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Review

Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects

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ABSTRACT

In addition to posing a serious risk to motorist safety, vehicle collisions with wildlife are a significant threat for many species. Previous spatial modeling has concluded that wildlife-vehicle collisions (WVCs) exhibit clustering on roads, which is attributed to specific landscape and road-related factors. We reviewed twenty-four published manuscripts that used generalized linear models to statistically determine the influence that numerous explanatory predictors have on the location of WVCs. Our motivation was to summarize empirical WVC findings to facilitate application of this knowledge to planning, and design of mitigation strategies on roads. In addition, commonalities between studies were discussed and recommendations for future model design were made. We summarized the type and measurement of each significant predictor and whether they potentially increased or decreased the occurrence of collisions with ungulates, carnivores, small-medium vertebrates, birds, and amphibians and reptiles. WVCs commonly occurred when roads bisect favorable cover, foraging, or breeding habitat for specific species or groups of species. WVCs were generally highest on road sections with high traffic volumes, or low motorist visibility, and when roads cut through drainage movement corridors, or level terrain. Ungulates, birds, small-medium vertebrates, and carnivore collision locations were associated with road-side vegetation and other features such as salt pools. In several cases, results were spurious due to confounding and interacting predictors within the same model. For example, WVCs were less likely to occur when a road bisected steep slopes; however, steep slopes may be located along specific road-types and habitat that also influence the occurrence of WVCs. In conclusion, this review showed that much of the current literature has gleaned the obvious, broad-scale relationships between WVCs and predictors from available data sets, and localized studies can provide unique and novel results. Future research requires specific modeling for each target species on a road-by-road basis, and measuring the predictive power of model results within similar landscapes. In addition, research that builds on the current literature by investigating rare anomalies and interacting variables will assist in providing sound comprehensive guidelines for wildlife mitigation planning on roads.

1. Introduction

As traffic volumes increase and roads permeate more and more natural areas, wildlife and vehicles often collide, becoming a prominent socio-economic and traffic safety issue (Hughes et al., 1996). For example, collisions with large mammals such as deer (*Odocoieus* spp.), moose (*Alces alces*) and elk (*Cervus elaphus*) occur at alarming rates in many regions of North America and Europe, increasing the risk of human and wildlife injury and fatality (Joyce and Mahoney, 2001; Bruinderink and Hazebroek, 1996; Bissonette et al., 2008). Conover et al. (1995) estimates that more than 1 million deer collide with vehicles each year in the United States and costs accumulate as a result of vehicular damage, loss of wildlife, and human injury and fatality (Bissonette et al., 2008).

Road ecologists have used available georeferenced locations of wildlife-vehicle collisions (WVCs) to determine distribution patterns along roads (Puglisi et al., 1974; Krisp and Durot, 2007; Ramp et al., 2005, 2006; Mountrakis and Gunson, 2009). These analyses have indicated that WVCs along roads are not random occurrences but are spatially clustered for vertebrate species, including ungulates (Puglisi et al., 1974; Hubbard et al., 2000; Joyce and Mahoney, 2001) and other vertebrate fauna (Clevenger et al., 2003; Ramp et al., 2006).

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As a result, road ecologists have used statistical modeling to determine what landscape-related characteristics, i.e., factors that influence animal distribution, abundance, and dispersal habits surrounding roads (Joyce and Mahoney, 2001; Malo et al., 2004; Dussault et al., 2006; Barrientos and Bolonio, 2009), as well as road-related predictors such as traffic volumes, road alignment, and road-side topography (Clevenger et al., 2003; Jaarsma et al., 2007; Barrientos and Bolonio, 2009) influence the risk of WVCs.

This information is useful to guide transportation professionals in the placement and design of relatively permanent mitigation structures, such as wildlife overpasses and underpasses with fencing, as well as less permanent measures such as seasonal wildlife signage, reduced speed limits, wildlife warning reflectors, road-side vegetation management, speed bumps, and public awareness programs (Pojar et al., 1975; Putman, 1997; Joyce and Mahoney, 2001; Al-Ghamdi and AlGadhi, 2004; Krisp and Durot, 2007). Research has shown that wildlife overpasses and underpasses with fencing have reduced WVCs and enabled large ungulate species (Clevenger and Waltho, 2000; Foster and Humphrey, 1995; Dodd et al., 2007; Mata et al., 2008) and smaller animals (Dodd et al., 2004; Woltz et al., 2008; Mata et al., 2008) to cross roads safely. The use of less permanent measures, such as wildlife signage, is still relatively experimental and their effectiveness is uncertain (Romin and Bissonette, 1996; D'Angelo et al., 2006; Huijser et al., 2007).

The next step is to integrate wildlife mitigation research and knowledge early into the road planning process. In the United States, policy has been developed that allows resource practitioners to participate in identifying road impacts on wildlife and ecosystems up to twenty years before the development and implementation phase of a new road, (see http://www.wildlifeandroads.org). Identified mitigation measures are then integrated into new road planning projects typically through the environmental impact assessment process. Alternatively, mitigation can be integrated post-road construction as new wildlife-motorist conflicts are identified.

We reviewed twenty-four published studies that examined the explanatory factors that influence WVCs to assess how current empirical results can be applied to mitigation planning, placement and design for wildlife on roads. Other motives were to examine common and novel results among studies and to identify to practical research needs. We also provide recommendations for alternate model designs that may be more applicable to mitigation planning. Research is occurring at a heightened pace (e.g., six of the reviewed studies published in 2009) alongside an increasing number of WVCs, emphasizing the need for novel solutions that will alleviate the negative impacts of roads on wildlife.

2. Methods

We reviewed 24 studies that used generalized linear models (GLMs), e.g., logistic or multiple regression, to quantitatively analyze the influence of environmental predictors on the response variable (WVC locations). The response variable refers to either an observed or random site-specific location or a density measurement for a defined length of road, e.g., 1 km. We limited our review to these studies as they provided the majority of empirical findings in the field and provided standardized methodology for comparisons between studies, i.e., all studies examined the interactions between predictors.

For each study we first assessed the significant predictors in each model and classified them as Landscape or Road-related. Landscape-level predictors measured wildlife behavior and distribution surrounding the road, e.g., habitat proportion in the road vicinity. Road-related predictors were features that influence the risk of a WVC when an animal is within the road verge or on the road, e.g. traffic volume.

We then determined the target species for each GLM model. In the case that a model was developed for a species group, e.g., several bird species, we used the dominant road-killed species as the target species. We classified each species into the following categories: (a) Ungulates, (b) Carnivores, (c) Small-medium Vertebrates, (d) Birds, and (e) Amphibians and Reptiles. Within each species group we listed all significant landscape-related predictors and classified them into the following groups: Forest (e.g., wooded areas), Open areas (e.g., grasslands), Urban areas (e.g., buildings or campgrounds), Agriculture, Open water (e.g., dams, lakes, wetlands), Landscape diversity, Public land (e.g., dispersion of natural areas), Species-specific habitat use (i.e., presence of landscape element utilized by a species) and Elevation. In addition we listed any significant Road-related predictor and classified them into the following groups: Road-side topography, Road-side vegetation, Jersey barrier or Guard-rail, Visibility/Curvature, Traffic volume/Speed limit, Road Pavement Width, Fencing, Crossing Structures, Reflectors, Median, Road Corridor, and Riparian Corridor. The presence of a bridge was included in the Riparian Corridor group.

We then defined each significant predictor by its type (presence, index, size, area, count, proportion, or proximity) and the scale of measurement when available (i.e., the buffer radius used to measure proportions). We also summarized whether the presence, proximity, higher proportion or count of the predictor surrounding the road potentially increased (+) or decreased (−) the number of WVCs. WVCs increased as proximity predictors, i.e., measured by the distance of a feature to a WVC, neared the collision site. For further interpretation about predictor type or its influence on wildlife collisions we referred to the discussions in each paper for clarification.

We focused our review on summarizing predictors that were deemed significant both statistically and through the author's discussion to provide a resource for transportation planners, resource agencies, and road ecologists. We then gleaned the most important results from the summary that could be applied to mitigation planning. We did not explicitly list non-significant predictors to maintain a suitable manuscript length and level of complexity for the intended audience, i.e. transportation planners. Instead, when pertinent we tallied the number of studies that included a predictor but perhaps surprisingly did not obtain a significant result.

3. Results

3.1. Landscape-related predictors

Table 1 shows a summary of the significant landscape predictors that influenced vehicle collisions with (a) Ungulates, (b) Carnivores, (c) Small-medium Vertebrates, (d) Birds, and (e) Amphibians and Reptiles. For simplicity, we described each significant predictor as increasing or decreasing the occurrence of WVCs although the cause and effect relationship may be more complex than this, i.e., several interacting variables contributing to this outcome. Forest and open habitat surrounding roads increased the number of ungulate collisions and agriculture and urban areas surrounding roads decreased the number of collisions. All seven studies that included landscape diversity in their models found it increased ungulate-vehicle collisions. Two studies found ungulate collisions increased when public land patches surrounded roads. One study found open water decreased the occurrence of moose-vehicle collisions (Table 1a).

Contrary to the ungulate group, it is difficult to generalize the predictors that influence vehicle collisions within the other species group, due to small sample size and the varying species-specific habitat requirements within their associated landscapes. However, there were some note-worthy commonalities between and within groups. The majority of the studies found the presence of urban

Table 1
Description of significant landscape-related predictors that increase (+) or decrease (−) the occurrence of wildlife-vehicle collisions. Predictors are first arranged by species group, second by predictor group, third by the influence (+ or −) that each feature has on wildlife-vehicle collisions, and last alphabetically by author.

Target species	Predictor description	+/−	Source
a.Ungulates			
Forest			
White-tailed Deer (*Odocoileus virginianus*)	Proximity to woodland greater than 0.8 km^2 or to tree lines connecting woodlands	+	Bashore et al., 1985
White-tailed Deer	Proximity to forest cover greater than 200 m	+	Finder et al., 1999
White-tailed Deer and Mule Deer (*Odocoileus hemionus*)	Density and size of forest (800 m)[a]	+	Finder et al., 1999
White-tailed Deer and Mule Deer	Presence of coniferous forest at kill site	+	Gunson et al., 2009
White-tailed Deer	Amount of woody patches with interior areas greater than 50 m from edge (800 m)	+	Hubbard et al., 2000
Roe Deer (*Capreolus capreolus L.*), Wild Boar (*Sus scrofa L.*), and Red Deer (*Cervus elaphus L.*)	Proportion of non-riparian forest cover (1000 m)	+	Malo et al., 2004
Roe Deer, Wild Boar, and Red Deer	Proximity to forest stand	+	Malo et al., 2004
Moose (*Alces alces*)	Proportion of coniferous forest (500 m)	+	Seiler, 2005
Moose	Proportion of deciduous forest (500 m)	+	Seiler, 2005
Moose	Proximity to forest edge	+	Seiler, 2005
Open areas			
White-tailed Deer	Size of grass patches (800 m)	+	Hubbard et al., 2000
Moose	Proportion open area (500 m)	+	Seiler, 2005
Open water			
Moose	Proportion wetlands (500 m)	−	Seiler, 2005
Agriculture			
White-tailed Deer	Proportion of crop fields, weighted by area and shape index (800 m)	−	Hubbard et al., 2000
Moose	Proportion agriculture (500 m)	−	Seiler, 2005
Urban areas			
White-tailed Deer	Area (ha) residences and commercial buildings	−	Bashore et al., 1985
Roe Deer, Wild Boar, and Red Deer	Proportion urban (1000 m)	−	Malo et al., 2004
White-tailed Deer and Mule Deer	Count of buildings (100 m)	−	Nielsen et al., 2003
Moose	Proportion urban areas (500 m)	−	Seiler, 2005
Landscape diversity			
White-tailed Deer	Count non-wooded; woody plant (<2 m tall), herbaceous vegetation and agricultural crops	+	Bashore et al., 1985
White-tailed Deer	Simpson diversity index (800 m)	+	Finder et al., 1999
White-tailed Deer and Mule Deer	Presence open-forest mix relative to open habitat	+	Gunson et al., 2009
Roe Deer, Wild Boar, and Red Deer	Shannon diversity index, forest and open habitat (1000 m)	+	Malo et al., 2004
White-tailed Deer and Mule Deer	Shannon diversity index (100 m)	+	Nielsen et al., 2003
White-tailed Deer	Presence of ecotone-one side of highway wooded, other side a field	+	Puglisi et al., 1974
Moose	Length land cover type edges (500 m)	+	Seiler, 2005
Moose	Count of intersections with forest edges	−	Seiler, 2005
Public land patches			
White-tailed Deer	Proportion public recreational land, e.g. wooded habitat (800 m)	+	Finder et al., 1999
White-tailed Deer and Mule Deer	Number patches of public land (mixed forest, shrub, grassland and wetland) (100 m)	+	Nielsen et al., 2003
Species-specific habitat use			
Moose	Presence brackish pools with moose utilization; salinity $\geq$ 300 ppm	+	Dussault et al., 2006
b. Carnivores			
Forest			
Stone Marten (*Martes foina*)	Percentage cork oak woodland at road-side	+	Grilo et al., 2009
Urban areas			
Hedgehog spp (*Erinaceus* spp.)	Percent built-up area along road	+	Orlowski and Nowak, 2006
European Polecat (*Mustela putorius L.*)	Proximity isolated house	−	Barrientos and Bolonio, 2009
Eurasian Badger (*Meles meles*)	Proportion urban area (500 m)	−	Grilo et al., 2009
Eurasian Badger	Proximity to other road(s)	−	Grilo et al., 2009
Red Fox (*Vulpes vulpes*)	Proportion urban area (500 m)	−	Grilo et al., 2009
Species-specific habitat use			
European Polecat	Proximity of rabbit burrow	+	Barrientos and Bolonio, 2009
c. Small-medium vertebrates			
Forest			
Opossum (*Didelphis virginiana*)	Area (m^2) forest/wood lot per 100 × 200 m section	+	Glista et al., 2007
Swamp Wallaby (*Wallabia bicolour*)	Proportion forest (704 m)	+	Ramp et al., 2005
Red-necked Wallaby (*Macropus rufogriseus*)	Proportion forest (704 m)	+	Ramp et al., 2005
Virginia Opossum (*Didelphis virginiana*)	Percentage forest (200 m)	−	Kanda et al., 2006
Eastern Grey Kangaroo (*Macropus giganteus*)	Proportion forest (714 m)	−	Ramp et al., 2005

Table 1 (*continued*)

Target species	Predictor description	+/−	Source
Common Wombat (*Vombatus ursinus*)	Proportion forest (320 m)	−	Roger and Ramp, 2009
Open areas			
Common Vole (*Microtus arvalis*) and Striped Field Mouse (*Apodemus agrarius*)	Percent open countryside along road	+	Orlowski and Nowak, 2006
Open water			
Kangaroo, Wombat, Feral animals e.g. European rabbit (*Oryctolagus cuniculus*)	Proximity to body of water, e.g. dam	+	Ramp et al., 2005
Urban areas			
Striped Field Mouse	Percent built-up along road	−	Orlowski and Nowak, 2006
Kangaroo, Wallaby, Wombat, Feral animals	Proximity to town	−	Ramp et al., 2005
Landscape diversity			
Common Wombat	Normalized difference vegetation index, higher values: mixed forest and grassland; lower values: pure forest and grassland	+	Roger and Ramp, 2009
Species-specific habitat use			
Common Wombat	Proximity of blackberry bush	+	Roger and Ramp, 2009
Common Wombat	Proximity of wombat burrow	+	Roger and Ramp, 2009
Common Wombat	Clustering of abandoned wombat burrows	+	Roger and Ramp, 2009
Common Wombat	Clustering of occupied wombat burrows	−	Roger and Ramp, 2009
Elevation			
Common Raven (*Corvus corax*)	GPS Elevation	−	Clevenger et al., 2003
Snowshoe Hare (*Lepus americanus*)	GPS Elevation	−	Clevenger et al., 2003
Virginia Opossum	Elevation contour	−	Kanda et al., 2006
Common Wombat	Elevation index (320 m)	−	Ramp et al., 2005
d. Birds			
Forest			
Tawny Owl (*Strix aluco*)	Proportion of cork oak forests (250 m)	+	Gomes et al., 2009
Barn Owl (*Tyto alba*)	Proportion pine plantation (250 m)	−	Gomes et al., 2009
Open water			
Barn Owl	Presence of permanent pond and reservoir (500 m)	+	Gomes et al., 2009
Tawny Owl	Presence of permanent pond and reservoir (500 m)	+	Gomes et al., 2009
Birds	Proximity to body of water, e.g. dam	+	Ramp et al., 2005
Agriculture			
Little Owl (*Athene noctua*)	Proportion of cereal crops (250 m)	+	Gomes et al., 2009
Barn Swallow (*Hirundo rustica*)	Number of reared cattle and livestock	+	Orlowski, 2005
Urban areas			
Little Owl	Proximity to localities (>100 inhabitants)	+	Gomes et al., 2009
Barn Swallow	Number of inhabitants	+	Orlowski, 2005
Barn Owl	Proportion urban area (250 m)	−	Gomes et al., 2009
Mixed habitat			
Common Raven	Presence open-forest mix and forest relative to open habitat	−	Clevenger et al., 2003
e. Amphibians and Reptiles			
Forest			
Ranids (*Ranid* spp.) and Common Garter Snake (*Thamnophis sirtalis*)	Area (m^2) forest/wood lot per 100 × 200 m section	+	Glista et al., 2007
Open water			
Ranids and Common Garter Snake	Area (m^2) water/wetlands (100 × 200 m)	+	Glista et al., 2007
Northern Leopard Frog (*Lithobates pipiens*) and Painted Turtle (*Chrysemys picta*)	Proportion of wetland (100 m)	+	Langen et al., 2009
Northern Leopard Frog and Painted Turtle	Presence of causeway (paired wetland on opposite sides of the road within 100 m)	+	Langen et al., 2009
Urban area			
Ranids and Common Garter Snake	Area (m^2) urban/residential (100 × 200 m)	−	Glista et al., 2007
Mixed habitat			
Common Garter Snake and Pond Slider (*Trachemys scripta*)	Presence of high, natural or semi-natural habitat	+	Shepard et al., 2008

[a] Refers to the buffer radius surrounding the WVC location.

areas decreased the risk of wildlife-vehicle collisions (Table 1), with the exception of two species, the Little Owl (*Athene noctua*) and Barn Swallow (*Hirundo rustica*), where urban areas increased the number of collisions (Table 1d). The number of non-ungulate vertebrate collisions increased with the presence of open water (Table 1b–e). Within the small-medium vertebrate group collisions increased for four species at low elevations (Table 1c). Three studies found a unique relationship between a species-specific habitat use and wildlife-vehicle collisions, i.e., presence of brackish pools increased the risk of moose-vehicle collisions, rabbit burrows increased the risk of European-Polecat collisions, and blackberry bushes and wombat burrows increased the risk of vehicle collisions with wombats (Table 1a–c).

3.2. *Road-related predictors associated with wildlife-vehicle collisions*

Table 2 summarizes the influence of Road-related predictors on vehicle collisions with (a) Ungulates, (b) Carnivores, (c) Small-medium vertebrates, and (d) Birds. Generally, flat terrain, increased traffic volumes and speed limits, increased road width, decreased visibility, and the presence of riparian and road corridors increased

Table 2
Description of significant road-related predictors that increase (+) or decrease (−) the occurrence of wildlife-vehicle collisions. Predictors are first arranged by species group, second by predictor group, third by the influence (+/−) that each factor has on wildlife-vehicle collisions, and last alphabetically by author.

Target species	Predictor	+/−	Source
a.Ungulates			
Road-side topography			
White-tailed Deer and Mule Deer	Maximum slope	−	Gunson et al., 2009
Roe Deer, Wild Boar, and Red Deer	Presence steep embankments; $\geq$ 2m high & a vertical/horizontal ratio $\geq$ 1	−	Malo et al., 2004
Roe Deer, Wild Boar, and Red Deer	Continuity of steep embankment	−	Malo et al., 2004
Moose	Topographic variation	−	Seiler, 2005
Moose	Mean slope of the terrain (1000 m)	+	Dussault et al., 2006
Jersey barrier/Guardrails			
White-tailed Deer and Mule Deer	Length of Jersey barrier (800 m)	−	Gunson et al., 2009
White-tailed Deer and Mule Deer	Proximity to Jersey barrier	−	Gunson et al., 2009
Roe Deer, Wild Boar, and Red Deer	Presence of guardrails	−	Malo et al., 2004
Roe Deer, Wild Boar, and Red Deer	Presence of continuous guardrails	−	Malo et al., 2004
Visibility			
White-tailed Deer	In-line visibility measured from distance of a 2 m high optical density board from highway centre line	+	Bashore et al., 1985
White-tailed Deer	Shortest visibility	−	Bashore et al., 1985
Traffic volume/Speed limit			
Moose	Annual Average Daily Traffic Volume (AADTV)	+	Seiler, 2005
Moose	Mean speed limit	+	Seiler, 2005
White-tailed Deer	Posted or mean speed limit	−	Bashore et al., 1985
Road pavement width			
White-tailed Deer	Number of lanes	+	Hubbard et al., 2000
Fencing			
White-tailed Deer	Presence of 7.5′ high fence located at the edge or within 25 yards of nearest wooded area, and grazing area highway side of fence	+	Puglisi et al., 1974
White-tailed Deer	Mean proportion of livestock fencing ($<$0.91 m) within 100 m	+	Bashore et al., 1985
Moose	Exclusion fencing	−	Seiler, 2005
Road corridor			
Roe Deer, Wild Boar, and Red Deer	Presence of cross roads	+	Malo et al., 2004
Moose	Count of intersecting private roads	+	Seiler, 2005
Moose	Length private roads (500 m)	+	Seiler, 2005
Riparian corridor			
Moose	Presence of valley with at least one slope $<$2%	+	Dussault et al., 2006
White-tailed Deer and Mule Deer	Width riparian corridor crossing road (800 m)	+	Finder et al., 1999
White-tailed Deer and Mule Deer	Proximity to drainage	+	Gunson et al., 2009
White-tailed Deer and Mule Deer	Count bridge	+	Hubbard et al., 2000
b. Carnivores			
Visibility			
European Polecat	Length of unbroken line on road	−	Barrientos and Bolonio, 2009
Curvature			
Common Genet (*Genetta genetta*) and Egyptian Mongoose (*Herpestes ichneumon*)	Proximity to nearest curve	+	Grilo et al., 2009
Traffic volume/Speed limit			
European Polecat	Posted speed limit	+	Barrientos and Bolonio, 2009
European Polecat	Monthly average daily traffic volume	+	Barrientos and Bolonio, 2009
Hedgehog spp (*Erinaceus europaeus* and *E. concolor*)	Daily traffic volume	+	Orlowski and Nowak, 2006
Common Shrew (*Sorex araneus*), and Least Weasel (*Mustela nivalis*)	Daily traffic volume	+	Orlowski and Nowak, 2006
Road Width			
Stone Marten	National road relative to highway	+	Grilo et al., 2009
Crossing structure			
Red Fox	Number of passages above and below grade	+	Grilo et al., 2009
Riparian corridor			
European Polecat	Length of bridge	+	Barrientos and Bolonio, 2009
c. Small-medium vertebrates			
Road-side vegetation			
Snowshoe Hare	Proximity to mean cover, trees and shrubs $>$1 m high	+	Clevenger et al., 2003
Swamp Wallaby	Percentage understory vegetation 5 m from road verge	−	Ramp et al., 2006
Swamp Wallaby	Percentage bare ground 5 m from road verge	−	Ramp et al., 2006
Road-side topography			
Snowshoe Hare	Raised road-side topography relative to flat	−	Clevenger et al., 2003
Snowshoe Hare	Raised-buried road-side topography relative to flat	−	Clevenger et al., 2003
Eastern Grey Kangaroo	Slope (°)	−	Ramp et al., 2005

Table 2 (*continued*)

Target species	Predictor	+/−	Source
Possum	Ridge top and mid slope relative to lowland	+	Taylor and Goldingay, 2004
Visibility			
Swamp Wallaby	Index of visibility distance, controlled by stopping distance	−	Ramp et al., 2006
Curvature			
Wombat	Curvature; measured from Euclidean distance	+	Ramp et al., 2005
Traffic volume/Speed Limit			
Armadillo (*Dasypus novemcinctus*)	Average hourly nightly traffic volume	+	Inbar and Mayer, 1999
Common Vole (*Microtus arvalis*),	Daily traffic volume	+	Orlowski and Nowak, 2006
Road width			
Swamp Wallaby	Verge width	−	Ramp et al., 2006
Crossing structure			
Snowshoe Hare	Proximity of wildlife crossing structure or drainage culvert	−	Clevenger et al., 2003
d. Birds			
Road-side topography			
Common Raven	Raised road-side topography relative to flat	−	Clevenger et al., 2003
Australian Magpie (*Gymnorhina tibicen*)	Ridge top relative to mid and lowland	+	Taylor and Goldingay, 2004
Road-side vegetation			
Barn Swallow	Length of road-side single line of trees	+	Orlowski, 2005
Little Wattlebird (*Anthochaera chrysoptera*)	Percentage understory vegetation 5 m from road verge	+	Ramp et al., 2006
Little Wattlebird	Percentage bare ground 5 m from road verge	−	Ramp et al., 2006
Little Wattlebird	Percentage canopy height 5 m from road verge	−	Ramp et al., 2006
Road width			
Canopy-dwelling bird & Noisy Miner (*Manorina melanocephala*)	3 lanes relative to 2 and 4 lanes	+	Taylor and Goldingay, 2004
Riparian Corridor			
Birds	Proximity to gully	+	Ramp et al., 2005
Visibility			
Canopy-dwelling bird	Open view	−	Taylor and Goldingay, 2004
Reflectors			
Little Owl	Presence of reflectors causing blindness	+	Gomes et al., 2009
Median			
Common Raven	Presence of median	+	Clevenger et al., 2003

the number of wildlife-vehicle collisions among all species groups. The presence of Jersey barriers and guardrails decreased the probability of ungulate-vehicle collisions, and one study found deer (*Odocoileus virginianus*)-vehicle collisions decreased with increased speed limits (Table 2a). Possum (*Trichosurus* spp.) and Australian magpie (*Gymnorhina tibicen*) collisions occurred most often along roads with steep road-side topography relative to lowlands (Tables 2c and d, respectively).

Two studies that included road-side livestock fencing in their models found this fencing-type increased the occurrence of ungulate-vehicle collisions and another study that looked specifically at wildlife exclusion fencing found a decrease in collisions with moose (Table 2a). Two studies included a measure of wildlife passages along roads in their models. Red Fox (*Vulpes vulpes*) collisions occurred when there were more passages present along the road and Snowshoe Hare (*Lepus americanus*) collisions occurred further from culverts or wildlife crossing structures (Tables 2b and c, respectively).

The results suggest road-side vegetation influenced birds and small-medium vertebrate collisions. In addition, Snowshoe hare collisions occurred when road-side cover was present, and collisions with Swamp Wallabies (*Wallabia bicolour*) and Barn Swallows occurred when forage was present. Results from one study found that bird collisions increased with canopy height.

4. Discussions

Direct comparisons among studies was a challenging task even among studies that used similar target species (see also Nielsen et al., 2003). Even though all studies used a similar GLM model type, the modeling process differed considerably, e.g., inclusion of a priori tests for multicollinearity, stepwise regression, and Akaikes Information Criterion. Other differences included the selection of target species in specific landscapes where WVC data collection varied across many spatial extents and road types, e.g., major and minor roads. A study by van Langevelde et al. (2009) showed that road-related characteristics influence rates of road mortality differently for major and minor roads. For these reasons, rather than focusing on commonalities between studies we chose to interpret our summary as it applies to mitigation planning.

4.1. Application of summary to mitigation planning

Intuitively, wildlife-motorist conflicts can be alleviated by avoiding natural landscape features and species-specific nesting, cover, or foraging habitat (e.g., Nielsen et al., 2003; Orlowski, 2005; Roger and Ramp, 2009) during route planning. For example, findings show a mixture of forest-open habitat surrounding a road will increase the occurrence of collisions with ungulates (e.g., Finder et al., 1999; Malo et al., 2004; Gunson et al., 2009) and the presence of wetlands will increase the risk of vehicle collisions with amphibians and reptiles (e.g., Glista et al., 2007; Langen et al., 2009). Realistically as the landscape becomes more permeated with roads it becomes more difficult to avoid natural areas used by targeted wildlife species. Other competing demands such as travel efficiency and avoidance of population and employment areas lead to further infringement on natural areas. Therefore transportation planners require solutions and strategies to mitigate impacts of roads on wildlife and increase motorist safety when predicted wildlife-motorist conflict zones cannot be avoided.

Other research, and five of the reviewed studies, found that ungulates use road and riparian corridors as movement pathways, increasing their risk of collisions with vehicles (e.g., Bellis and Graves, 1971; Feldhammer et al., 1986; Finder et al., 1999; Malo et al., 2004; Seiler, 2005; Dussault et al., 2006; Gunson et al., 2009). The risk of collisions at riparian and road intersections can be reduced by facilitating wildlife passage (Seiler, 2005) through existing culverts or bridges. For example, bridges can be extended beyond their stream widths to create wildlife pathways or embankments along riparian corridors (Clevenger and Waltho, 2000), and wildlife shelving along culverts can facilitate passage by terrestrial small-medium vertebrates (Foresman, 2003).

Wildlife movements tend to travel along a path of least resistance (see examples in Boone et al., 1996; Schippers et al., 1996; Larkin et al., 2004), therefore it is not surprising that several studies showed the risk of wildlife-vehicle collisions increased when roads bisected level terrain (e.g., Clevenger et al., 2003; Malo et al., 2004; Ramp et al., 2005). On a large scale it is not feasible to re-route large sections of road to avoid areas of level terrain that are associated with wildlife movements. Therefore, an accurate understanding of where and when wildlife migration routes and movement patterns occur in association with roads will provide opportunities to identify locations for effective and dynamic mitigation strategies (Mountrakis and Gunson, 2009).

This review showed that wildlife is often attracted to road-sides that provide shrub for cover, foraging opportunities, and support abundant prey species thereby increasing their risk of interactions with oncoming vehicles. Road-side vegetation management that creates an inhospitable environment and changes the behavior of target species impacted by roads can play a large role in providing mitigation solutions. For example, Grosman et al. (2009) modeled a reduction in moose-vehicle collisions when salt pools were removed from road-sides. In addition, a study by Ramp et al. (2006) suggest road-side vegetation that is at least vehicular height may alter bird flight paths away from oncoming vehicles.

The presence of road features, such as Jersey barriers, and guardrails may have an influential role in wildlife-vehicle collision rates. We are not aware of any previously published studies that assess how barriers influence collisions with small-medium vertebrates. However, five ungulate studies included Jersey barriers or guardrails in their models, and two of these found their presence decreased the number of collisions on roads. It is inconclusive whether these results are due to the barriers themselves or their association with steep topography and/or curved road sections (Gunson et al., 2009). Other road features such as medians may encourage animals, e.g., birds and ungulates, to cross roads at these locations to access safe habitat or resources (Clevenger et al., 2003; Bellis and Graves, 1971).

4.2. *Modeling considerations for mitigation planning*

There were several examples illustrating that when models focused on species-specific habitat requirements near roads results were more applicable to localized mitigation strategies. For example, Dussault et al. (2006) found small brackish pools surrounding roads increased moose-vehicle collisions in Quebec. Applied field research and modeling simulations have shown road-side salt-pool management is an effective mitigation solution to alleviate moose-vehicle crossings and collisions (Leblond et al., 2007; Grosman et al., 2009). Barrientos and Bolonio (2009) also showed that European Polecat collisions occurred when rabbit burrows were abundant on the road-side, necessitating management strategies that will control rabbit colonization near roads.

It was evident from this review that explanatory factors interact with each other in the multivariate modeling process, complicating mitigation management solutions. For example, vehicle collisions with all wildlife typically occurred when visibility was obstructed either by road curvature (Bashore et al., 1985) or sight-line distance (Barrientos and Bolonio, 2009). Therefore it seems logical that increasing visibility along roads should decrease collisions. However, even though visibility increases along straight sections of roads, WVC risk increases because motorists will typically travel at higher speeds (e.g., Barrientos and Bolonio, 2009). Furthermore, it may seem sensible to clear vegetation along roads to increase motorist visibility; however, this could be counter-productive because clearing not only increases traffic speed, but creates foraging ground and shrub cover for ungulates and smaller vertebrates attracting wildlife to road-sides (Gunson et al., 2009).

In several studies road-side topography interacted with other predictors such as road type for Stone Martens (Grilo et al., 2009), vegetation for opossums (Taylor and Goldingay, 2004) and the placement of Jersey barriers and guardrails for ungulates (Gunson et al., 2009). Furthermore, collisions with small-medium vertebrates occurred at low elevations, most likely due to favorable habitat type (Kanda et al., 2006). A consideration for future modeling would be to control for one variable when including two known interacting predictors, i.e., measure road-side topography and or elevation at sites with similar vegetation composition surrounding roads.

Seven of eighteen studies (44%) that included traffic volume, road width, and posted speed in their models found that these factors were associated with increased WVCs (e.g., Orlowski and Nowak, 2006; Barrientos and Bolonio, 2009), and one study found that deer collisions decreased as the posted speed limit increased (Bashore et al., 1985). A possible explanation for these mixed results is that the temporal resolution of the traffic volume data set may not have matched when a particular species is most prone to WVCs. For example, Shepard et al. (2008) report that the time of day when snakes are most active does not coincide with daily traffic peaks so it is possible that traffic volume is a significant factor on snake mortality over shorter time scales than what they examined. Bissonette and Kassar (2008) also document mixed results from studies analysing the relationship between traffic volume and wildlife-vehicle collisions, which they attribute to the use of unsuitable temporal scale domains for explanatory variables. Complicating matters even further, in some cases the relationship between traffic volume and WVCs are not linear (Seiler, 2004; Jaarsma et al., 2006) as traffic can create a 'barrier' effect impeding animal movement across roads (Forman and Alexander, 1998; Eigenbrod et al., 2008).

Several studies included ambiguous predictor definitions that hinder interpretation of model results and their ability to be applied to mitigation planning. For example, the influence of wildlife crossing structures embedded in the road on WVCs is meaningful; however results are difficult to interpret if more than one type, i.e., culverts and larger wildlife underpasses (Clevenger et al., 2003) and above and below grade structures (Grilo et al., 2009), are included in the definition. This is especially valid because species and species groups use specific crossing structure designs differently (Clevenger and Waltho, 2000; Clevenger et al., 2003; Mata et al., 2008).

Vehicle collisions with birds, small-medium vertebrates, and amphibians and reptiles tend to increase when open water, e.g., reservoir, pond, or wetland is present surrounding road sections. This relationship is not well known for ungulates and one study in this review found that as wetlands increased moose-vehicle collisions decreased (Seiler, 2005). This is somewhat surprising because moose tend to be associated with wetlands in the landscape (Cederlund and Okarma, 1988). In addition, four other studies that examined the influence of open water on ungulate-vehicle collisions did not have a significant result. In all these studies wetlands was analyzed at a coarse scale, using a Geographic Information System and land-use data, and a more detailed description and measurement, e.g., type, and configuration surrounding roads (see Langen et al., 2009) may provide more conclusive results.

5. Conclusions

Model designs are often developed with readily available wildlife-collision data sets where many of the obvious, broad-scale patterns associated with collisions have already been documented. Modeling should measure localized, species-specific predictors that are well-defined, easing interpretation of results by practitioners and road planners for application to road mitigation projects. This can be further achieved by statistically teasing apart the many interacting and uncertain relationships between WVC occurrence and the processes influencing them. Finally, more localized models should consider measuring predictors that match the temporal scale of when WVCs are most likely to occur in addition to the spatial scale, e.g., home range of the target species.

Vehicle collisions with wild animals pose a serious human safety issue and contribute to a significant loss in wildlife population numbers. Sufficient funds and resources are required to evaluate mitigation schemes derived from road ecology research. In turn, this will provide a feedback mechanism for adaptive research and applied management that can assist transportation agencies in complying with road safety and environment (i.e. endangered species acts) regulations. Confidence in the application of models to mitigation projects will be enhanced if they have been validated to assess their predictive power on other road sections in similar landscapes (e.g., Seiler, 2005). Furthermore, the development of practical and applicable models for transportation projects requires a multi-disciplinary approach that includes transportation decision-makers and engineers in the modeling process.

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References

Al-Ghamdi, A.S., AlGadhi, S.A., 2004. Warning signs as countermeasures to camel-vehicle collisions in Saudi Arabia. Accident Analysis and Prevention 36, 749–760.

Barrientos, R., Bolonio, L., 2009. The presence of rabbits adjacent to roads increases polecat road mortality. Biodiversity Conservation 18, 405–418.

Bashore, T.L., Tzilkowski, W.M., Bellis, E.D., 1985. Analysis of deer-vehicle collision sites in Pennsylvania. Journal of Wildlife Management 49, 769–774.

Bellis, E.D., Graves, H.B., 1971. Highway fences as deterrents to deer-vehicle collisions. Transportation Research Record 674, 53–58.

Bissonette, J.A., Kassar, C.A., 2008. Locations of deer-vehicle collisions are unrelated to traffic volume or posted speed limit. Human Wildlife Conflicts 2, 122–130.

Bissonette, J.A., Kassar, C.A., Cook, L.J., 2008. Assessment of costs associated with deer-vehicle collisions: human death and injury, vehicle damage, and deer loss. Human Wildlife Conflicts 2, 17–27.

Boone, R.B., Hunter, M.L., Cook, L.J., 1996. Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. Landscape Ecology 11, 51–64.

Bruinderink, G.W.T.A., Hazebroek, E., 1996. Ungulate traffic collisions in Europe. Conservation Biology 10, 1059–1067.

Cederlund, G., Okarma, H., 1988. Home range and habitat use of adult female moose. Journal of Wildlife Management 52, 336–343.

Clevenger, A.P., Waltho, N., 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14, 47–56.

Clevenger, A.P., Chruszcz, B., Gunson, K.E., 2003. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. Biological Conservation 109, 15–26.

Conover, M.R., Pitt, W.C., Kessler, K.K., DuBow, T.J., Sanborn, W.A., 1995. Review of human injuries, illnesses and economic losses caused by wildlife in the U.S. Wildlife Society Bulletin 23, 407–414.

D'Angelo, G.J., D'Angelo, J.G., Gallagher, G.R., Osborn, D.A., Miller, K.V., Warren, R.J., 2006. Evaluation of wildlife warning reflectors for altering white-tailed deer behavior along roadways. Wildlife Society Bulletin 34, 1175–1183.

Dodd, C.K., Barichivich, W.J., Smith, L.L., 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118, 619–631.

Dodd, N.L., Gagnon, J.W., Manzo, A.L., Schweinsburg, R.E., 2007. Video surveillance to assess highway underpass use by elk in Arizona. Journal of Wildlife Management 71, 637–645.

Dussault, C., Roulin, M., Courtois, R., Ouellet, J.P., 2006. Temporal and spatial distribution of moose-vehicle accidents in the Laurentides Wildlife Reserve, Quebec, Canada. Wildlife Biology 12, 415–426.

Eigenbrod, F., Hecnar, S.J., Fahrig, L., 2008. The relative effects of road traffic and forest cover on anuran populations. Biological Conservation 141, 35–46.

Feldhammer, G.A., Gates, J.E., Harman, D.M., Loranger, A.J., Dixon, K.R., 1986. Effects of interstate highway fencing on white-tailed deer activity. Journal of Wildlife Management 50, 497–503.

Finder, R.A., Roseberry, J.L., Woolf, A., 1999. Site and landscape conditions at white-tailed deer/vehicle collision locations in Illinois. Landscape and Urban Planning 44, 77–85.

Foresman, K., 2003. Small mammal use of modified culverts on the Lolo south project of western Montana-an update. International Conference of Ecology and Transportation, Lake Placid, New York, 342–343.

Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29, 206–231.

Foster, M.L., Humphrey, S.R., 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin 23, 95–100.

Glista, D.J., DeVault, T.L., DeWoody, J.A., 2007. Vertebrate road mortality predominantly impacts amphibians. Herpetological Conservation and Biology 3, 77–87.

Gomes, L., Grilo, C., Silva, C., Mira, A., 2009. Identification methods and deterministic factors of owl roadkill hotspot locations in Mediterranean landscapes. Ecological Research 24, 355–370.

Grilo, C., Bissonette, J.A., Margarida, S., 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. Biological Conservation 142, 301–313.

Grosman, P.D., Jaeger, J.A.G., Biron, P.M., Dussault, C., Ouellet, J., 2009. Reducing moose-vehicle collisions through salt pool removal and displacement : an agent based modeling approach. Ecology & Society 14 [online] URL: http://www.ecologyandsociety.org/vol14/iss2/art17/.

Gunson, K.E., Clevenger, A.P., Ford, A.T., Bissonette, J.A., Hardy, A., 2009. A comparison of data sets varying in spatial accuracy used to predict the locations of wildlife-vehicle collisions. Environmental Management 44, 268–277.

Hubbard, M.W., Danielson, B.J., Schmitz, R.A., 2000. Factors influencing the location of deer-vehicle accidents in Iowa. Journal of Wildlife Management 64, 707–712.

Hughes, W.E., Saremi, A.R., Paniati, J.F., 1996. Vehicle-animal crashes: an increasing safety problem. Institute of Transportation Engineers Journal 66, 24–28.

Huijser, M.P., McGowen, P., Fuller, J., Hardy, A., Kociolek, A., Clevenger, A.P., Smith, D., Ament, R., 2007. Wildlife-vehicle Collision Reduction Study. Report to U.S. Congress. U.S. Department of Transportation, Federal Highway Administration, Washington, D.C.

Inbar, M., Mayer, R.T., 1999. Spatio-temporal trends in armadillo diurnal activity and road-kills in central Florida. Wildlife Society Bulletin 27, 865–872.

Jaarsma, C.F., van Langevelde, F., Botma, H., 2006. Flattened fauna and mitigation: traffic victims related to road, traffic, vehicle, and species characteristics. Transportation Research Part D: Transport and Environment 11, 264–276.

Jaarsma, C.F., van Langevelde, F., Baveco, J.M., van Tupen, M., Arisz, J., 2007. Model for rural transportation planning considering simulating mobility and traffic kills in the badger *Meles meles*. Ecological Informatics 2, 73–82.

Joyce, T.L., Mahoney, S.P., 2001. Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. Wildlife Society Bulletin 29, 281–291.

Kanda, L.L., Fuller, T.K., Sievert, P.R., 2006. Landscape associations of road-killed virginia ppossums (*Diderphis virginiana*) in Central Massachusetts. American Midland Naturalist 156, 128–134.

Krisp, J.M., Durot, S., 2007. Segmentation of lines based on point densities-An optimisation of wildlife warning sign placement in southern Finland. Accident Analysis Prevention 39, 38–46.

Langen, T.A., Ogden, K.M., Schwarting, L.L., 2009. Predicting hot spots of herpetofauna road mortality along highway networks. Journal of Wildlife Management 73, 104–114.

van Langevelde, F., Dooremalen, C., Jaarsma, C.F., 2009. Traffic mortality and the role of minor roads. Journal of Environmental Management 90, 660–667.

Larkin, J.L., Maehr, D.S., Hoctor, T.S., Orlando, M.A., Whitney, K., 2004. Landscape linkages and conservation planning for the black bear in west-central Florida. Animal Conservation 7, 23–34.

Leblond, M., Dussault, C., Ouellet, J., Poulin, M., Courtois, R., Fortin, J., 2007. Management of roadside salt pools to reduce moose-vehicle collisions. Journal of Wildlife Management 71, 2304–2310.

Malo, J.E., Suarez, F., Diez, A., 2004. Can we mitigate animal-vehicle accidents using predictive models? Journal of Applied Ecology 41, 701–710.

Mata, C.I., Hervas, J., Herranz, F., Suarez, F., Malo, J.E., 2008. Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. Journal of Environmental Management 88, 407–415.

Mountrakis, G., Gunson, K.E., 2009. Multi-scale spatiotemporal analyses of moose-vehicle collisions: a case study in northern Vermont. International Journal of Geographic Information Systems 23, 1389–1412.

Nielsen, C.K., Anderson, R.G., Grund, M.D., 2003. Landscape influences on deer-vehicle accident areas in an urban environment. Journal of Wildlife Management 67, 46–51.

Orlowski, G., 2005. Factors affecting road mortality of the Barn Swallows *Hirundo rustica* in farmland. Acta Ornithologica 40, 117–125.

Orlowski, G., Nowak, L., 2006. Factors influencing mammal roadkills in the agricultural landscape of south-western Poland. Polish Journal of Ecology 54, 283–294.

Pojar, T.M., Prosencer, R.A., Reed, D.F., Woodard, T.N., 1975. Effectiveness of a lighted, animated deer crossing sign. Journal of Wildlife Management 39, 87–91.

Puglisi, M.J., Lindzey, J.S., Bellis, E.D., 1974. Factors associated with highway mortality of white-tailed deer. Journal of Wildlife Management 38, 799–807.

Putman, R.J., 1997. Deer and road traffic accidents: options for management. Journal of Environmental Management 51, 43–57.

Ramp, D.J., Caldwell, J., Edwards, K.A., Warton, D., Croft, D.B., 2005. Modelling of wildlife fatality hotspots along the snowy mountain highway in New South Wales, Australia. Biological Conservation 126, 474–490.

Ramp, D., Wilson, V.K., Croft, D.B., 2006. Assessing the impacts of roads in peri-urban reserves: road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. Biological Conservation 129, 348–359.

Roger, E., Ramp, D., 2009. Incorporating habitat use in models of fauna fatalities on roads. Diversity and Distributions 15, 222–231.

Romin, L.A., Bissonette, J.A., 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24, 276–283.

Schippers, P., Verbroom, J., Knappen, J.P., Apeldoorn, R.C.V., 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. Ecography 19, 97–106.

Seiler, A., 2004. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. Wildlife Biology 10, 301–313.

Seiler, A., 2005. Predicting locations of moose-vehicle collisions in Sweden. Journal of Applied Ecology 42, 371–382.

Shepard, D.B., Dreslik, M.J., Benjamin, C.J., Phillips, C.A., 2008. Reptile road mortality around an oasis in the Illinois corn desert with emphasis on the endangered eastern massasauga. Copeia 2, 350–359.

Taylor, B.D., Goldingay, R.L., 2004. Wildlife road-kills on three major roads in north-eastern New South Wales. Wildlife Research 31, 83–91.

Woltz, H.W., Gibbs, J.P., Ducey, P.K., 2008. Road crossing structures for amphibians and reptiles: informing design through behavioral analysis. Biological Conservation 141, 2745–2750.