alpha \cdot x)$ , where  $\alpha$   
147 controlled road sinuosity. We computed an index of sinuosity for each simulated road as the ratio of  
148 the road’s length to 30 (i.e. the  $x$  axis’ length). A sinuosity index of 1 indicated a straight road, and  
149 the index increased as the road became more and more sinuous. The number of vehicles on the road  
150 at any given time followed a Poisson distribution (Breiman, 1963) and all vehicles moved at  
151 constant speed. For animal movement, we used biased correlated random walks (BCRW; Turchin,  
152 1998), a combination of correlated random walks where animals have a directional persistence and  
153 therefore avoid backtracking, and of biased random walks, where animals are attracted to one or  
154 several centers of attraction spatially defined on the simulation plane. BCRW are highly flexible  
155 models proven to fit animal trajectories at different spatial scales for a range of terrestrial species in  
156 heterogeneous landscapes: individuals can be biased toward a home range (Red deer *Cervus*  
157 *elaphus*, Berthelot et al., 2020), or resources such as larval hosts plants (Butterfly *Plebejus*  
158 *icarioides fender*, Bailey et al., 2018) and food (Elk *Cervus canadensis*, Fortin et al., 2005).

160 Animals moved on the plane from time steps  $t = 0$  to  $T$  according to a BCRW:

$$x_a(t) = x_a(t - 1) + \cos(\theta_t) \cdot d$$

$$y_a(t) = y_a(t - 1) + \sin(\theta_t) \cdot d$$

$$x_a(0) \sim U(0,30)$$

$$y_a(0) \sim U(0,30)$$

161 with  $(x_a, y_a)$  the coordinates of the animal on the simulation plane, step length  $d$  drawn from a  
 162 zero-truncated normal distribution  $N(\mu, 0.5)$ ,  $\mu$  the mean animal speed (km.h<sup>-1</sup>), and  $U(0, 30)$  the  
 163 uniform distribution between 0 and 30. We computed the direction of the walk  $0 \leq \theta_t \leq 2\pi$  as the  
 164 mean between the *correlated* direction  $\theta_t^c \sim N(\theta_{t-1}^c, \sigma^2 = 5)$  with  $\theta_0^c$  randomly drawn between 0  
 165 and  $2\pi$ , and the *biased* direction  $\theta^b$ , the direction of the nearest attraction center. It resulted that the  
 166 direction of the walk was the outcome of two competing processes: the *persistence*, the animal's  
 167 internal propensity to walk without backtracking in a given direction  $\theta_0^c$ , and the *attraction* toward  
 168 the nearest attraction center. The relative importance of the *attraction* with respect to the *persistence*  
 169 was defined by the associated weight of attraction  $w$  (Duchesne et al., 2015). Accordingly,  $w$   
 170 controlled the strength with which animals are attracted to the attraction center:  $w = 0$  produces  
 171 unbiased correlated random walks (no attraction), and  $w \rightarrow \infty$  tends towards biased random walks.  
 172 In practice, for high values of  $w$  the animal made a beeline towards the nearest center of attraction  
 173 because the *attraction* to the nearest center takes over the *persistence* of the correlated walk in  
 174 orienting the walk. Once the animal reached the attraction center, it orbited around it, as a result of  
 175 the *persistence* pulling away in its own direction while the attraction component brought the animal  
 176 back towards the center. In consequence, high values of  $w$  would imply less spread-out orbiting  
 177 behaviours, mimicking animals staying in proximity of the attraction center (see fig. S1 in  
 178 supplementary material).

179

We defined an animal-vehicle collision as a time-step during which the distance between an animal  
 and a vehicle was less than 5 meters (Euclidean distance). If that condition was satisfied, the animal  
 182 died and stopped moving, while the car continued to move along the road. For each collision, a new  
 183 animal would enter the plane in order to keep the animal density constant. In this model, we did not  
 184 implement any sort of behavioural reactions from the animals to an oncoming vehicle, or from the  
 185 driver in the presence of an animal on the road or roadside. However, we discuss these mechanisms  
 186 in section 4 of the supplementary material. Given its stochastic nature, the model was run  $N = 1000$

187 times to produce a mean collision number and estimate an individual probability of collision. The  
188 simulation used R package *Rcpp* (Eddelbuettel & Balamuta, 2018).

189

## 190 **2.2 Behavioural scenarios of animal movement and space use**

191 We considered 5 different scenarios designed to mimic real-life animal behaviours described in the  
192 literature (fig. 2).

### 193 *2.2.1 Scenario 0: no influence of the road*

194 In scenario 0, the weight of attraction  $w$  was set at 0 resulting in animals performing (unbiased)  
195 correlated random walks (CRW). In CRW, successive steps directions are correlated, resulting in a  
196 directional bias: the animal walked forward and rarely backtracked. CRW have been used to  
197 describe the movement of several species (Mouse *Apodemus sylvaticus*: Benhamou 1991, Reindeer  
198 *Rangifer tarandus*: Marell, Ball & Hofgaard 2002, Red fox *Vulpes vulpes*, Snowshoe hare *Lepus*  
199 *americanus*: Siniff & Jessen 1969). CRW imply that animals did not factor in the presence of a road  
200 or moving vehicles in their movement, which could be especially prevalent on smaller or unpaved  
201 roads (Brehme et al., 2013). This simple movement model also served as a null model, *i.e.* a  
202 scenario without attractive or repellent effects of road presence on animal movement.

### 203 *2.2.2 Scenario 1: habitat fragmentation*

204 All animals started the simulation run in the top-left corner of the simulation plane, always above  
205 the road, while the single attraction center ( $w = 1.5$ ) was randomly located below the road. The  
206 resulting BCRW simulated a migration of individuals between patches during which they had no  
207 choice but to cross the road. This scenario could match many migrating species such as amphibians  
208 converging towards open waters for reproduction (Hels & Buchwald, 2001; Sillero, 2008), large  
209 mammals migrating to their summer or winter ranges (Avgar et al., 2014) or crab species moving  
210 back to sea during breeding migrations (Ryu & Kim, 2020).

### 211 *2.2.3 Scenarios 2 & 3: attraction to the road*

212 Scenario 2 emerged from the frequently reported attraction to roads in many species: salt licking on  
213 roadsides by large mammalian herbivores (Fraser & Thomas, 1982), use of roads and roadsides for  
214 foraging or hunting (Diurnal raptors: Meunier et al., 2000; Passerines: D'Amico et al., 2013) or  
215 carnivores scavenging on carrion from animals hit by vehicles (Schwartz et al., 2018; Ratton et al.,  
216 2014). Arguably, this scenario could encompass the case of reptiles that bask on warm road surfaces  
217 (Meek, 2009). Attraction centers ( $w = 3$ ) were placed every 300m on the road, such that animals  
218 converged towards the closest attraction center. Once an animal had reached an attraction center, it

219 would orbit around until another attraction center in the vicinity became the new closest center, at  
220 which point the animal would leave its current attraction center to walk towards the new one. Little  
221 by little, an animal would visit several attraction centers during a simulation run, and would often  
222 walk on or in close proximity to the road while moving in-between attraction centers.

223 Scenario 3 is a slightly modified version of scenario 2, intended for animals with flying abilities  
224 (birds, bats...) and using roads as corridors for long-range displacements; or for hunting because  
225 roads “drive” preys in the landscape (Kerth & Melber, 2009; Schwartz et al., 2018). Flying animals  
226 often make low-altitude flights to catch a prey or land on the road to feed (Grilo et al., 2014; see  
227 also the ‘leap and strike’ hunting behaviour of owls: Norberg & Norberg, 1970; Southern, 1954). To  
228 this end, we added a third dimension  $z_a$  describing the altitude of the animals to their existing  $(x_a, y_a)$   
229 position on the plane. The altitude was a function of the distance to the nearest attraction center:  
230  $z_a(t) = \exp(0.3 * ||d||) - 1$ , with  $||d||$  the Euclidean distance between the animal and the closest  
231 attraction center. This distribution of altitudes entailed that animals got progressively closer to the  
232 ground as they approached the attraction center. In consequence, they were only susceptible to  
233 collision when within a radius of 5m around a center of attraction.

#### 234 2.2.4 Scenario 4: road avoidance

235 The last scenario accommodated animal movement for road avoidance behaviours. Road avoidance  
236 has been reported in several species (Grizzly bear *Ursus arctos*: Mace et al., 1996; Wild boar *Sus*  
237 *scrofa* and Red deer *Cervus elaphus*: D’Amico et al., 2016), possibly resulting from chemical, noise  
238 pollution, or road surface avoidance (Andrews & Gibbons, 2005; Schaub et al., 2008; Jaeger et al.,  
239 2005). Building upon scenario 2, we only modified the attraction angle to be computed as  $\theta^b +$   
240  $180^\circ$ , meaning that the animal moved away from the center instead of towards it.

241

242

243

### 244 2.3 Qualitative predictions of the model

245 For each of the scenarios described above, we derived qualitative predictions for 6 parameters of  
246 interest, by running the simulation at different values of this parameter while holding everything  
247 else constant. The parameters of interest were: animal mean speed, vehicle speed, animal density,  
248 traffic volume, weight of attraction centers  $w$  (scenarios 1 through 4 only) and road sinuosity (Table  
249 2).

250 Mean animal travel speed values covered the observed speed range of most terrestrial species (from  
251 slowest to fastest, migrating amphibians: Hels & Buchwald 2001, foraging badger *Meles meles*: San  
252 et al. 2007, migrating ungulates: Berger et al. 2006; Singh & Ericsson 2014). Considering that this  
253 range is wide, we extracted mean travel speed estimations for several species from the literature  
254 (Rowcliffe et al., 2016; Farley et al., 1993) and set our baseline at the mean value of 5 km.h<sup>-1</sup>.  
255 Vehicle speed encompassed slow vehicles up to high-speed trains, and the baseline was set at the  
256 current speed limit on main roads in France (80 km.h<sup>-1</sup>). Local animal densities, traffic volume  
257 ranges and baselines were mostly dictated by computational limitations, although the baseline of  
258 250 vehicles.hour<sup>-1</sup> is representative of average sized roads in France (French Ministry of  
259 Ecological Transition, 2022). Finally, road sinuosity was investigated following observed  
260 sinuosities which are publicly available for the road network of Ireland (Transport Infrastructure  
261 Ireland, 2022).

262 The weight of attraction  $w$  in BCRW scenarios was a dimensionless unit ranging from 1 (attraction  
263 to centers is equal to the correlated direction of the walk, spread-out orbiting behaviour around  
264 attraction center) to 20 (when attraction was 20 times more important in walk orientation, animals  
265 walked in nearly straight paths toward the attraction center and stayed mostly in place once it was  
266 reached). Baseline values for  $w$  were scenario-dependent as  $w = 5$  for scenario 1 ensured that over  
267 90% of animals cross the road in less than 12 hours, and  $w = 3$  for scenarios 2 and 3 ensured that  
268 animals would effectively visit several attraction centers during the simulation run.

269 Two types of results were extracted from simulation runs: the mean number of collisions recorded  
270 over the course of a 12 hours run, and the individual probability of collision for animals.  
271 Considering that new individuals replaced dead animals, not all animals were present from the start  
272 of the simulation run and exposure to vehicles was not constant across all animals. Consequently,  
273 we estimated the individual probability of collision from a logistic regression (0: alive, 1: hit by a  
274 vehicle) as a function of the parameter under study, and where the time of arrival in the simulation  
275 was entered as an offset predictive variable (Agresti & Coull, 2002).

276

277

Table 2: Model parameters of interest, relating to animal and vehicle movement and that appear to be pivotal factors driving collision numbers according to most studies (Table 1). While the effects of one parameter on collisions are being explored, all other parameters assume their baseline values. To produce quantitative and qualitative predictions, we explored a range of values contained within biologically relevant intervals for each parameter.

| Parameter of interest | Baseline value | Explored range |
|-----------------------|----------------|----------------|
|-----------------------|----------------|----------------|

|                |   |  |              |
|----------------|---|--|--------------|
| <b>ANIMAL</b>  | Mean speed (km.h <sup>-1</sup> )          | 5  | 0.1 – 30     |
|                | Density (ind.km <sup>-2</sup> )           | 0.016  | 0.001 – 0.03 |
|                | <i>w</i>                                  | 5 ( <i>scenario 1</i> ) ; 3 ( <i>scenarios 2-4</i> ) | 1 - 20       |
| <b>VEHICLE</b> | Speed (km.h <sup>-1</sup> )               | 80   | 30 – 300     |
|                | Traffic volume (vehicle.h <sup>-1</sup> ) | 30   | 10 – 250     |
|                | Road sinuosity index                      | 1 ( <i>straight road</i> )                           | 1 – 3.5      |

278

## 279 **2.4 Sensitivity analyses of collision number**

280 Sensitivity analyses were conducted on each scenario, following a one-at-a-time approach, meaning  
 281 that we measured the variation in collision numbers while keeping all input factors fixed except the  
 282 one that is being perturbed (Saltelli et al., 2019). In practice, we computed the mean number of  
 283 collisions  $y_{xI}$  for factor of interest  $x$  at a reference value  $x_I$ , and after 10% increase in value (denoted  
 284  $x_2$ ). To explore possible non-linearity, we repeated this for several reference values  $x_I$  within the  
 285 relevant range of  $x$  (see section 2.3 for parameter ranges). We then defined the sensitivity measure  
 286 as  $OR_{x1} = y_{x2} / y_{x1}$ , *i.e.*, the odd ratio of the collision probabilities that results from a 10% increase  
 287 of parameter  $x$  at reference value  $x_I$ . For example, an  $OR_{x1}$  of 1 indicated no change in the odds of  
 288 collisions between parameter values  $x_I$  and  $x_I+10\%$ , while  $OR_{x1} > 1$  indicated greater odds of  
 289 collision after a 10% increase in parameter  $x$ . The overall strength of the influence of parameter  $x$  on  
 290 the collision number in its relevant range was defined by how far the mean of the ratios ( $OR_{mean}$ ) for  
 291 all tested values of  $x$  deviated from 1 (*e.g.*,  $OR_{mean} = 1$  indicated no overall influence of factor  $x$  on  
 292 collision numbers).

293

## 294 **3. Results**

### 295 **3.1 Qualitative model predictions**

296 Applying baseline values to all parameters of interest, mean collision rate ranged from 0.16 to 17.2  
 297 animal-vehicle collisions over 12 hours (individual probabilities of collision for animals: 0.4% -  
 298 45.6%). As expected, the movement of animals had major effects on the probability for an animal to  
 299 get hit by a vehicle (fig. 3). With baseline parameter values, animals attracted to the road (scenarios  
 300 2 and 3) were hit more often than in any other scenario, with an increase in the odds of collision for  
 301 terrestrial animals (scenario 2) compared to flying animals such as birds and bats (scenario 3).  
 302 Compared to the null model (scenario 0, roaming with no attraction/avoidance of the road),  
 303 migrating animals crossing the road exactly once (scenario 1) were hit more often, while the odds of

304 collisions for active road avoidance (scenario 4) were reduced. This ranking between scenarios was  
305 not always maintained for other values of the tested parameters.

306 Overall, response functions of parameters had similar shapes whether the outcome was measured as  
307 the mean number of collisions or as the individual probability of collision, except for animal  
308 density. Vehicle speed had no effect on collision numbers and probabilities in any of the scenarios  
309 (fig. 3b and 4b). Animal density was positively and linearly associated with collision numbers,  
310 which translated into a constant individual probability of collision no matter the local abundance in  
311 animals (fig. 3d and 4d). The influence of the remaining parameters (animal speed, weight of  
312 attraction, traffic volume and road sinuosity) was non-linear and/or scenario-dependent.

313 Traveling faster reduced collision numbers and probabilities for migrating animals (scenario 1) but  
314 had the opposite effect on roaming and road-avoiding animals (scenarios 0 and 4). In scenarios with  
315 road-attracted animals, collision occurrences increased with mean animal speed up to moderate  
316 speed values, after which the relation was reversed (fig. 3A and 4a). Higher volumes of traffic on  
317 the road increased collision numbers and probabilities, although scenarios 0, 2, 3 and 4 presented  
318 inflection points after which the increase in collision occurrences slowed down, which was not  
319 observed within the explored range of traffic volume for scenario 1 (fig. 3C and 4c). Similarly,  
320 increasingly sinuous roads had moderate to low positive effects on collision number and probability  
321 in all but one scenario: scenario 3 yielded no apparent effect of road sinuosity (fig. 3f and 4f).  
322 Finally, increasing weights of attraction (or repulsion for scenario 4) led to more collisions (and  
323 higher individual probabilities) in scenarios 2 and 3 with inflection points around  $w = 5$ , but  
324 increasing  $w$  values were associated to less collisions and lower probabilities of WVC in scenarios 1  
325 and 4 (fig. 3e and 4e).

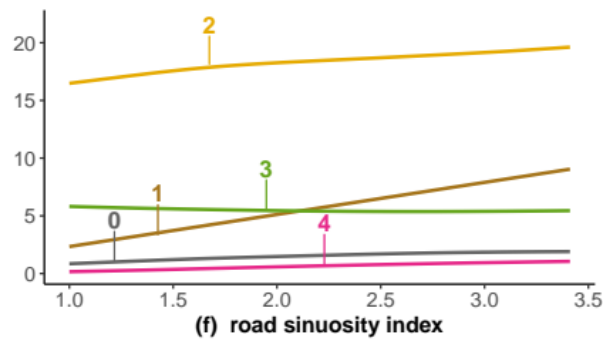
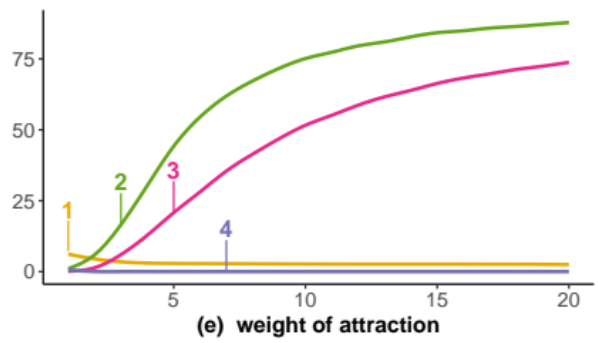
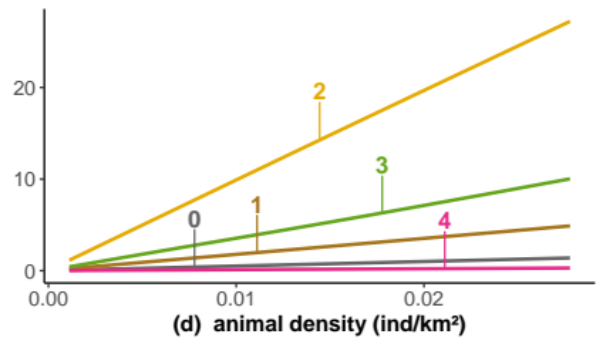
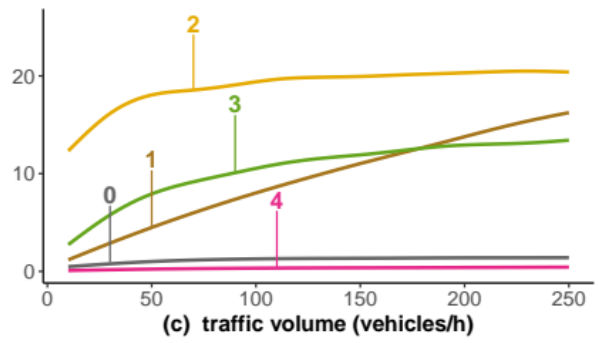
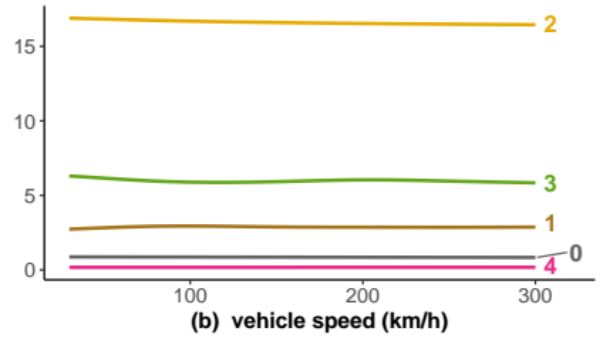
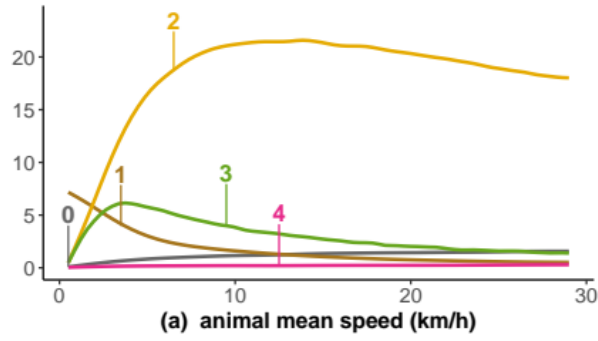
326

### 327 **3.2 Sensitivity analyses**

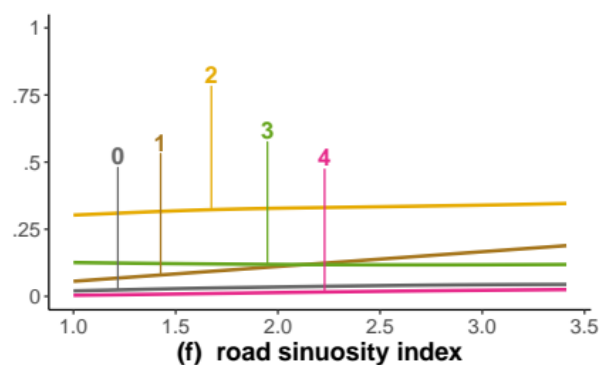
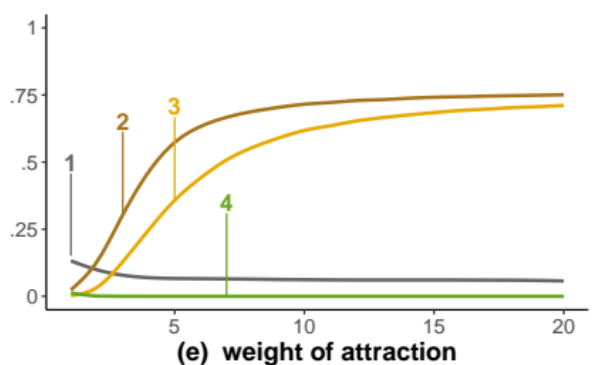
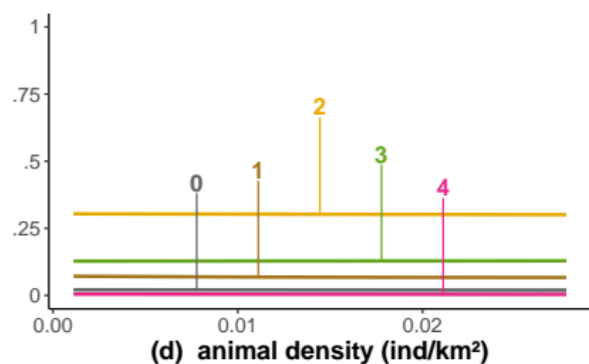
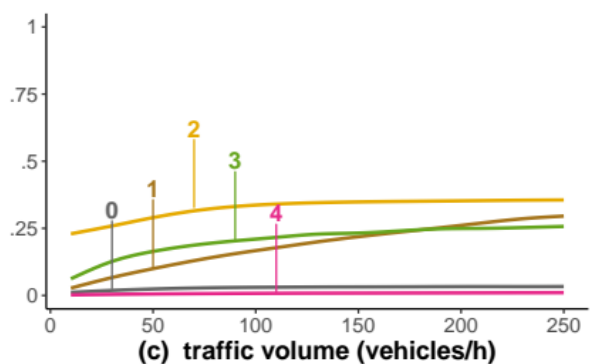
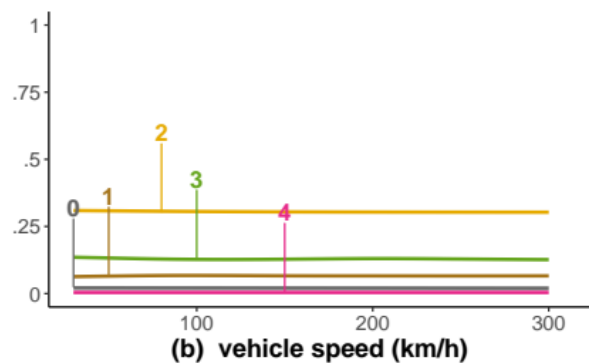
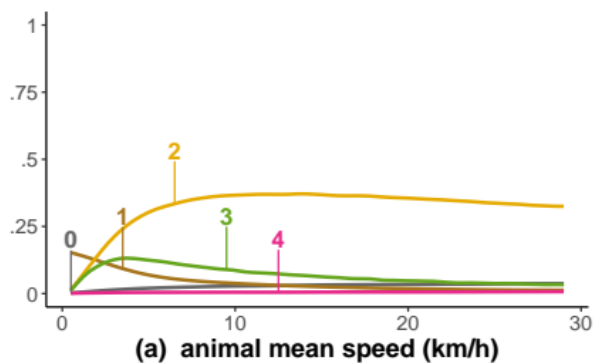
328 For roaming animals (scenario 0), the most influential parameter was the animal density ( $OR_{\text{mean}} =$   
329 1.091) followed by animal speed ( $OR_{\text{mean}} = 1.032$ ). In all other scenarios (scenarios 1, 2, 3 and 4),  
330 the weight of attraction  $w$  had the largest influence (respectively  $OR_{\text{mean}} = 0.888, 2.019, 1.155$  and  
331 0.843) followed by animal density (respect.  $OR_{\text{mean}} = 1.098, 1.095, 1.101$  and 1.108). The least  
332 influential parameters were traffic volume for scenario 0 ( $OR_{\text{mean}} = 0.996$ ), vehicle speed for  
333 scenarios 1 and 3 (respect.  $OR_{\text{mean}} = 1.01, 1.006$ ) and road sinuosity for scenarios 2 and 4 (respect.  
334  $OR_{\text{mean}} = 0.998, 0.993$ ). Using  $OR_{\text{mean}}$  is, however, a simplified view of the non-linear effect of  
335 parameters, as it was sometimes pulled in one direction by one or a few extreme OR values. For  
336 example, some parameters such as the weight of attraction/repulsion generally had a substantial

337 influence on collision numbers at lower values ( $w = 1$ ) while higher  $w$  values yielded OR values  
338 closer to 1 (fig. 5).

mean number of collisions over 12h



individual probability of collision



1

2

343

## 344 **4. Discussion**

345 Road mortality of wildlife is a pervasive and widespread cause of biodiversity loss across the world  
346 that should be seriously considered in wildlife management and conservation programs. In spite of  
347 its ecological importance and relevance, we are still lacking a strong formalization of WVC to grasp  
348 what are its main biological, ecological and anthropogenic determinants. By combining earlier  
349 encounter models with the current knowledge about movement ecology, our work should help  
350 formulating qualitative predictions for reducing the number of WVC or predict which species  
351 should be at greater risks of being hit by vehicles.

352 Our simulations show how collision numbers and probabilities differ markedly with the movement  
353 and behaviour of animals, such as migration or home-ranging, or with their locomotion (terrestrial  
354 vs. flight). We suggest that this contrast in mortality risk between individuals with different  
355 movement types could lead to contrasting selection forces on animal habitat use with regard to road  
356 avoidance or attraction. Knowledge about animal movement of species should be an essential part  
357 of WVC studies as it seems to be the most influential variable on WVC occurrence in the absence  
358 of reaction from vehicle drivers and animals.

359

### 360 **4.1 Effects of animal movement on WVC risks**

361 WVC broadly results from two competing mechanisms: the number of times an individual will  
362 cross or stay close to a road, and the time spent at risk of collision when on the road while crossing,  
363 foraging or basking. Both mechanisms are modulated by patterns of space use (in our simulation,  
364 the different scenarios of movement behaviour), and their modulations through the weight of  
365 attraction/repulsion  $w$  and the speed at which animals travel. Obviously, individuals actively  
366 avoiding roads (scenario 4) should be the least at risk of collision with a vehicle and, conversely,  
367 terrestrial individuals attracted to the road for foraging or basking (scenario 2) should be the most at  
368 risk. This is in line, for example, with Western green lizards (*Lacerta bilineata*) being road-killed in  
369 higher proportions than the other sympatric lizard species that do not bask on roads (Meek, 2009).  
370 Flying carrion feeders (mostly diurnal and nocturnal raptors) are less likely to be killed than their  
371 terrestrial counterparts, a difference that may be further widened by some species' cognition and  
372 ability to successfully evade oncoming vehicles, as is the case with corvids (Mukherjee et al., 2013;  
373 Lima et al., 2015). Nevertheless, we show here that other parameters of both animal and vehicle  
374 movement can modulate these conclusions. For example, slow moving animals (less than  $15\text{km}\cdot\text{h}^{-1}$ )  
375 were more often hit when migrating (scenario 1) than roaming freely (scenario 0), but the reverse  
376 was true for faster animals (fig. 3a).

377 By mimicking the presence of attractive or repulsive areas for animals in the landscape, the  
378 attraction/repulsion weight ( $w$ ) ultimately controls the time spent in the vicinity of the road, which  
379 is positively correlated to collision numbers and probabilities. The relationship between  $w$  and the  
380 time spent on the road is easily interpreted for scenarios of road attraction (scenarios 2 and 3,  $w$  is  
381 positively correlated to time on road surface) and avoidance (scenario 4,  $w$  value is negatively  
382 correlated to time on road surface). When animals travel from a departure point to an attraction  
383 center (scenario 1), the time spent crossing is negatively correlated to  $w$ : high  $w$  values means  
384 straight trajectories between departure and attraction center, and thus less time on the road.

385 Collision risks in animals roaming freely in a landscape (scenario 0, no  $w$  variable) are dictated by  
386 their speed: the faster the animal, the more it explores its environment during a simulation run and  
387 thus encounter roads more often, even though each crossing becomes concurrently less dangerous  
388 as fast animals cross the road in less time (see fig. S2 in supplementary material). For the same  
389 reason, when animals cross the road only once (scenario 1), we would also expect the animal travel  
390 speed to be a key variable in decreasing collision numbers. However, this was not reflected by the  
391 sensitivity analyses, the most likely explanation being that the mean sensitivity  $OR_{\text{mean}}$  for travel  
392 speed in scenario 1 is pulled up by the odds ratio for very low travel speeds (odds ratio  $OR_{0.5}$   
393 comparing collisions at 0.5 and 0.55  $\text{km}\cdot\text{h}^{-1}$ ) where more animals would cover the distance between  
394 their departure point and the road during the simulation when traveling at 0.55  $\text{km}\cdot\text{h}^{-1}$  compared to  
395 0.5  $\text{km}\cdot\text{h}^{-1}$  (fig. 5). Nevertheless, these results demonstrate that the cumulative time spent on or near  
396 roads by animals, through repeated road encounters and/or a long time spent on the road at each  
397 encounter (modulated here by patterns of space use, animal speed, and biased random walk  
398 parameter  $w$ ), is the most influential parameter driving collisions probabilities for an animal, and  
399 has more importance than road characteristics such as traffic volume or speed.

400 These findings are consistent with studies exploring the relationship between landscape features and  
401 roadkill hot-spots: factors such as the presence of attractive habitats on roadsides as well as a high  
402 connectivity landscapes conducive to wide ranges of movement are often linked to high road  
403 mortality (Table 1, see also de Freitas et al. 2013; de Freitas et al. 2015). Similarly, the temporal  
404 distribution of roadkill is dictated by the level of activity, and periods of high mobility such as rut,  
405 mating or migrating seasons are especially risky for animals (Table 1). Larger home ranges and  
406 exploratory behaviours contribute to higher fitness for individuals by increasing foraging  
407 opportunities (Andersson, 1978), but the presence of roads (also applicable to aircrafts, ships or  
408 trains) in a landscape lead to costs in the form of road mortality, and selection pressure may lead to  
409 road avoidance (Meisingset et al., 2013; Jaeger et al., 2005; Husby & Husby, 2014) or collision  
410 avoidance strategies (Lima et al., 2015; Brown and Bomberger Brown, 2013).

## 411 **4.2 Effect of animal density on WVC risks**

412 The impact of spatial and temporal variations in animals density has been repeatedly reported as a  
413 significant driver of WVC (Joyce & Mahoney, 2001; Taylor et al., 2010; Saint-Andrieux et al.,  
414 2020). Some authors suggested that the number of carcasses on roads could serve as an index of  
415 animal abundance (Seiler & Helldin, 2006; George et al., 2011). We show that this relationship is  
416 linear but strongly modulated by animal movement (fig. 3): compared to animals with no attraction  
417 or avoidance towards roads, the slope of the relation between local density and roadkill number is 8  
418 times greater for terrestrial animals attracted to roads, and about 70 times smaller when there is road  
419 avoidance. When dealing with different species, or with large temporal or spatial scales in which  
420 animal movement might be modified by biological seasons and/or landscape features, WVC counts  
421 are meaningless, unless the average movement of animals is precisely known. Furthermore, all  
422 slopes deviates from isometry ( $\beta < 1$ ), suggesting that the number of casualties on the roads  
423 underestimates high population abundances.

424 If animal density has an impact on collision numbers, it has no effect on the probability of collision  
425 for the individual: WVC are coincidental and have no upper threshold for the number of roadkill,  
426 contrary to, for example, a predator looking to feed on a set number of prey. Because of this, there  
427 is no mechanism of dilution, or “safety in numbers”, in which we might expect a lower collision  
428 risk for the individual in a large group of conspecifics (Lehtonen & Jaatinen, 2016). We need to  
429 mention that changes in local density have documented effects on individual behaviour which were  
430 not explored in the model, and that could in turn affect movement and hence, WVC indirectly  
431 (Kjellander et al., 2004; Dahle & Swenson, 2003; Sword, 2005).

432

## 433 **4.3 Effects of traffic volume on WVC risks**

434 A general consensus arises in the literature on the number of WVCs increases with road traffic  
435 (Fahrig et al., 1995; Rosen & Lowe, 1994; Inbar & Mayer, 1999; Joyce & Mahoney, 2001). This  
436 correlation is, however, much discussed with some authors proposing a linear relationship (Fahrig et  
437 al., 1995); and others a barrier effect (high-traffic roads having fewer WVCs than less frequented  
438 roads because animals avoid the noise and other disturbances they generate: Seiler & Helldin, 2006;  
439 Clewenger et al., 2002; van Langevelde et al., 2009). Others explained the lower-than-expected  
440 number of collisions reported on some high-traffic roads by a depletion of local animal populations  
441 due to roadkill (Ascensao et al., 2019). Those arguments may be unnecessary given our results: the  
442 theoretical relationship between traffic and WVCs can be non-linear even in the absence of traffic-

443 dependent road avoidance or source-sink dynamics, and roads with heavy traffic would not  
444 necessarily have higher collision rates than intermediate roads.

445 Whatever assumption we make on animal movement, the number and the individual probability of  
446 WVC grow asymptotically within the explored range of traffic (fig. 3c and 4c). This observation  
447 agrees with the mechanistic model of WVCs by Hels & Buchwald (2001) that too predicts a  
448 logarithmic relationship between traffic volume and WVC occurrence. A noticeable difference  
449 between the two models is that while the probability of dying animals asymptotically approaches 1  
450 for Hels & Buchwald's model, the asymptotic number and probability of WVC lie below a 100% in  
451 all our simulations. Note that no asymptote is visible in scenario 1 (habitat fragmentation), which  
452 possibly results from the limited range of traffic volume we considered due to computational  
453 limitations (major highways worldwide can see up to 15 000 vehicles per hour).

454

#### 455 **4.4 Effects of vehicle speed on WVC risks**

456 In our model, the speed of the moving vehicles is unrelated to the number and individual risk of  
457 WVC over the simulated range of speed (0–300 km.h<sup>-1</sup>, see fig. 3b and 4b). At first sight, a lack of  
458 effect of vehicle speed may appear at odds with the previous theoretical models suitable for WVC,  
459 but it is not: in the ideal gas model (Hutchinson & Waser, 2007), the equations for encounters  
460 feature the length of the path of the molecule (speed × time spent moving) rather than the speed  
461 itself. In our model, the distance travelled by a vehicle is constant: they move from one end of the  
462 road to the other, and a higher speed does not equate with a longer distance travelled, therefore  
463 speed does not increase WVC risks. In contrast, on the subject of the animal's speed, when higher  
464 speed means longer travel distances (for scenarios 0 and 4; scenarios 1, 2 and 3 are more complex  
465 as the movement is also directed), it leads to higher WVC occurrences and risks. In addition, the  
466 distance travelled by vehicles was increased by simulating more tortuous roads (high sinuosity  
467 index), and the number and probabilities of collision for animals increased as well (fig. 3f and 4f),  
468 as expected under the ideal gas framework. Therefore, vehicle speed alone did not impact collision  
469 risks in the model.

470 Empirically, speed is regarded as a significant component of WVCs: the faster the vehicles, the  
471 more likely is a collision with an animal (Table 1, see also Farmer & Brooks 2012; Hobday &  
472 Minstrell 2008). Vehicles moving at high speeds are most of the time traveling on multi-lane  
473 highways with heavy traffic, and the reported association between WVCs and vehicle speed may  
474 therefore be confounded with traffic density that we find to be a stronger driver of WVC, or road  
475 width which relates to the time required to cross the road.

476 For flying carrion feeders (scenario 3) only, sinuosity is not or slightly negatively correlated to  
477 WVC numbers and individual probabilities. We do not have a satisfactory answer to this, but  
478 suggest that the Euclidean distance between two attraction centers placed on the road changes with  
479 road sinuosity and could impact (with our method of simulating flight) the altitude and therefore the  
480 collision risk, which is why terrestrial animals (scenario 2) are not impacted. Road sinuosity can  
481 also be treated as a measure of the density of roads, i.e. the surface of road per unit of area, where  
482 sinuous roads equate to a higher density than straight roads. In that sense, we show that the density  
483 of roads is positively correlated to WVC number and risks for most scenarios of movement.

484

#### 485 **4.5 Model limits**

486 We find that the time spent on the road is the critical factor driving WVC number and probabilities  
487 independently of space use patterns, and consequently behaviours we did not implement but that  
488 modify the time the animal spends on the road surface (road avoidance, pausing on the road,  
489 speeding away from vehicles, evading oncoming vehicles, see Jacobson et al. 2016; Lima et al.  
490 2015) are likely to be key components of WVC occurrences. As previously discussed, some of these  
491 behaviours, such as intentional collision avoidance, are complex and may be difficult to simulate  
492 realistically (Broadhurst & Kanade, 2005; Kuge et al., 2000). Although this was not the focus of  
493 this work, we briefly investigated the effects of some of these mechanisms on WVC risks based on  
494 the different scenarios of movement already implemented in the model (Table S4).

495 For example, road avoidance dependant on characteristics such as traffic volume, or conversely,  
496 habituation to traffic would translate into modifications of the probability of coming into contact  
497 with the road, controlled in the model by the strength of avoidance of the road  $w$  under scenario of  
498 animal movement 4 (road avoidance). The relationships between  $w$  and the number and individual  
499 probability of collision with a vehicle have been explored in the model: increasing the strength of  
500 road avoidance  $w$  (e.g., with increasing intensities of road traffic) decreases the risks and numbers  
501 of WVC, and low values of  $w$  (e.g., habituation to traffic) leads to increased numbers and risks of  
502 WVC (fig. 3e and 4e). Therefore, the effect of these mechanisms can be understood in terms of  
503 modifications in parameters that have already been explored in the model. In particular, increasing  
504 values of road avoidance  $w$  with road traffic may lead to relation between WVC risks and traffic to  
505 be an inverted U-shaped curve where roads of intermediate traffic volume are more dangerous than  
506 high-traffic and low-traffic roads, as conceptualized by Seiler (2006) and Jacobson et al. (2016).

507 We also investigated the possibility for vehicle drivers and animals to evade oncoming collisions  
508 (Sup. Material). We show that adding driver or animal reactions to oncoming vehicles – reduced

509 here to a probability of successful collision avoidance depending on vehicle speed – does not  
510 change the qualitative results regarding the effects of animal movement on collision risks although  
511 the absolute risks did (fig. S4b and S4c). However, behaviours not implemented in the model, such  
512 the possibility of evading oncoming collisions, may account for discrepancies between empirical  
513 findings and model predictions. For example, while the model did not predict that vehicle speed  
514 affects collision risks, reducing speed limits on road has proven efficient in reducing WVC (Hobday  
515 & Minstrell, 2008; Jones, 2000), possibly because decreased speeds may afford sufficient time for  
516 both animals and drivers to evade potential collisions.

517 The main focus of this work was the movement of the animals, and we reduced “collisions” to the  
518 number of times an animal and a vehicle were located less than 5 meters away from each other. This  
519 will likely overestimate collision probabilities, especially for smaller-bodied species that can easily  
520 fit in-between car tires (Hels & Buchwald, 2001; van Langevelde & Jaarsma, 2005). This is a  
521 classical simplification from the ideal gas model that we expect will not alter the general patterns  
522 we report, but simply move all the curves down. Finally, we designed the simulation to have  
523 constant animal density, which does not allow for population depletion dynamics (justified by the  
524 limited temporal scale of 12 hours per simulation run). Based on our conclusions, the total number  
525 of roadkill would decrease linearly with population decline but have no impact on individual  
526 probabilities of collision (fig. 3d and 4d).

527

## 528 **4.6 Conclusion**

529 Empirical studies focusing on animal behaviour and movement in addition to other biological traits,  
530 road-side habitat type and road characteristics can give valuable insights as to why some species are  
531 more often killed on roads than others. We show here that animal behaviour in the presence of roads  
532 is a key component of roadkill occurrences, and that understanding space use patterns can give  
533 insights on the vulnerability of a species to roadkill. Although this model is not intended to provide  
534 quantitative predictions of roadkill for particular species, we show that future predictive models  
535 should incorporate components of movement ecology to properly address road mortality. Animal  
536 behaviours in the proximity of transport infrastructures could also be of interest in evolutionary  
537 studies, an aspect of road ecology that is lacking so far in the literature (Brady & Richardson, 2017).

538

## 539 **Acknowledgments**

540 This work was performed using the computing facilities of the CC LBBE/PRABI. We thank Simon  
541 Benhamou, Jean-Michel Gaillard and Marion Valeix for comments on previous drafts of this work.

### 542 **Author Contributions**

543 Annaëlle Bénard: coding work and analysis of the data generated, lead writing of the manuscript,  
544 equal contribution to the methodology. Thierry Lengagne and Christophe Bonenfant: equal  
545 contribution to the methodology, writing, reviewing and editing of the manuscript. All authors  
546 contributed critically to the drafts and gave final approval for publication.

547

### 548 **Open research statement**

549 Code is provided via the following link: [https://gitlab.in2p3.fr/annaelle.benard/a-simulation-of-](https://gitlab.in2p3.fr/annaelle.benard/a-simulation-of-animal-vehicle-collisions)  
550 [animal-vehicle-collisions](https://gitlab.in2p3.fr/annaelle.benard/a-simulation-of-animal-vehicle-collisions). No data were collected for this study.

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**Supplementary Material**

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583 **Section 4 - Regarding drivers' reaction to oncoming collisions and animals' reactions to traffic and**  
584 **oncoming vehicles.**  
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586 The model presented in this paper focuses on animal and vehicle movement in landscapes.  
587 Therefore, it does not consider the possibility of vehicle drivers reacting to the presence of an  
588 animal on the road or roadside, such as braking or swerving. Likewise, we do not consider potential  
589 behaviours from animals: fleeing the road surface or taking off before impact (Brown & Bomberger  
590 Brown, 2013; Lima et al., 2015), road avoidance depending on the intensity of traffic (Seiler &  
591 Helldin 2006) or habituation to traffic (Legagneux & Ducatez, 2013).

592  
593 Although the investigation of these behaviours and choices made in the face of a danger was not the  
594 focus of this work, some of these behavioural responses by the driver or the animals were somewhat  
595 already embedded in the different scenarios of movement already implemented in the model (Table  
596 S4). For example, traffic-dependent road avoidance and habituation to road traffic would translate  
597 into modifications of the probability with which animals come into contact with the road's surface  
598 (Jaeger et al., 2005). In our model, this probability is best modelled by changes in the strength of  
599 avoidance of the road  $w$  under scenario of animal movement 4 (road avoidance): high values of  
600 avoidance result in lower probabilities that animal will approach the road. The relationships  
601 between  $w$ , and the number and individual probability of collision with a vehicle, have been  
602 explored in the model: increasing the strength of road avoidance  $w$  (e.g., with increasing intensities  
603 of road traffic) decreases the risks and numbers of WVC, and low values of  $w$  (e.g., habituation to  
604 road traffic where animal no longer avoid roads and roadsides) leads to increased numbers and risks  
605 of WVC (fig. 3e and 4e). Therefore, introducing new mechanisms of road avoidance and  
606 habituation in the model would have predictable impacts on the simulation results.

607  
608 Other mechanisms, such as reactions to oncoming collisions, may be more difficult to incorporate  
609 into the model. Indeed, animal reaction to oncoming collision may differ depending on the species'  
610 cognitive abilities or adaptive behaviours (Lima et al., 2015), morphological traits (Brown &  
611 Bomberger Brown, 2013), and vehicle speed (Legagneux & Ducatez, 2013). Collision avoidance on  
612 the driver's part is modulated by driver decisions (Kuge et al., 2000; Broadhurst & Kanade, 2005),  
613 vehicle characteristics (e.g., weight, tyres) and speed (Samson et al., 2022), and road characteristics  
614 (Samuelraj et al., 2018). Because of this complexity, incorporating realistic animal or driver  
615 reactions into a mechanistic model is complex and would take our study far from our original idea  
616 of exploring the effect of animal movement only on WVC.

617

618 We nevertheless introduced here the outcome of of these mechanisms into our modelling to test  
 619 whether the main conclusions from the model regarding the impact of animal and vehicle  
 620 trajectories on WVC would differ or not.

621

622 Table S4: Animal and driver behaviours not currently implemented in the wildlife-vehicle collision  
 623 model. The model presented in this work focuses on realistic animal and vehicle movement, but  
 624 does not incorporate elements related to animal and vehicle drivers reactions to oncoming collisions  
 625 or road traffic.

626

|               | <b>Mechanism</b>   | <b>Possibility of inclusion in the model</b>   | <b>Impact</b>  |
|---------------|--|--|--|
| <b>Animal</b> | Road avoidance dependent on traffic, or other road characteristics | Road avoidance (parameter $w$ , scenario 4 – road avoidance) increasing with intensity of a pre-determined characteristic.                           | Similar to scenario 4: number and individual probability of WVC decrease with increasing $w$ (fig. 3e and fig. 4e, scenario 4).                            |
|               | Habituation  | Increasing levels of habituation to traffic translated into decreasing levels of avoidance of the road (parameter $w$ , scenario 4 – road avoidance) |  |
|               | Adaptive reactions to oncoming collisions (e.g., fleeing the road) | Increasing levels of habituation to vehicles lead to a reduction in collision avoidance strategies, such as fleeing from oncoming traffic.           | Difficult to predict. In general, high probabilities of successfully evading oncoming collisions will reduce the number and individual probability of WVC. |
| <b>Driver</b> | Evasive manoeuvres (e.g., braking, swerving)                       | Complex mechanisms that depend on species, vehicles and road characteristics, would need to be implemented as independent mechanisms in the model.   |  |

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## 629 **Methods**

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631 We present here an additional model of WVC that incorporates the possibility for animal or drivers  
 632 to avoid an oncoming collision. We reduced the mechanism of collision avoidance to a probability  
 633 of successfully evading an oncoming collision that depended on the speed of the vehicle. Faster  
 634 vehicles lead to a decreased window of time to flee the road for animals (Legagneux & Ducatez,  
 635 2013), or to brake/swerve for vehicle drivers (braking distance is also increased, Samson et al.,  
 636 2022), and therefore the probability of being able to avoid the collision is decreased (fig. S4a). In  
 637 this model, the probability of evading collisions was high (> 98%) for vehicles moving at speeds of  
 638 10 km.h<sup>-1</sup> or less, and decreased with vehicle speed to < 5% for vehicles moving at or over 100  
 639 km.h<sup>-1</sup>. For each oncoming collision (animal and vehicle located < 5 meters apart), we drew from a

640 Bernoulli distribution with parameter  $p = \text{probability of evading collision depending on vehicle}$   
641 *speed*, to determine whether the collision happened or was avoided. The rest of the model and  
642 simulation parameters (parameters baseline values, scenarios of movement, number of runs) were  
643 kept identical to the main body of this manuscript. We ran the model for two parameters of interest:  
644 a  $p$  that is not involved in the implemented mechanism of collision avoidance (mean  
645 animal speed) and a parameter that is involved in the mechanism (vehicle speed).

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## 648 **Results and Discussion**

649 We show the mean number of collisions for varying mean speeds of animals (fig. S4b) and vehicles  
650 (fig. S4c). When testing the impact of mean animal speed on WVC, the baseline value for vehicle  
651 speed is  $80 \text{ km.h}^{-1}$  (Table 2), and therefore the probability of avoiding an oncoming collision is  
652 constant at around 83%. Therefore, the mean number of collisions for each scenario of movement is  
653 decreased in the model implementing the possibility of evading collisions (fig. S4b) compared to  
654 the results showed on the original model (fig. 3a). However, the shape of the curves for each  
655 scenario and the ranking of each scenario were not changed compared to the original model, and  
656 thus the main conclusions of our work regarding the importance of animal speed and the impact of  
657 animal trajectories on WVC remain unchanged, with only the quantitative results shifted downward.

658 The speed of the vehicle had little to no impact on WVC numbers in the original model (fig. 3b).  
659 However, in the new model with probabilities of evading collisions, we see an increase in mean  
660 WVC numbers with increasing vehicle speeds (fig. S4c). Results interpretation is straightforward,  
661 as the probability of a collision happening increases with the speed of the vehicle: the observed  
662 impact of vehicle speed on the number of collisions reflects the probability of collision (*i.e.*,  $1 -$   
663  $\text{probability of evading collision}$ , fig. S4a). Indeed, as vehicle speed increases and probability of  
664 collision nears 1 (probability of evading collision nears 0, fig. S4a), the mean number of collisions  
665 for each scenario of movement tends toward the values we found in the original model (fig. 3b).  
666 Therefore, the ranking between each scenario of movement was unchanged.

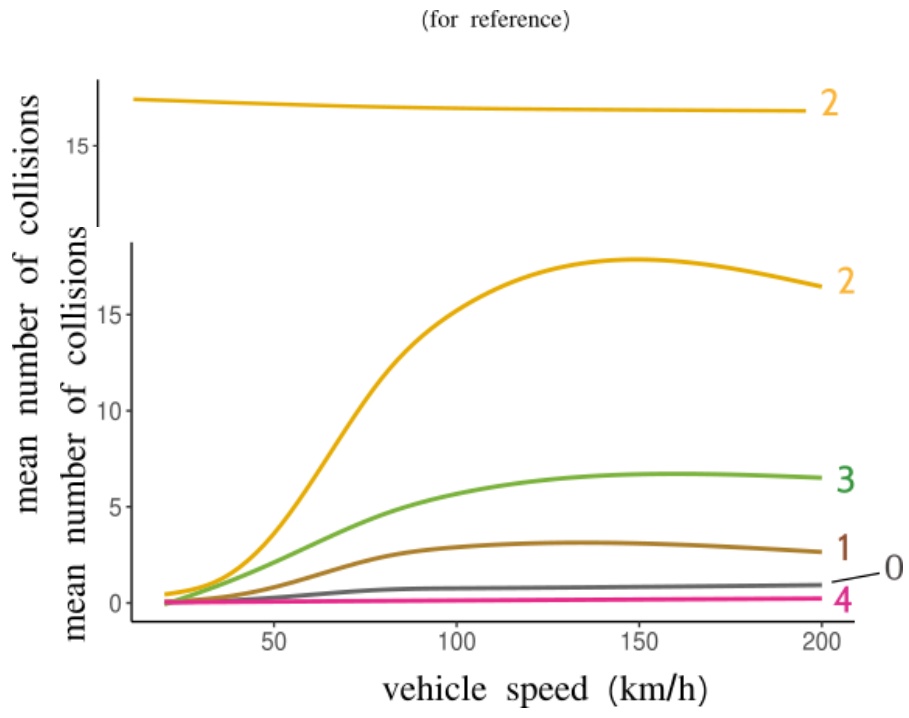
667 In conclusion, we find that this new model yielded results similar to the original model presented in  
668 the main body of this work when testing the effect of a parameter not involved in oncoming  
669 collision avoidance (mean animal speed), with the curves for mean number of WVC per scenario of  
670 movement simply shifted downwards. This conclusion should hold for all other parameters of  
671 interest not implicated into the mechanism (road sinuosity, animal density, strength of  
672 attraction/avoidance  $w$ , volume of traffic) where vehicle speed is similarly held constant at  $80 \text{ km.h}^{-1}$

673 <sup>1</sup>. In regard to the speed of vehicles, which directly influenced the probability of avoiding collisions,  
674 we found that the mean number of WVC represented the distribution of collision avoidance  
675 probabilities we defined in the model.

676 This mechanism is an oversimplified representation of reality, and effectively modelling animal or  
677 driver behaviour for avoiding collisions with oncoming vehicles is a complex task well beyond the  
678 scope of this study. The inclusion of this new collision avoidance mechanism does not alter the key  
679 findings and conclusions drawn in the model regarding the effects of animal movement on wildlife-  
680 vehicle collisions.

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