



An Analytical Framework of the Factors Affecting Wildlife–Vehicle Collisions and Barriers to Movement

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Abstract: Road mortalities caused by wildlife-vehicle collisions (WVCs) are the most obvious negative effect of roads on wildlife. Identifying the influencing factors and summarizing the spatialtemporal patterns of WVCs have been important research trends in recent decades. However, most studies have only considered a portion of the factors, and there remains a lack of a relatively complete framework, including the numerous factors of WVCs, as well as the underlying transmission mechanisms between factors. In this study, an analytical framework incorporating a wide range of previously discussed factors is constructed. The framework not only displays the possible direction of the influence of each factor on WVCs, but also summarizes some important potential explanations under some circumstances and reveals the main interactions between certain types of factors. From one perspective, the factors affecting WVCs can be divided into four categories: species characteristics, road and traffic characteristics, landscape and environmental characteristics, and driver-related factors and specific human activities. From another perspective, the factors affecting WVCs can be mainly categorized as those related to entering roads and those related to leaving roads safely. The study begins with a discussion of three important sub-frameworks: factors promoting road crossing, factors related to barriers to movement, and factors related to safe crossing. Finally, a suggestion is provided to promote the research on WVCs globally.

Keywords: wildlife–vehicle collisions (WVCs); crossing willingness; crossing avoidance; crossing ability; road ecology

1. Introduction

As massive-scale infrastructure constructed by human beings, roads have profound impacts on wildlife. The main negative effects of roads on wildlife include wildlife–vehicle collisions (WVCs), barriers to movement, various forms of pollution (e.g., noise, light, chemical contaminants, and dust), other indirect disturbances on wildlife due to changing geology and hydrology patterns, the spread of invasive species and diseases, and human activities encroaching on more habitats. These effects correspond to habitat loss, fragmentation, and degradation [1]. Although a road itself is a linear structure, its effect zone may extend perpendicularly up to hundreds to thousands of meters [2,3]. Even the positive effects on wildlife provided by roads may become ecological traps for some species or their predators [4,5].

WVCs are the most obvious negative effect of roads on wildlife. Enormous numbers of wildlife road-kills are documented each year and must be underestimated to a large extent due to the carcass persistence time (affected by scavengers, traffic, and weather), low detectability, and subsequent death away from roads [6–10]. Scientists have estimated that approximately 194 million birds and 29 million mammals may be killed on roads in Europe each year [11]. WVCs have serious consequences for wildlife populations. Road mortality can be a primary cause of death for some species in some regions [2,12–15], can reduce species abundance near roads [16–18], can limit genetic diversity [19], and can pose



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). extinction threats to certain wildlife [20]. One study identified four populations that could become extinct in 50 years if the observed levels of road-kill mortalities persist [20].

Identifying the influencing factors and summarizing the spatial-temporal patterns of WVCs have been major research trends in recent decades and are of great importance for mitigation measures. While numerous factors have been discussed, most empirical studies have considered only a small portion of the factors, and the few relevant review studies have also tended to focus on only some types of factors and the influence direction of each single factor [21]. There remains a lack of a relatively complete framework comprising a wide range of factors of WVCs as well as the underlying transmission mechanisms [22]. Indeed, the factors influencing WVCs may vary by geographical location and circumstance and can be species-specific. It remains necessary to present a relatively complete framework comprising a large number of factors affecting WVCs as well as the transmission mechanisms between some factors. This can help guide empirical studies to more comprehensively considering various possible related factors in specific circumstances, thus improving the general principles of empirical models as compared to the selection of only a single set of factors of interest. The objective of the present work is to establish an analytical framework including a wide range of previously discussed factors, determine the possible influence direction of each factor, summarize potential explanations under certain circumstances, and reveal the interactions between factors.

2. Materials and Methods

In order to find the various factors affecting WVCs that have been studied, an electronic literature search was conducted primarily by using the Web of Science. Possible combinations between the following four groups of keywords were attempted: (1) "road" or "highway" or "motorway" or "expressway", with (2) "wildlife" or "animal" or "mammal" or "reptile" or "amphibian" or "bird" (invertebrates are not considered in this study), with (3) "collision" or "kill" or "mortality", with (4) "factor" or "variable" or "spatial" or "temporal". To find the factors related to road crossing or barriers to movement, combinations including the following three groups of keywords were attempted: (1) "road" or "highway" or "motorway" or "expressway", with (2) "wildlife" or "animal" or "mammal" or "reptile" or "amphibian" or "bird", with (3) "cross" or "movement" or "barrier" or "avoidance". Reference lists from the published literature, especially relevant review articles, were also checked.

We excluded pieces of the literature that did not explore factors. For those factors affecting WVCs that were frequently discussed in previous studies, we attempted to include sufficiently relevant pieces of the literature to support our framework. Three types of literature were also included with emphasis; namely, those discussing factors rarely mentioned in previous relevant reviews, those drawing conclusions about the influence direction of some factors that differed from most studies, and those providing representative interpretations for the influence direction of factors.

In total, one hundred and fifty studies were incorporated as the foundation to establish the whole analytical framework, which includes numerous factors, their representative interpretations, and main interactions.

3. Factors Promoting Road Crossing

Many internal and external factors can improve the road crossing willingness or entering opportunities of wildlife (Figure 1). In this section, only certain main factors are briefly summarized to lay a foundation for the whole framework of WVCs, and more relevant factors are discussed in the later section concerning WVCs.



Increase crossing willingness or entering opportunities

Figure 1. The outline of the sub-framework of factors promoting road crossing.

Mobility is a very basic internal factor. The higher mobility of wildlife can increase their probability of encountering roads, for example, rodents with high mobility cross roads more frequently than less-mobile rodents [23]. Generally, large species are likely to be more mobile than small species, and carnivores are likely to be more mobile than herbivores or omnivores [24]. Larger snakes, for instance, cross roads more frequently than smaller ones [25,26]. Habitat generalists, which move across various habitats, may have a greater likelihood of road crossing than habitat specialists [27,28]. Males of many species have larger movement ranges and cross roads more frequently than females [29–33]. On the contrary, females of some species are more likely to cross roads than males [34,35]. The nearby population density affects the basic probability of road-entering opportunities. Several types of road use can lead wildlife to enter roads [5]. Seasonal life-history traits, such as reproductive behaviors (e.g., rutting and mating), migration, dispersal, and hibernating in different roosts, may enlarge the scope of activities and increase the likelihood of road crossing, even for some species that rarely cross roads in their daily movement [36]. Following regular migration routes regardless of the road network is also a common phenomenon [35].

Typical external factors that may significantly promote many types of wildlife to cross roads include roadside vegetation [37], preferred habitats surrounding the area [35,38,39], and the presence of crossing structures [40], among others.

4. Factors Related to Barriers to Movement

Barriers to movement can be regarded as the opposite aspect of the promotion of road crossing. On the one hand, barriers to movement reduce the crossing willingness of some wildlife, which is manifested as road crossing avoidance. For example, as mentioned previously, high mobility means more opportunities to encounter roads, but it does not necessarily mean more road crossing for each species, as the behavior of crossing avoidance is supposed to be taken into account. On the other hand, physical road obstacles such as fences can inhibit entering opportunities. The effect of barriers to movement helps to reduce the risk of WVCs. In addition, it should be noted that the reason why barriers to movement are given a high position in the proposed framework lies in the fact that they represent another significant negative impact of roads on wildlife. They have serious impacts on wildlife populations, such as limiting gene flow and reducing genetic diversity for populations on opposite roadsides [18,41–44]. Hence, it is especially valuable to further analyze the factors related to barriers to movement (Figure 2).



Figure 2. The outline of the sub-framework of factors related to barriers to movement.

Crossing avoidance can be attributed to avoiding the road itself (physical presence) or avoiding traffic. A wide range of small species avoids crossing roads regardless of the traffic [44,45]. Even narrow, unpaved roads limit the road crossing of some small species [12,36,46–48]. Explanatory factors for avoiding the road itself can at least be further classified as gap avoidance or sensitivity to the road substrate. Some wildlife, such as forest-dependent species [36], avoid the gap created by road clearance [44,46,48], possibly due to anti-predator behavior, environmental contrast between forest interiors and roads, or site fidelity [46,49,50]. D'Amico et al. (2016) attributed the road gap avoidance of red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) to long-term vehicle avoidance based on their memory [51]. Some species are sensitive to road materials [52,53]. For instance, San Diego pocket mice (*Chaetodipus fallax*) and cactus mice (*Peromyscus eremicus*) cross dirt roads but avoid crossing paved roads with a similar width, likely due to the odor emitted by the material of the pavement surface [52].

The crossing willingness of many wildlife species is negatively correlated with the traffic volume; such species include badgers (*Meles meles*) [54], hedgehogs (*Erinaceus europaeu*) [55], grizzly bears (*Ursus arctos*) [56], black bears (*Ursus americanus*) [57], red foxes (*Vulpes vulpes*) [58], and some ungulates [59–61]. This is likely due to noise or being alert to vehicles based on anti-predatory behaviors [58,62]. Furthermore, the degree of crossing avoidance may be weakened by the need to move to preferred habitats [63]. For instance, when grizzly bears [64] or elk (*Cervus elaphus*) [63] tend to move to higher-quality habitats, they are more likely to cross roads with high traffic.

Numerous studies indicate that the degree of crossing avoidance of a number of species is positively correlated with road width [29,49,65–73]. This is usually not related to the moving ability, as species are able to traverse for distances longer than the road width [49]. Actually, as the main factors affecting crossing avoidance, gaps, materials, and traffic all have internal consistency with the road width. Moreover, via a meta-analysis, Chen and Koprowski (2019) demonstrated that the degree of crossing avoidance is negatively related to the body mass of species [73].

Finally, numerous species avoid the road-effect zone due to various disturbances. The relationship between road-effect zone avoidance and road-crossing avoidance seems to be subtle. Many small species use road verges but avoid crossing roads. Conversely, some species, for example, wolverines (*Gulo gulo luscus*), avoid the road-effect zone unless they have to cross roads [74]. Siers et al. (2016) pointed out that the distance to roads might be used to predict the road crossing of species, excluding those with high crossing avoidance [26]. The specific relationship between road-effect zone avoidance and road-crossing avoidance of different species still requires more detailed research in the future.

5. Factors Related to Safe Crossing

Once wildlife ventures onto a road, many factors are associated with the probability of a safe exit on the other side (Figure 3). External factors may include road design, traffic volume, vehicle speed, time of day, weather, and driver-related factors, which will be discussed together with WVCs in the following section. Here, the focus is placed on discussing the internal factors associated with crossing ability, including the traversing speed, traversing route, evasive capacity, i.e., the ability to avoid collisions with approaching vehicles, timing of crossing, and others.



Figure 3. The outline of the sub-framework of factors related to safe crossing.

Slow-moving species spend more time on roads, thus increasing the risk of WVCs. When crossing roads, some species move faster than normal; these species include grizzly bears [75], moose (Alces alces) [39], elk [76], and black bears [57]. Snakes usually cross roads perpendicularly, i.e., they take the shortest possible route, which helps to reduce the crossing time [25,77]. Lima et al. (2015) divided the process of avoiding collisions with oncoming vehicles into three steps: vehicle detection, threat assessment, and evasive behavior [78]. Vehicle detection is mainly based on the sensory capacities of a species and is affected by external factors such as vehicle speed. Some species might be accustomed to vehicles and do not perceive them as threats. Evasive behavior is related to the antipredator behavior of a species. Properly moving away from the path of oncoming vehicles is usually an effective evasive response [78], but not every species has this ability. Several species, such as some amphibians [79], tend to freeze when facing approaching vehicles, possibly due to inappropriate antipredator behavior [78]. Hedgehogs may curl up into a ball when facing danger, and this behavior on roads increases the risk of WVCs [80]. Lee et al. (2010) found that the flight response of some kangaroos toward approaching vehicles makes them more vulnerable to WVCs than does keeping stationary (of course, not in the path of the vehicle) because the flight is unpredictable and might lead them to the path of oncoming vehicles [81]. The timing of crossing is correlated to the traffic avoidance mentioned previously. Several species tend to cross roads at night because of traffic avoidance, including grizzly bears [56] and Canada lynxes (Lynx canadensis) [82]. The flight pattern, especially the flight height, can influence the risk of WVCs for birds [83,84]. Finally, some species may become more adapted to roads with time and learn to improve their crossing ability [13]. Medrano-Vizcaíno et al. (2022) found that long-lived animals have a reduced risk of WVCs, in part due to the greater opportunity to learn crossing skills [85].

6. Factors Related to WVCs

6.1. Species Characteristics

Species characteristics affecting WVCs include the nearby population density, the crossing willingness or entering opportunity, the crossing ability, and morphological and life-history traits. Morphological and life-history traits include mobility, body size, diet type, gender, age, health, body length, group size, various road uses (e.g., foraging or thermoregulation on roads), reproductive and breeding behaviors, seasonal migrations, post-breeding dispersal, and movements to hibernation locations (Table 1).

	Factors	References
Species characteristics	Nearby population density	[86–91]
		Increase:
	Crossing willingness or	[5,23-40]
	entering opportunity	Decrease (barrier to movement):
		[12,26,29,36,44-74]
	Crossing ability	[13,25,39,56,57,75-85]
	Morphological and life-history traits:	
	mobility, body size, diet type, gender,	
	age, health, body length, group size,	
	various road uses (e.g., foraging or	
	thermoregulation on roads),	[2,5,29,31,33,34,80,84,85,92–101]
	reproductive and breeding behaviors,	
	seasonal migrations, post-breeding	
	dispersal, movements to	
	hibernation locations	

Table 1. The species characteristics affecting WVCs.

Numerous studies have found that the local population density is a crucial factor influencing WVCs [86–91]. As mentioned previously, larger species and carnivores are likely to be more mobile, but the specific effects on WVCs must be considered in combination with other factors. Several studies indicate that medium-sized mammals have the highest risk of WVCs, and the comparatively lower risk of WVCs of larger mammals can be explained by a lower population density, better crossing ability, and higher visibility for drivers [85,92,95,98]. Regarding birds, Møller et al. (2011) and Medrano-Vizcaíno et al. (2022) found that the WVCs of birds are positively correlated with body mass [84,85], while Morelli et al. (2020) came to the opposite conclusion [100]. There is also no consistent conclusion about the relationship between diet type and the risk of WVCs for mammals, as the dominant factors considered in different studies [80,92,95,96,98,99], such as mobility, population density, and foraging on roads, were not identical. The gender difference in the WVCs of certain species mainly results from the different crossing frequencies between males and females (bias toward males: e.g., [29,31,33]; bias toward females: e.g., [34]). Crossing roads in groups may reduce the risk of WVCs because of increased vigilance [96]. Nevertheless, Pfeiffer et al. (2020) pointed out that when white-tailed deer (Odocoileus *virginianus*) cross roads in groups, despite the increased total vigilance of the group, the vigilance of individuals in the group might decrease [101]. In addition, individuals in large groups tend to catch up with others on opposite sides of roads, thus increasing the risk of WVCs [93]. As a rare study involving the relationship between health conditions and WVCs, Møller et al. (2011) found that the risk of WVCs is higher in bird species with blood parasite infections [84]. Various road uses, such as foraging (e.g., predation, scavenging), movement, and thermoregulation, can increase the density and road crossing of wildlife, which may enhance the risk of WVCs [2,5]. For example, the presence of prey on roadsides may increase the risk of WVCs of predators [94,97]. In northern latitudes, just after dawn, birds often sit on tarmac roads, which are warmer than dew-laden roadside vegetation.

6.2. Road and Traffic Characteristics

Road and traffic characteristics affecting WVCs include road design, road age, traffic volume, and vehicle speed. Road design includes the road class, road width, road curvature, road embankments, road verges, medians, road lights, roadside vegetation, and mitigation measures (Table 2).

	Factors	References
Road and traffic characteristics	Road design: road class, road width, road curvature, road embankments, road verges, medians, road lights, roadside vegetation, mitigation measures	[21,35,39,40,55,60,62,68,82,83, 99,102–133]
	Road age Traffic volume Vehicle speed	[72] [21,55,58,60,62,88,134–138] [21,116,139]

Table 2. The road and traffic characteristics affecting WVCs.

Wider roads mean spending more time crossing, a higher traffic volume means fewer intervals to cross, and a higher vehicle speed means less time to react [62,115,116]. Although curves may lower the visibility of drivers [103], they may also reduce vehicle speed [60,128] and enhance drivers' attention [121]. Indeed, the majority of studies indicate that WVCs are positively correlated with road width, number of lanes, road class, traffic volume, and speed limit and are negatively correlated with road curvature [21]. Conversely, a high traffic volume can reduce the crossing willingness of some species and lower the risk of WVCs [58,60,62,88,134–137]. Additionally, it should not be overlooked that high traffic may depress the nearby population density via high road mortality, which causes road-kill hotspots to move to low-traffic segments [55,138]. Furthermore, high traffic may also make corpses disappear faster [55]. The negative relationship between the road width and the WVCs of certain species can be primarily attributed to the crossing avoidance of wide roads [118,123]. Husby (2016) conducted a rare study demonstrating a negative relationship between vehicle speed and the WVCs of birds, and the interpretation was that the sound of high-speed vehicles might alert birds earlier or that these vehicles might hit birds harder and throw them further off roads without detection [139].

Raised roads or roadsides with high embankments decrease the risk of WVCs of many species [68,104,128], but this may not be the case for birds [83]. Lao et al. (2011) and Valero et al. (2015) found that an increased shoulder width increases the likelihood of WVCs of some species [109,119]. Vegetated medians increase the WVCs of a number of species because they may attract species for food or protection or may reduce the width of the gap for crossing [68,128,131]. Even rigid median barriers may enhance the risk of WVCs by trapping wildlife on roads [113]. Road lights attract some species while repelling others [62]. Those who are attracted to roads by artificial lights may have a higher risk of WVCs [110,112,129,130]. Moreover, vehicle headlights may dazzle some nocturnal birds [83,128] or may cause some species to freeze, such as possums (*Trichosurus vulpecula*) and hedgehogs [55].

Roadside vegetation can be an attractive habitat to a wide range of wildlife or can act as a corridor for movement. A large number of species prefer to cross roads at sites hidden by vegetation cover, which may limit the awareness of drivers or wildlife [35,39,82,99,104,108,115,126]. Actually, the majority of studies show a positive correlation between roadside vegetation and WVCs [21]. In detail, the structure of roadside vegetation may also have an impact. For example, dense vegetation may force birds to fly higher and decrease the risk of WVCs [106,128]. When incubating birds nesting in low roadside vegetation flush from their nests, they often fly low over the open road and are very vulnerable to WVCs. Galantinbo et al. (2022) found that wood mice (*Apodemus sylvaticus*) are more likely to cross roads near taller shrubs or after firebreak openings [132].

Road fences are a very effective mitigation measure to reduce WVCs [40,102,105,111, 120,122,124,133]. Moreover, WVCs are likely to be concentrated at fence ends because of the funnel effect of fences [40,102,122,125,131]. Similarly, Cserkész et al. (2013) noted the high rate of WVCs near crossing structures due to fence gaps [114]. Fences may also become

As mentioned previously, species may improve their crossing ability with time. The road age may correlate with the change in local abundance or the interaction behavior (e.g., habituation) with roads [72].

6.3. Landscape and Environmental Characteristics

Landscape and environmental characteristics affecting WVCs include the surrounding habitat and landscape, topography, weather, time of day, day of the week, and month of the year (Table 3).

Table 3. The landscape and environmental characteristics affecting WV	/Cs.
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	Factors	References
	Surrounding habitat and	[7,10,21,60,80,104,107,108,118,126,
	landscape	129,130,135,136,140-147]
Landscape and environmental characteristics	Topography	[21,35,57,135,148,149]
	Weather	[88,103,112,150-156]
	Temporal factors: time of day, day of the week, month of the year	[9,60,68,93,130,136,150,151,157–163]

The likelihood of WVCs increases when roads intersect suitable habitats [118,129,144]. Most studies indicate that the amount and proximity of surrounding habitats (e.g., forest, grassland, wetland, water areas, agricultural land) are positively correlated with WVCs [10,21,126,135,140]. Furthermore, many studies have posited that the diversity of landscapes or habitat types may prompt the movement of wildlife and increase WVCs [21,104,108]. However, Puig et al. (2012) found that homogeneous landscapes on both sides of roads could increase WVCs of many medium-sized mammals due to higher crossing attempts, while heterogeneous landscapes were found to reduce WVCs [146]. Several studies indicate that the presence of national parks nearby raises the risk of WVCs [21], which is due to high species abundance in protected areas [80] or high traffic caused by tourism [7]. There is no major consensus on the correlation between developed areas and the risk of WVCs [21]. The explanations supporting a positive correlation include a higher abundance of some species attracted by exploiting anthropogenic resources, more nervous behavior, higher traffic density, and lower driver awareness in developed areas [60,80,130,136,141,142,145,147]. The explanations supporting a negative correlation mainly include the low density of some species in built areas due to the avoidance of human disturbance [107,143,144]. When linear topographies or landscapes (e.g., riparian structures, ditches, drainages, slopes, ridges) funnel wildlife to roads, they may increase the risk of WVCs [135,148]. The relationships between the slope or height of the surrounding terrain and WVCs seem to be complex [21,35,57,149].

Various climatic factors concerning WVCs have been discussed in relevant studies, including the temperature, humidity, precipitation, snow cover, wind, barometric pressure, fog, drought, extreme weather, photoperiod, and moon phase (e.g., Refs. [88,103,112,150–156]). For instance, Dussault et al. (2006) found more WVCs of moose during days with high temperatures and atmospheric pressure, possibly due to increased nocturnal activity or seeking open areas to avoid biting insects [150].

The seasonal distribution and the time distribution of the day of WVCs are mainly influenced by the activity patterns of wildlife. The day distribution of the week of WVCs is mainly influenced by the traffic volume. A large number of studies have demonstrated that seasonal peaks of road crossing and WVCs are consistent with seasonal life-history patterns [9,68,93,130,136,151,157,159,160]. Furthermore, numerous studies have found that the WVCs of some wildlife, such as ungulates and red foxes, are higher in dark periods because these species are more active during the night, and the WVCs are intensified by poor driver visibility [93,150,158,159,162,163]. Many studies have found that WVCs are

more frequent on weekends due to higher traffic [60,93,150,159]. Similarly, WVCs can be more numerous on holidays because of a higher traffic volume [161].

6.4. Driver-Related Factors and Specific Human Activities

The driver-related factors affecting WVCs include visibility, attention, reaction, and attitude (Table 4). Driver-related factors usually correspond to some other factors. For example, the visibility of drivers can be affected by the body size and color of wildlife, the driving speed, the road curvature, roadside vegetation, the weather, and the time of day. Moreover, the attention of drivers may decrease on straight roads [164] or at certain periods of time. The reaction of drivers is related to their visibility, attention, driving skill, driving speed, vehicle type, and the predictability of the crossing behavior of wildlife. The attitudes of drivers toward WVCs may vary with the species, and drivers may even hit certain species (e.g., snakes) intentionally [165–168]. Some human activities in certain periods of the year, such as hunting, may promote the activity of some wildlife and increase the risk of WVCs [10,60,129,159].

Table 4. Driver-related factors and specific human activities affecting WVCs.

	Factors	References
Driver-related	Visibility, attention, reaction, attitude	[164–168]
Specific human activities	E.g., hunting, littering	[10,60,129,159]

7. Conclusions and Recommendations

Based on the preceding discussion, Figure 4 integrates the two analytical perspectives of factors affecting WVCs. The figure presents the comprehensive factors affecting WVCs and the main transmission mechanisms.



Figure 4. The comprehensive factors affecting WVCs and the main transmission mechanisms.

The interactions between factors are quite complex, and factors in the four groups often influence each other. For example, factors concerning landscape and environment characteristics, such as the surrounding habitat, landscape, and temporal factors, can affect traffic, driver-related factors, life-history traits, crossing willingness, and nearby population density. A high traffic volume reduces the crossing willingness or nearby population density of some species. Roadside vegetation or vegetated medians increase the road use and crossing willingness of some species, while wider roads decrease the crossing willingness and fences or high embankments limit entering opportunities. Factors within one group may also influence each other. For example, morphological and life-history traits influence the nearby population density, crossing willingness, and crossing ability of species.

In this study, a relatively complete framework of factors related to WVCs was integrated. The framework includes a wide range of factors affecting WVCs, the possible influence direction of each factor, potential explanations under different circumstances, and interactions between factors. This framework can be used to make theoretical contributions and provide more perspectives for relevant empirical studies. In addition, although numerous internal and external factors associated with WVCs have been discussed, more undocumented variables and the interactions between known variables have yet to be revealed. This can be remedied by the use of better quantitative models in the future.

It is advised that research on the factors affecting WVCs be carried out in combination with specific locations and species. Based on this, the main key factors can be distinguished, and targeted and practical mitigation approaches to tackle WVCs can be provided. To date, different types of wildlife crossing structures have been built in many countries and areas, such as overpasses, underpasses, and canopy crossings, and plenty of studies have proven that these structures have effectively reduced the WVCs of almost all wildlife [2,133,169].

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References

- van der Ree, R.; Smith, D.J.; Grilo, C. The ecological effects of linear infrastructure and traffic: Challenges and opportunities of rapid global growth. In *Handbook of Road Ecology*; van der Ree, R., Smith, D.J., Grilo, C., Eds.; John Wiley & Sons: Hoboken, NJ, USA, 2015; pp. 1–9.
- Forman, R.T.T.; Sperling, D.; Bissonette, J.A.; Clevenger, A.P.; Cutshall, C.D.; Dale, V.H.; Fahrig, L.; France, R.; Goldman, C.R.; Heanue, K.; et al. *Road Ecology: Science and Solutions*; Island Press: Washington, DC, USA, 2003.
- Cooke, S.C.; Balmford, A.; Johnston, A.; Newson, S.E.; Donald, P.F. Variation in abundances of common bird species associated with roads. J. Appl. Ecol. 2020, 57, 1271–1282. [CrossRef]
- 4. Ascensão, F.; LaPoint, S.; van der Ree, R. Roads, traffic and verges: Big problems and big opportunities for small mammals. In *Handbook of Road Ecology*; van der Ree, R., Smith, D.J., Grilo, C., Eds.; John Wiley & Sons: Hoboken, NJ, USA, 2015; pp. 325–333.
- 5. Hill, J.E.; De Vault, T.L.; Belant, J.L. A review of ecological factors promoting road use by mammals. *Mammal Rev.* 2021, *51*, 214–227. [CrossRef]
- 6. Santos, S.M.; Carvalho, F.; Mira, A. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE* **2011**, *6*, e25383. [CrossRef] [PubMed]
- 7. Arévalo, J.E.; Honda, W.; Arce-Arias, A.; Häger, A. Spatiotemporal variation of roadkills show mass mortality events for amphibians in a highly trafficked road adjacent to a national park, Costa Rica. *Rev. Biol. Trop.* **2017**, *65*, 1261–1276. [CrossRef]
- 8. Monge-Nájera, J. Road kills in tropical ecosystems: A review with recommendations for mitigation and for new research. *Rev. Biol. Trop.* **2018**, *66*, 722–738. [CrossRef]
- Wright, P.G.R.; Coomber, F.G.; Bellamy, C.C.; Perkins, S.E.; Mathews, F. Predicting hedgehog mortality risks on British roads using habitat suitability modelling. *PeerJ* 2020, 7, e8154. [CrossRef] [PubMed]
- 10. Aquino, A.G.H.E.O.; Nkomo, S.L. Spatio-temporal patterns and consequences of road kills: A review. *Animals* **2021**, *11*, 799. [CrossRef]
- 11. Grilo, C.; Koroleva, E.; Andrášik, R.; Bíl, M.; González-Suárez, M. Roadkill risk and population vulnerability in European birds and mammals. *Front. Ecol. Environ.* **2020**, *18*, 323–328. [CrossRef]
- 12. Trombulak, S.C.; Frissell, C.A. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* 2000, 14, 18–30. [CrossRef]

- 13. Coffin, A.W. From roadkill to road ecology: A review of the ecological effects of roads. *J. Transp. Geogr.* 2007, *15*, 396–406. [CrossRef]
- 14. Williams, S.T.; Collinson, W.; Patterson-Abrolat, C.; Marneweck, D.G.; Swanepoel, L.H. Using road patrol data to identify factors associated with carnivore roadkill counts. *PeerJ* **2019**, *7*, e6650. [CrossRef]
- 15. Garcês, A.; Queiroga, F.; Prada, J.; Pires, I. A review of the mortality of wild fauna in Europe in the last century: The consequences of human activity. *J. Wildl. Biodivers.* **2020**, *4*, 34–55. [CrossRef]
- 16. Fahrig, L.; Pedlar, J.H.; Pope, S.E.; Taylor, P.D.; Wegner, J.F. Effect of road traffic on amphibian density. *Biol. Conserv.* **1995**, *73*, 177–182. [CrossRef]
- 17. Jack, J.; Rytwinski, T.; Fahrig, L.; Francis, C.M. Influence of traffic mortality on forest bird abundance. *Biodivers. Conserv.* 2015, 24, 1507–1529. [CrossRef]
- 18. Teixeira, F.Z.; Rytwinski, T.; Fahrig, L. Inference in road ecology research: What we know versus what we think we know. *Biol. Lett.* **2020**, *16*, 20200140. [CrossRef]
- 19. Jackson, N.D.; Fahrig, L. Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biol. Conserv.* **2011**, *144*, 3143–3148. [CrossRef]
- Grilo, C.; Borda-de-Agua, L.; Beja, P.; Goolsby, E.; Soanes, K.; le Roux, A.; Koroleva, E.; Ferreira, F.Z.; Gagné, S.A.; Wang, Y.; et al. Conservation threats from roadkill in the global road network. *Glob. Ecol. Biogeogr.* 2021, 30, 2200–2210. [CrossRef]
- Pagany, R. Wildlife-vehicle collisions—Influencing factors, data collection and research methods. *Biol. Conserv.* 2020, 251, 108758.
 [CrossRef]
- Clevenger, A.P.; Barrueto, M.; Gunson, K.E.; Caryl, F.M.; Ford, A.T. Context-dependent effects on spatial variation in deer-vehicle collisions. *Ecosphere* 2015, 6, 47. [CrossRef]
- 23. Ji, S.; Jiang, Z.; Li, L.; Li, C.; Zhang, Y.; Ren, S.; Ping, X.; Cui, S.; Chu, H. Impact of different road types on small mammals in Mt. Kalamaili Nature Reserve. *Transp. Res. Part D Transp. Environ.* **2017**, *50*, 223–233. [CrossRef]
- 24. Carbone, C.; Cowlishaw, G.; Isaac, N.J.B.; Rowcliffe, J.M. How Far Do Animals Go? Determinants of Day Range in Mammals. *Am. Nat.* 2005, *165*, 290–297. [CrossRef]
- Andrews, K.M.; Gibbons, J.W. How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia* 2005, 4, 772–782. [CrossRef]
- 26. Siers, S.R.; Reed, R.N.; Savidge, J.A. To cross or not to cross: Modeling wildlife road crossings as a binary response variable with contextual predictors. *Ecosphere* **2016**, *7*, e01292. [CrossRef]
- Grilo, C.; Molina-Vacas, G.; Fernández-Aguilar, X.; Rodriguez-Ruiz, J.; Ramiro, V.; Porto-Peter, F.; Ascensão, F.; Román, J.; Revilla, E. Species-specific movement traits and specialization determine the spatial responses of small mammals towards roads. *Landsc. Urban Plan.* 2018, 169, 199–207. [CrossRef]
- Fabrizio, M.; Di Febbraro, M.; D'Amico, M.; Frate, L.; Roscioni, F.; Loy, A. Habitat suitability vs landscape connectivity determining roadkill risk at a regional scale: A case study on European badger (Meles meles). *Eur. J. Wildl. Res.* 2019, 65, 7. [CrossRef]
- 29. Schwab, A.C.; Zandbergen, P.A. Vehicle-related mortality and road crossing behavior of the Florida panther. *Appl. Geogr.* 2011, *31*, 859–870. [CrossRef]
- 30. Bond, A.R.F.; Jones, D.N. Roads and macropods: Interactions and implications. Aust. Mammal. 2014, 36, 1–14. [CrossRef]
- Poessel, S.A.; Burdett, C.L.; Boydston, E.E.; Lyren, L.M.; Alonso, R.S.; Fisher, R.N.; Crooks, K.R. Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. *Biol. Conserv.* 2014, 180, 224–232. [CrossRef]
- 32. Karelus, D.L.; McCown, J.W.; Scheick, B.K.; van de Kerk, M.; Bolker, B.M.; Oli, M.K. Effects of environmental factors and landscape features on movement patterns of Florida black bears. *J. Mammal.* **2017**, *98*, 1463–1478. [CrossRef]
- Moore, L.J.; Petrovan, S.O.; Baker, P.J.; Bates, A.J.; Hicks, H.L.; Perkins, S.E.; Yarnell, R.W. Impacts and potential mitigation of road mortality for hedgehogs in Europe. *Animals* 2020, 10, 1523. [CrossRef]
- 34. Steen, D.A.; Aresco, M.J.; Beilke, S.G.; Compton, B.W.; Condon, E.P.; Dodd, C.K.; Forrester, H.; Gibbons, J.W.; Greene, J.L.; Johnson, G.; et al. Relative vulnerability of female turtles to road mortality. *Anim. Conserv.* **2006**, *9*, 269–273. [CrossRef]
- 35. Meisingset, E.L.; Loe, L.E.; Brekkum, Ø.; Van Moorter, B.; Mysterud, A. Red deer habitat selection and movements in relation to roads. *J. Wildl. Manag.* 2013, 77, 181–191. [CrossRef]
- Chen, H.L.; Koprowski, J.L. Barrier effects of roads on an endangered forest obligate: Influences of traffic, road edges, and gaps. Biol. Conserv. 2016, 199, 33–40. [CrossRef]
- 37. van der Hoeven, C.A.; de Boer, W.F.; Prins, H.H.T. Roadside conditions as predictor for wildlife crossing probability in a Central African rainforest. *Afr. J. Ecol.* **2009**, *48*, 368–377. [CrossRef]
- Dodd, N.L.; Gagnon, J.W.; Boe, S.; Schweinsburg, R.E. Assessment of elk highway permeability by using Global Positioning System telemetry. J. Wildl. Manag. 2007, 71, 1107–1117. [CrossRef]
- 39. Dussault, C.; Ouellet, J.; Laurian, C.; Courtois, R.; Poulin, M.; Breton, L. Moose movement rates along highways and crossing probability models. *J. Wildl. Manag.* 2007, *71*, 2338–2345. [CrossRef]
- 40. Helldin, J.O.; Petrovan, S.O. Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. *PeerJ* 2019, 7, e7518. [CrossRef]
- 41. Epps, C.W.; Palsbøll, P.J.; Weyhausen, J.D.; Roderick, G.K.; Ramey, R.R., II; McCullough, D.R. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecol. Lett.* **2005**, *8*, 1029–1038. [CrossRef]

- 42. Marsh, D.M.; Page, R.B.; Hanlon, T.J.; Corritone, R.; Little, E.C.; Seifert, D.E.; Cabe, P.R. Effects of roads on patterns of genetic differentiation in red-backed salamanders, Plethodon cinereus. *Conserv. Genet.* 2008, *9*, 603–613. [CrossRef]
- Clark, R.W.; Brown, W.S.; Stechert, R.; Zamudio, K.R. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. *Conserv. Biol.* 2010, 24, 1059–1069. [CrossRef]
- Ascensão, F.; Mata, C.; Malo, J.E.; Ruiz-Capillas, P.; Silva, C.; Silva, A.P.; Santos-Reis, M.; Fernandes, C. Disentangle the causes of the road barrier effect in small mammals through genetic patterns. *PLoS ONE* 2016, 11, e0151500. [CrossRef]
- 45. McGregor, R.L.; Bender, D.J.; Fahrig, L. Do small mammals avoid roads because of the traffic? *J. Appl. Ecol.* **2008**, 45, 117–123. [CrossRef]
- Laurance, S.G.W.; Stouffer, P.C.; Laurance, W.F. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conserv. Biol.* 2004, 18, 1099–1109. [CrossRef]
- Eigenbrod, F.; Hecnar, S.J.; Fahrig, L. Accessible habitat: An improved measure of the effects of habitat loss and roads on wildlife populations. *Landsc. Ecol.* 2008, 23, 159–168. [CrossRef]
- 48. Macpherson, D.; Macpherson, J.L.; Morris, P. Rural roads as barriers to the movements of small mammals. *Appl. Ecol. Environ. Res.* **2011**, *9*, 167–180. [CrossRef]
- 49. Rico, A.; Kindlmann, P.; Sedláček, F. Barrier effects of roads on movements of small mammals. Folia Zool. 2007, 56, 1–12.
- 50. Paterson, J.E.; Baxter-Gilbert, J.; Beaudry, F.; Carstairs, S.; Chow-Fraser, P.; Edge, C.B.; Lentini, A.M.; Litzgus, J.D.; Markle, C.E.; McKeown, K.; et al. Road avoidance and its energetic consequences for reptiles. *Ecol. Evol.* **2019**, *9*, 9794–9803. [CrossRef]
- 51. D'Amico, M.; Périquet, S.; Román, J.; Revilla, E. Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *J. Appl. Ecol.* **2016**, *53*, 181–190. [CrossRef]
- 52. Brehme, C.S.; Tracey, J.A.; McClenaghan, L.R.; Fisher, R.N. Permeability of roads to movement of scrubland lizards and small mammals. *Conserv. Biol.* 2013, 27, 710–720. [CrossRef]
- 53. Robson, L.E.; Blouin-Demers, G. Eastern hognose snakes (*Heterodon platirhinos*) avoid crossing paved roads, but not unpaved roads. *Copeia* **2013**, *3*, 507–511. [CrossRef]
- Clarke, G.P.; White, P.C.L.; Harris, S. Effects of roads on badger *Meles meles* populations in south-west England. *Biol. Conserv.* 1998, 86, 117–124. [CrossRef]
- 55. Brockie, R.E.; Sadleir, R.M.F.S.; Linklater, W.L. Long-term wildlife road-kill counts in New Zealand. N. Z. J. Zool. 2009, 36, 123–134. [CrossRef]
- 56. Northrup, J.M.; Pitt, J.; Muhly, T.B.; Stenhouse, G.B.; Musiani, M.; Boyce, M.S. Vehicle traffic shapes grizzly bear behaviour on amultiple-use landscape. *J. Appl. Ecol.* **2012**, *49*, 1159–1167. [CrossRef]
- 57. Zeller, K.A.; Wattles, D.W.; Conlee, L.; Destefano, S. Response of female black bears to a high-density road network and identification of long-term road mitigation sites. *Anim. Conserv.* **2021**, *24*, 167–180. [CrossRef]
- 58. Grilo, C.; Ferreira, F.Z.; Revilla, E. No evidence of a threshold in traffic volume affecting road-kill mortality at a large spatiotemporal scale. *Environ. Impact Assess. Rev.* 2015, *55*, 54–58. [CrossRef]
- 59. Alexander, S.M.; Waters, N.M.; Paquet, P.C. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. *Can. Geogr.* **2005**, *49*, 321–331. [CrossRef]
- Zuberogoitia, I.; del Real, J.; Torres, J.J.; Rodríguez, L.; Alonso, M.; Zabala, J. Ungulate vehicle collisions in a peri-urban environment: Consequences of transportation infrastructures planned assuming the absence of ungulates. *PLoS ONE* 2014, 9, e107713. [CrossRef] [PubMed]
- 61. Jacobson, S.L.; Bliss-Ketchum, L.L.; de Rivera, C.E.; Smith, W.P. A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere* 2016, 7, e01345. [CrossRef]
- 62. van Langevelde, F.; Jaarsma, C.F. Using traffic flow theory to model traffic mortality in mammals. *Landsc. Ecol.* **2004**, *19*, 895–907. [CrossRef]
- 63. Gagnon, J.W.; Theimer, T.C.; Dodd, N.L.; Boe, S.; Schweinsburg, R.E. Traffic volume alters elk distribution and highway crossings in Arizona. *J. Wildl. Manag.* 2007, *71*, 2318–2323. [CrossRef]
- 64. Chruszcz, B.; Clevenger, A.P.; Gunson, K.E.; Gibeau, M.L. Relationships among grizzly bears, highways and habitat in the Banff-Bow Valley, Alberta, Canada. *Can. J. Zool.* **2003**, *81*, 1378–1391. [CrossRef]
- 65. Oxley, D.J.; Fenton, M.B.; Carmody, G.R. The effects of roads on populations of small mammals. J. Appl. Ecol. **1974**, 11, 51–59. [CrossRef]
- Richardson, J.H.; Shore, R.F.; Treweek, J.R.; Larkin, S.B.C. Are major roads a barrier to small mammals? J. Zool. 1997, 243, 840–846.
 [CrossRef]
- 67. Rondinini, C.; Doncaster, C.P. Roads as barriers to movement for hedgehogs. Funct. Ecol. 2002, 16, 504–509. [CrossRef]
- Clevenger, A.P.; Chruszczc, B.; Gunson, K.E. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biol. Conserv.* 2003, 109, 15–26. [CrossRef]
- 69. Goosem, M. Fragmentation impacts caused by roads through rainforests. Curr. Sci. 2007, 93, 1587–1595.
- 70. Tremblay, M.A.; St. Clair, C.C. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. *J. Appl. Ecol.* **2009**, *46*, 1314–1322. [CrossRef]
- 71. van der Ree, R.; Cesarini, S.; Sunnucks, P.; Moore, J.L.; Taylor, A. Large gaps in canopy reduce road crossing by a gliding mammal. *Ecol. Soc.* **2010**, *15*, 35. [CrossRef]

- 72. Fensome, A.G.; Mathews, F. Roads and bats: A meta-analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Rev.* 2016, 46, 311–323. [CrossRef]
- Chen, H.L.; Koprowski, J.L. Can we use body size and road characteristics to anticipate barrier effects of roads in mammals? A meta-analysis. *Hystrix* 2019, 30, 1–7. [CrossRef]
- Scrafford, M.A.; Avgar, T.; Heeres, R.; Boyce, M.S. Roads elicit negative movement and habitat-selection responses by wolverines (*Gulo gulo luscus*). *Behav. Ecol.* 2018, 29, 534–542. [CrossRef]
- 75. Waller, J.S.; Servheen, C. Effects of transportation infrastructure on grizzly bears in northwestern Montana. *J. Wildl. Manag.* 2005, 69, 985–1000. [CrossRef]
- Prokopenko, C.M.; Boyce, M.S.; Avgar, T. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. J. Appl. Ecol. 2017, 54, 470–479. [CrossRef]
- 77. Shine, R.; Lemaster, M.; Wall, M.; Langkilde, T.; Mason, R. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). *Ecol. Soc.* **2004**, *9*, *9*. [CrossRef]
- Lima, S.L.; Blackwell, B.F.; DeVault, T.L.; Fernández-Juricic, E. Animal reactions to oncoming vehicles: A conceptual review. *Biol. Rev.* 2015, 90, 60–76. [CrossRef]
- 79. Mazerolle, M.J.; Huot, M.; Gravel, M. Behavior of amphibians on the road in response to car traffic. *Herpetologica* **2005**, *61*, 380–388. [CrossRef]
- Akrim, F.; Mahmood, T.; Andleeb, S.; Hussain, R.; Collinson, W.J. Spatiotemporal patterns of wildlife road mortality in the Pothwar Plateau, Pakistan. *Mammalia* 2019, *83*, 487–495. [CrossRef]
- Lee, E.; Croft, D.B.; Ramp, D. Flight response as a causative factor in kangaroo-vehicle collisions. In *Macropods: The Biology* of Kangaroos, Wallabies and Rat-Kangaroos; Coulson, G., Eldridge, M., Eds.; CSIRO Publishing: Collingwood, Australia, 2010; pp. 301–311.
- Baigas, P.E.; Squires, J.R.; Olson, L.E.; Ivan, J.S.; Roberts, E.K. Using environmental features to model highway crossing behavior of Canada lynx in the Southern Rocky Mountains. *Landsc. Urban Plan.* 2017, 157, 200–213. [CrossRef]
- 83. Erritzoe, J.; Mazgajski, T.D.; Rejt, L. Bird casualties on European roads—A review. Acta Ornithol. 2003, 38, 77–93. [CrossRef]
- Møller, A.P.; Erritzøe, H.; Erritzøe, J. A behavioral ecology approach to traffic accidents: Interspecific variation in causes of traffic casualties among birds. Zool. Res. 2011, 32, 115–127. [CrossRef]
- 85. Medrano-Vizcaíno, P.; Grilo, C.; Pinto, F.A.S.; Carvalho, W.D.; Melinski, R.D.; Schultz, E.D.; González-Suárez, M. Roadkill patterns in Latin American birds and mammals. *Glob. Ecol. Biogeogr.* **2022**, *31*, 1756–1783. [CrossRef]
- Caceres, N.C. Biological characteristics influence mammal road kill in an Atlantic Forest-Cerrado interface in south-western Brazil. *Ital. J. Zool.* 2011, 78, 379–389. [CrossRef]
- 87. Orłowski, G. Spatial distribution and seasonal pattern in road mortality of the common toad Bufo bufo in an agricultural landscape of south-western Poland. *Amphib. Reptil.* **2007**, *28*, 25–31. [CrossRef]
- Rolandsen, C.M.; Solberg, E.J.; Herfindal, I.; Van Moorter, B.; Sæther, B. Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density? *Ecosphere* 2011, 2, 113. [CrossRef]
- 89. D'Amico, M.; Román, J.; de los Reyes, L.; Revilla, E. Vertebrate road-kill patterns in Mediterranean habitats: Who, when and where. *Biol. Conserv.* 2015, 191, 234–242. [CrossRef]
- 90. Ascensão, F.; Desbiez, A.L.J.; Medici, E.P.; Bager, A. Spatial patterns of road mortality of medium-large mammals in Mato Grosso do Sul, Brazil. *Wildl. Res.* 2017, 44, 135–146. [CrossRef]
- 91. Saint-Andrieux, C.; Calenge, C.; Bonenfant, C. Comparison of environmental, biological and anthropogenic causes of wildlifevehicle collisions among three large herbivore species. *Popul. Ecol.* **2020**, *62*, 64–79. [CrossRef]
- 92. Ford, A.T.; Fahrig, L. Diet and body size of North American mammal road mortalities. *Transp. Res. Part D Transp. Environ.* 2007, 12, 498–505. [CrossRef]
- Eloff, P.; van Niekerk, A. Temporal patterns of animal-related traffic accidents in the Eastern Cape, South Africa. S. Afr. J. Wildl. Res. 2008, 38, 153–162. [CrossRef]
- Barrientos, R.; Bolonio, L. The presence of rabbits adjacent to roads increases polecat road mortality. *Biodivers. Conserv.* 2009, 18, 405–418. [CrossRef]
- 95. Barthelmess, E.L.; Brooks, M.S. The influence of body-size and diet on road-kill trends in mammals. *Biodivers. Conserv.* 2010, 19, 1611–1629. [CrossRef]
- 96. Cook, T.C.; Blumstein, D.T. The omnivore's dilemma: Diet explains variation in vulnerability to vehicle collision mortality. *Biol. Conserv.* **2013**, *167*, 310–315. [CrossRef]
- Planillo, A.; Mata, C.; Manica, A.; Malo, J.E. Carnivore abundance near motorways related to prey and roadkills. *J. Wildl. Manag.* 2018, 82, 319–327. [CrossRef]
- Hill, J.E.; DeVault, T.L.; Belant, J.L. Research note: A 50-year increase in vehicle mortality of North American mammals. *Landsc.* Urban Plan. 2020, 197, 103746. [CrossRef]
- Jamhuri, J.; Edinoor, M.A.; Kamarudin, N.; Lechner, A.M.; Ashton-Butt, A.; Azhar, B. Higher mortality rates for large- and medium-sized mammals on plantation roads compared to highways in Peninsular Malaysia. *Ecol. Evol.* 2020, 10, 12049–12058. [CrossRef]
- Morelli, F.; Rodríguez, R.A.; Benedetti, Y.; Delgado, J.D. Avian roadkills occur regardless of bird evolutionary uniqueness across Europe. *Transp. Res. Part D Transp. Environ.* 2020, 87, 102531. [CrossRef]

- 101. Pfeiffer, M.B.; Iglay, R.B.; Seamans, T.W.; Blackwell, B.F.; DeVault, T.L. Deciphering interactions between white-tailed deer and approaching vehicles. *Transp. Res. Part D Transp. Environ.* **2020**, *79*, 102251. [CrossRef]
- 102. Clevenger, A.P.; Chruszcz, B.; Gunson, K.E. Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildl. Soc. B.* 2001, 29, 646–653.
- Lee, E.; Klöcker, U.; Croft, D.B.; Ramp, D. Kangaroo-vehicle collisions in Australia's sheep rangelands, during and following drought periods. *Aust. Mammal.* 2004, 26, 215–226. [CrossRef]
- 104. Malo, J.E.; Suárez, F.; Díez, A. Can we mitigate animal-vehicle accidents using predictive models? J. Appl. Ecol. 2004, 41, 701–710. [CrossRef]
- Aresco, M.J. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a North Florida lake. J. Wildl. Manag. 2005, 69, 549–560. [CrossRef]
- 106. Orłowski, G. Roadside hedgerows and trees as factors increasing road mortality of birds: Implications for management of roadside vegetation in rural landscapes. *Landsc. Urban Plan.* **2008**, *86*, 153–161. [CrossRef]
- Colino-Rabanal, V.J.; Lizana, M.; Peris, S.J. Factors influencing wolf *Canis lupus* roadkills in Northwest Spain. *Eur. J. Wildl. Res.* 2011, 57, 399–409. [CrossRef]
- Found, R.; Boyce, M.S. Predicting deer-vehicle collisions in an urban area. J. Environ. Manag. 2011, 92, 2486–2493. [CrossRef]
 [PubMed]
- 109. Lao, Y.; Wu, Y.; Corey, J.; Wang, Y. Modeling animal-vehicle collisions using diagonal inflated bivariate Poisson regression. *Accid. Anal. Prev.* **2011**, *43*, 220–227. [CrossRef]
- 110. Seshadri, K.S.; Ganesh, T. Faunal mortality on roads due to religious tourism across time and space in protected areas: A case study from south India. *For. Ecol. Manag.* **2011**, *262*, 1713–1721. [CrossRef]
- 111. Bissonette, J.A.; Rosa, S. An evaluation of a mitigation strategy for deer-vehicle collisions. Wildl. Biol. 2012, 18, 414–423. [CrossRef]
- 112. Coelho, I.P.; Teixeira, F.Z.; Colombo, P.; Coelho, A.V.P.; Kindel, A. Anuran road-kills neighboring a peri-urban reserve in the Atlantic Forest, Brazil. *J. Environ. Manag.* **2012**, *112*, 17–26. [CrossRef]
- Clevenger, A.P.; Kociolek, A.V. Potential impacts of highway median barriers on wildlife: State of the practice and gap analysis. *Environ. Manag.* 2013, 52, 1299–1312. [CrossRef]
- 114. Cserkész, T.; Ottlecz, B.; Cserkész-Nagy, Á.; Farkas, J. Interchange as the main factor determining wildlife-vehicle collision hotspots on the fenced highways: Spatial analysis and applications. *Eur. J. Wildl. Res.* **2013**, *59*, 587–597. [CrossRef]
- 115. Barthelmess, E.L. Spatial distribution of road-kills and factors influencing road mortality for mammals in Northern New York State. *Biodivers. Conserv.* 2014, 23, 2491–2514. [CrossRef]
- 116. Meisingset, E.L.; Loe, L.E.; Brekkum, Ø.; Mysterud, A. Targeting mitigation efforts: The role of speed limit and road edge clearance for deer-vehicle collisions. *J. Wildl. Manag.* **2014**, *78*, 679–688. [CrossRef]
- 117. Baxter-Gilbert, J.H.; Riley, J.L.; Lesbarrères, D.; Litzgus, J.D. Mitigating reptile road mortality: Fence failures compromise ecopassage effectiveness. *PLoS ONE* **2015**, *10*, e0120537. [CrossRef] [PubMed]
- 118. Gagné, S.A.; Bates, J.L.; Bierregaard, R.O. The effects of road and landscape characteristics on the likelihood of a Barred Owl (*Strix varia*)-vehicle collision. *Urban Ecosyst.* **2015**, *18*, 1007–1020. [CrossRef]
- 119. Valero, E.; Picos, J.; Álvarez, X. Road and traffic factors correlated to wildlife–vehicle collisions in Galicia (Spain). *Wildl. Res.* **2015**, 42, 25–34. [CrossRef]
- 120. Huijser, M.P.; Fairbank, E.R.; Camel-Means, W.; Graham, J.; Watson, V.; Basting, P.; Becker, D. Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife-vehicle collisions and providing safe crossing opportunities for large mammals. *Biol. Conserv.* **2016**, *197*, 61–68. [CrossRef]
- 121. Ranapurwala, S.I.; Mello, E.R.; Ramirez, M.R. A GIS-based matched case-control study of road characteristics in farm vehicle crashes. *Epidemiology* **2016**, *27*, 827–834. [CrossRef]
- 122. Rytwinski, T.; Soanes, K.; Jaeger, J.A.G.; Fahrig, L.; Findlay, C.S.; Houlahan, J.; van der Ree, R.; van der Grift, E.A. How effective is road mitigation at reducing road-kill? A meta-analysis. *PLoS ONE* **2016**, *11*, e0166941. [CrossRef]
- 123. Bitušík, P.; Kocianová-Adamcová, M.; Brabec, J.; Malina, R.; Tesák, J.; Urban, P. The effects of landscape structure and road topography on mortality of mammals: A case study of two different road types in Central Slovakia. *Lynx Ser. Nova* 2017, 48, 39–51. [CrossRef]
- Colley, M.; Lougheed, S.C.; Otterbein, K.; Litzgus, J.D. Mitigation reduces road mortality of a threatened rattlesnake. Wildl. Res. 2017, 44, 48–59. [CrossRef]
- 125. Markle, C.E.; Gillingwater, S.D.; Levick, R.; Chow-Fraser, P. The true cost of partial fencing: Evaluating strategies to reduce reptile road mortality. *Wildl. Soc. Bull.* 2017, 41, 342–350. [CrossRef]
- 126. Bíl, M.; Andrášik, R.; Dul'a, M.; Sedoník, J. On reliable identification of factors influencing wildlife-vehicle collisions along roads. J. Environ. Manag. 2019, 237, 297–304. [CrossRef] [PubMed]
- Boyle, S.P.; Dillon, R.; Litzgus, J.D.; Lesbarrères, D. Desiccation of herpetofauna on roadway exclusion fencing. *Can. Field Nat.* 2019, 133, 43–48. [CrossRef]
- Canal, D.; Camacho, C.; Martin, B.; de Lucas, M.; Ferrer, M. Fine-scale determinants of vertebrate roadkills across a biodiversity hotspot in Southern Spain. *Biodivers. Conserv.* 2019, 28, 3239–3256. [CrossRef]
- 129. Dean, W.R.J.; Seymour, C.L.; Joseph, G.S.; Foord, S.H. A review of the impacts of roads on wildlife in semi-arid regions. *Diversity* **2019**, *11*, 81. [CrossRef]

- 130. Kreling, S.E.S.; Gaynor, K.M.; Coon, C.A.C. Roadkill distribution at the wildland-urban interface. *J. Wildl. Manag.* 2019, *83*, 1427–1436. [CrossRef]
- Plante, J.; Jaeger, J.A.G.; Desrochers, A. How do landscape context and fences influence roadkill locations of small and mediumsized mammals? J. Environ. Manag. 2019, 235, 511–520. [CrossRef]
- Galantinbo, A.; Santos, S.; Eufrázio, S.; Silva, C.; Carvalho, F.; Alpizar-Jara, R.; Mira, A. Effects of roads on small-mammal movements: Opportunities and risks of vegetation management on roadsides. J. Environ. Manag. 2022, 316, 115272. [CrossRef]
- 133. van der Ree, R.; Gagnon, J.W.; Smith, D.J. Fencing: A valuable tool for reducing wildlife-vehicle collisions and funnelling fauna to crossing structures. In *Handbook of Road Ecology*; van der Ree, R., Smith, D.J., Grilo, C., Eds.; John Wiley & Sons: Hoboken, NJ, USA, 2015; pp. 159–171.
- 134. Mazerolle, M.J. Amphibian road mortality in response to nightly variations in traffic intensity. *Herpetologica* **2004**, *60*, 45–53. [CrossRef]
- 135. Seiler, A. Predicting locations of moose-vehicle collisions in Sweden. J. Appl. Ecol. 2005, 42, 371–382. [CrossRef]
- 136. Grilo, C.; Bissonette, J.A.; Santos-Reis, M. Spatial-temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. *Biol. Conserv.* 2009, 142, 301–313. [CrossRef]
- 137. Kušta, T.; Keken, Z.; Ježek, M.; Holá, M.; Šmid, P. The effect of traffic intensity and animal activity on probability of ungulatevehicle collisions in the Czech Republic. *Saf. Sci.* **2017**, *91*, 105–113. [CrossRef]
- 138. Teixeira, F.Z.; Kindel, A.; Hartz, S.M.; Mitchell, S.; Fahrig, L. When road-kill hotspots do not indicate the best sites for road-kill mitigation. *J. Appl. Ecol.* 2017, *54*, 1544–1551. [CrossRef]
- 139. Husby, M. Factors affecting road mortality in birds. Ornis Fenn. 2016, 93, 212–224.
- 140. Ashley, E.P.; Robinson, J.T. Road mortality of amphibians, reptiles and other wildlife on the long point causeway, Lake Erie, Ontario. *Can. Field Nat.* **1996**, *110*, 403–412.
- 141. Ramp, D.; Caldwell, J.; Edwards, K.A.; Warton, D.; Croft, D.B. Modelling of wildlife fatality hotspots along the snowy mountain highway in New South Wales, Australia. *Biol. Conserv.* 2005, *126*, 474–490. [CrossRef]
- 142. Farrell, M.C.; Tappe, P.A. County-level factors contributing to deer-vehicle collisions in Arkansas. *J. Wildl. Manag.* 2007, 71, 2727–2731. [CrossRef]
- Sudharsan, K.; Riley, S.J.; Campa III, H. Relative risks of deer-vehicle collisions along road types in Southeast Michigan. *Hum. Dimens. Wildl.* 2009, 14, 341–352. [CrossRef]
- 144. Gunson, K.E.; Mountrakis, G.; Quackenbush, L.J. Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. *J. Environ. Manag.* **2011**, *92*, 1074–1082. [CrossRef]
- 145. Neumann, W.; Ericsson, G.; Dettki, H.; Bunnefeld, N.; Keuler, N.S.; Helmers, D.P.; Radeloff, V.C. Difference in spatiotemporal patterns of wildlife road-crossings and wildlife vehicle collisions. *Biol. Conserv.* **2012**, *145*, 70–78. [CrossRef]
- Puig, J.; Ariño, A.H.; Sanz, L. The link between roadkills distribution and the surrounding landscape in two highways in Navarre, Spain. *Environ. Eng. Manag. J.* 2012, *11*, 1171–1178. [CrossRef]
- McCance, E.C.; Baydack, R.K.; Walker, D.J.; Leask, D.N. Spatial and temporal analysis of factors associated with urban deer-vehicle collisions. *Hum. Wildl. Interact.* 2015, 9, 119–131. [CrossRef]
- 148. Finder, R.A.; Roseberry, J.L.; Woolf, A. Site and landscape conditions at white-tailed deer/vehicle collision locations in Illinois. *Landsc. Urban Plan.* **1999**, 44, 77–85. [CrossRef]
- 149. Borkovcová, M.; Mrtka, J.; Winkler, J. Factors affecting mortality of vertebrates on the roads in the Czech Republic. *Transp. Res. Part D Transp. Environ.* **2012**, 17, 66–72. [CrossRef]
- 150. Dussault, C.; Poulin, M.; Courtois, R.; Ouellet, J. Temporal and spatial distribution of moose-vehicle accidents in the Laurentides Wildlife Reserve, Quebec, Canada. *Wildl. Biol.* **2006**, *12*, 415–425. [CrossRef]
- 151. Langen, T.A.; Machniak, A.; Crowe, E.K.; Mangan, C.; Marker, D.F.; Liddle, N.; Roden, B. Methodologies for surveying herpetofauna mortality on rural highways. *J. Wildl. Manag.* **2007**, *71*, 1361–1368. [CrossRef]
- Ramp, D.; Roger, E. Frequency of animal-vehicle collisions in NSW. In *Too Close for Comfort: Contentious Issues in Human-Wildlife Encounters*; Lunney, D., Munn, A., Meikle, W., Eds.; Royal Zoological Society of New South Wales: Sydney, Australia, 2008; pp. 118–126.
- 153. Shepard, D.B.; Dreslik, M.J.; Jellen, B.C.; Phillips, C.A. Reptile road mortality around an oasis in the Illinois corn desert with emphasis on the endangered Eastern Massasauga. *Copeia* 2008, 2008, 350–359. [CrossRef]
- 154. Carvalho, C.F.; Custódio, A.E.I.; Júnior, O.M. Influence of climate variables on roadkill rates of wild vertebrates in the cerrado biome, Brazil. *Biosci. J.* 2017, *33*, 1632–1641. [CrossRef]
- 155. Colino-Rabanal, V.J.; Langen, T.A.; Peris, S.J.; Lizana, M. Ungulate: Vehicle collision rates are associated with the phase of the moon. *Biodivers. Conserv.* 2018, 27, 681–694. [CrossRef]
- 156. Lee, E. The Ecological Effects of Sealed Roads in Arid Ecosystems. Ph.D. Thesis, University of New South Wales, Sydney, Australia, 2006.
- 157. Morelle, K.; Lehaire, F.; Lejeune, P. Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network. *Nat. Conserv.* 2013, *5*, 53–73. [CrossRef]
- 158. Chen, X.; Wu, S. Examining patterns of animal-vehicle collisions in Alabama, USA. *Hum. Wildl. Interact.* **2014**, *8*, 235–244. [CrossRef]

- 159. Steiner, W.; Leisch, F.; Hackländer, K. A review on the temporal pattern of deer-vehicle accidents: Impact of seasonal, diurnal and lunar effects in cervids. *Accid. Anal. Prev.* 2014, *66*, 168–181. [CrossRef]
- 160. Garrah, E.; Danby, R.K.; Eberhardt, E.; Cunnington, G.M.; Mitchell, S. Hot spots and hot times: Wildlife road mortality in a regional conservation corridor. *Environ. Manag.* 2015, *56*, 874–889. [CrossRef]
- Kazemi, V.D.; Jafari, H.; Yavari, A. Spatio-temporal patterns of wildlife road mortality in Golestan national park-north east of Iran. Open J. Ecol. 2016, 6, 312–324. [CrossRef]
- 162. Özcan, A.U.; Özkazanç, N.K. Identifying the hotspots of wildlife-vehicle collision on the Çankırı-kırıkkale highway during summer. *Turk. J. Zool.* 2017, *41*, 722–730. [CrossRef]
- 163. Laliberté, J.; St-Laurent, M. In the wrong place at the wrong time: Moose and deer movement patterns influence wildlife-vehicle collision risk. *Accid. Anal. Prev.* 2020, *135*, 105365. [CrossRef]
- 164. Joyce, T.L.; Mahoney, S.P. Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. *Wildl. Soc. Bull.* **2001**, 29, 281–291.
- 165. Ashley, E.P.; Kosloski, A.; Petrie, S.A. Incidence of intentional vehicle-reptile collisions. *Hum. Dimens. Wildl.* **2007**, *12*, 137–143. [CrossRef]
- 166. Beckmann, C.; Shine, R. Do drivers intentionally target wildlife on roads? Austral Ecol. 2012, 37, 629–632. [CrossRef]
- Kioko, J.; Kiffner, C.; Phillips, P.; Patterson-Abrolat, C.; Collinson, W.; Katers, S. Driver knowledge and attitudes on animal vehicle collisions in Northern Tanzania. *Trop. Conserv. Sci.* 2015, *8*, 352–366. [CrossRef]
- Crawford, B.A.; Andrews, K.M. Drivers' attitudes toward wildlife-vehicle collisions with reptiles and other taxa. *Anim. Conserv.* 2016, 19, 444–450. [CrossRef]
- 169. Wang, Y.; Qu, J.; Han, Y.; Du, L.; Wang, M.; Yang, Y.; Cao, G.; Tao, S.; Kong, Y. Impacts of linear transport infrastructure on terrestrial vertebrate species and conservation in China. *Glob. Ecol. Conserv.* **2022**, *38*, e02207. [CrossRef]

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