

EFFECTS OF LANDSCAPE STRUCTURE ON CONSERVATION OF SPECIES AND BIODIVERSITY (M BETTS, SECTION EDITOR)

# Effects of Road Density and Pattern on the Conservation of Species and Biodiversity

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Abstract The development and presence of roads can reduce landscape permeability, lead to habitat loss, and increase habitat fragmentation. It is these fundamental changes in landscape structure that can have both direct and indirect impacts on the conservation of species and biodiversity. In this review, I examine 215 research studies conducted between 2011 and 2015 that explore the impacts of roads and road networks on a wide range of species. I divided these studies into four main categories: 1) the direct effects of roads on wildlife, 2) the indirect effects of roads on wildlife, 3) the consequences of road networks on wildlife populations, and 4) survey design and mitigation including both innovations and evaluations. I found that the majority of studies (38%) explored the indirect effects of roads on wildlife, including displacement, fitness consequences, and road crossing ability of wildlife. Nevertheless, despite there being a pressing need to understand how existing road networks impact wildlife and how increasing road density may influence local and regional population persistence, only 10% of the studies considered the implications of road networks on wildlife. However, there is an increasing trend towards the development of predictive models that can be used for a better understanding of road network impacts, assess landscape connectivity, and devise

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Victoria J. Bennett v.bennett@tcu.edu mitigation. This review also highlighted the continued need to devise and evaluate mitigation measures so transportation authorities and conservation practitioners may be better equipped to address the ecological implications of roads and proposed road development.

**Keywords** Barrier effects · Habitat fragmentation · Landscape permeability · Road mitigation · Road networks · Wildlife-vehicle collisions

# Introduction

For three decades now the field of road ecology has brought to light the impacts that roads and road networks have on the landscape, its wildlife, and subsequent ecosystem stability [1, 2]. This paper presents seminal reviews from associating the presence of roads with the direct mortality of wildlife, hindering wildlife movement both physically and behaviorally, and the loss and degradation of habitat, all of which can have farreaching implications for regional population dynamics, species diversity, and ecosystem function [3-5]. To date, very few landscapes remain devoid of roads, and as human populations continue to increase it is likely that road density will increase as well, whether it be by new developments, road improvements, or road expansion schemes. There is, therefore, a pressing need to employ what we have learnt and use it to identify the species and habitats that are most vulnerable to the negative impacts of roads, consolidate the different mitigation strategies we have tried and tested, and establish where our knowledge is still lacking in order to recommend further research. In this quantitative review, I attempt to address these priorities.

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# Methods

This review is based on peer-reviewed publications obtained from an ISI Web of Knowledge database search of all articles from 2011 to 2015, which present research on the effects of roads and traffic on wildlife. My search was not limited to location or taxa. I used "roads", "traffic", "transportation infrastructure", "vehicle", and "anthropogenic disturbance" as key search words, along with "wildlife" or "animal".

For this review, I divided all research found into four main categories, which considered 1) the direct effects of roads on wildlife, 2) the indirect effects of roads on wildlife, 3) the consequences of road networks on wildlife populations, and 4) survey design and mitigation including both innovations and evaluations. These categories are discussed in more detail below. However, to summarize the former two categories: the direct and indirect impacts of roads on wildlife include studies that focus on the effect of a single road or a select number of roads (for comparison) on wildlife individuals, such as wildlife-vehicle collisions, avoidance, and attraction. Note that they do not explicitly study the effects of roads on population persistence. Instead, studies considered in the third category, the consequences of road networks on wildlife populations, do address the larger scale impacts of roads (e.g., within a landscape) on population persistence. The final category, survey design and mitigation, considers studies that present innovative ideas, and/or evaluate mitigation intended to reduce the impacts of roads on wildlife.

## Results

I found a total of 215 studies presenting research on the effects of roads and road networks on wildlife (see Appendix A for the full list of literature). These studies included animals from a wide range of taxa, with 86 studies focusing specifically on mammals (39%), 36 on birds (16%), 23 on reptiles (11%), 17 on amphibians (8%), five on invertebrates (2%), and three on fish (1%). The remaining studies considered multiple species across a variety of taxonomic groups (comprising 23%). A total of 57 studies documented research on species of conservation concern (26%), and almost half of these studies included species listed as threatened or endangered (26 of 57).

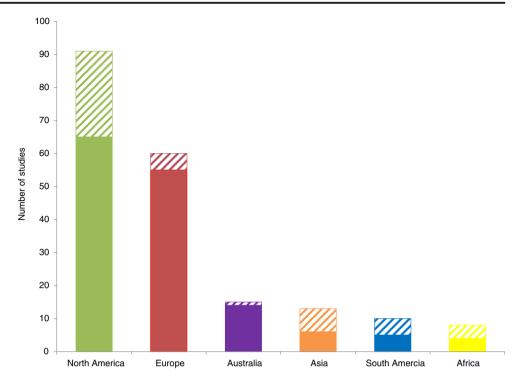
The majority of studies were conducted in North America (46%) and Europe (30%), but there were studies from all over the world, including Australia, Africa, Asia, and South America (Fig. 1). Moreover, 24% of studies were undertaken in protected areas (such as Biosphere Reserves, national parks, wildlife refuges, and nature reserves; Fig. 1) and a further nine studies involved a controlled experiment in a laboratory or field setting.

Of the four categories listed, a total of 55 studies specifically explored the direct impacts of roads on wildlife, 73 investigated the indirect impacts, nine studies considered both direct and indirect impacts, 15 explored the consequences of road networks on wildlife populations, 58 focused on survey design and mitigation, and finally five studies tested and recommended new techniques to explore the consequences of road networks on wildlife (i.e., a combination of categories 3 and 4).

## **Direct Impacts of Roads on Wildlife**

The direct mortality of wildlife through wildlife-vehicle collisions has been the most widely acknowledged impact of roads over the last three decades, not only because such fatalities are noticeable to the general public, but because these types of wildlife encounters can affect public safety, particularly when large herbivores and carnivores are involved. Of the 64 studies that explored direct mortality, 25% were conducted to quantify road-related mortality in large mammals (16 of 64), predominately moose and other large deer species [6-8]. While wildlife-vehicle collisions with large mammals continue to be reported, there appears to be a shift in research towards devising solutions and improving existing mitigation for such species (see Survey Design and Mitigation section). Furthermore, many research studies were focused on identifying and quantifying road-related mortality in species whose population persistence could be affected. For example, of the 27 studies that investigated road-related mortality in up to three related species, 15 studies involved species of conservation concern, while the remaining 12 studies considered the common and widespread species that are often reported in wildlife-vehicle collisions. Amphibians appeared to generate the most concern, with a number of multiple-taxa studies finding that they made up the highest percentage of roadkills (as much as 80% recorded, [9–12]). Studies warn that with many amphibian populations already declining globally any additional nonnatural mortality could further impact population persistence [13]. The reason as to why amphibians in general appear to be more vulnerable to wildlife-vehicle collisions than other taxa has been related to their ecology and life history. Three studies confirmed that road mortality of amphibians peaked as they attempted to cross roads during their migration in the spring from terrestrial hibernacula to aquatic breeding habitats [11, 12, 14]. These studies recommended that mitigation could be implemented during this seasonal activity period in order to reduce amphibian road-mortality rates; however, a study conducted on Fowler's toad (Anaxyrus fowleri) cautioned that road mortality may not always be limited to seasonal migrations [15].

Yet, even within a taxon many of the studies conducted over multiple species found that road mortality was speciesspecific [16, 17]. For example, a study that explored variations in road mortality rates of 11 species of mammalian carnivore found that stone martens (*Martes foina*), European otters Fig. 1 Number of road-related studies conducted in each continent from 2011 to 2015. The cross-hatched sections of each bar represent the number of studies conducted in protected areas



(Lutra lutra), and red foxes (Vulpes vulpes) were most frequently documented [18]. It was suggested that the higher number of roadkills among these species most likely reflected their life-history phenologies. Thus, understanding the life history traits and associated factors that make some species more vulnerable to wildlife-vehicle collisions than others would certainly allow us to devise more targeted mitigation along certain roads. In fact, many of the research studies undertaken on road mortality tended to explore the differences between and within species with the intention of informing more targeted mitigation. For instance, studies considered in this review found that a variety of species-associated factors influenced the rate of wildlife-vehicle collisions, such as age (particularly dispersing juveniles; [19-23]), activity patterns (such as nocturnal and migratory activities; [6, 7, 24, 25]), season (primarily breeding season; [12, 26–29]), gender (such as males ranging further in the breeding season in search a mate; [23, 26, 30-32]), diet preferences (e.g., one study found that omnivorous mammals and herbivorous birds were most vulnerable; [33]), mobility (including low-flying species; [15, 21, 34, 35]), behavioral responses (e.g., certain species do not respond to oncoming traffic; [15, 36]), and home range size (i.e., the larger the home range the higher the probability of crossing a road; [37]). Another study found that species that were more inconspicuous on the roads were more vulnerable to wildlife-vehicle collisions [38].

A number of studies also demonstrated the importance of habitat variables, such as distance of suitable habitat from the road and local topography. For example, one study that used radio-telemetry to track two species of snake in the Grasslands National Park in Canada found that road mortality rates were positively correlated with distance from their hibernacula [39]. Such studies can certainly be used to inform future road development. Furthermore, a total of six studies related increased road mortality rates of wildlife, not including amphibians, with distances from wetlands or water sources (e.g., [17]). Research included in this review also highlighted two concerns, 1) that maintained road-side habitat provided quality forage, nesting resources or breeding habitat for many species, thus attracting wildlife, which in turn increased their risk of wildlife-vehicle collisions [21, 31, 32, 40], and 2) that road mortality increased with proximity to a protected area [9, 10]. The latter indicates that any existing road or future road development in proximity to a protected area has the potential to impact the species that area may be attempting to protect.

In addition, many road mortality studies have tried to identify road characteristics that may be more readily associated with wildlife-vehicle-collisions. The most predominate characteristic among the studies reviewed was traffic volume. A total of 22 of the 64 studies conducted found that increasing traffic volume was positively correlated with road mortality rates of wildlife across all taxonomic groups. Furthermore, some national parks have already demonstrated that an increase in traffic volume as a result of a rise in tourism has led to an equivalent increase in wildlife-vehicle-collisions [10, 19, 41]. With tourism numbers expected to continue to escalate, there are real concerns for how this trend will impact wildlife populations in protected areas.

Finally, other road characteristics that were studied included gap width [42–44] and traffic speed [27, 43, 44], both found to be positively correlation with road mortality, and road sinuosity with straighter roads leading to more wildlifevehicle collisions [32, 43, 45]. Transportation authorities and conservation practitioners can use these kinds of data to inform roadway design and develop targeted strategies that will reduce wildlife encounters.

#### Indirect Impacts of Roads on Wildlife

The presence of roads can have a wide variety of indirect impacts on wildlife ranging from changes in habitat quality to influencing behavior. Of the 82 studies that explored the indirect impacts of roads on wildlife, 30% explored whether the abundance and distribution of wildlife near roads varied due to behavioral avoidance (known as displacement), 29% investigated the fitness consequences associated with wildlife being near roads, 29% focused on the ability of wildlife to physically and behaviorally cross roads, and the remaining 12% looked into the habituation or attraction of wildlife to roads.

The ability or frequency at which individuals cross roads will likely remain a priority in the field of road ecology, as a road can reduce landscape permeability by acting as a barrier or filter to movement and, therefore, has the potential to influence population persistence. One study highlighted that the barrier effects of roads are a particular concern for species that migrate, such as the pronghorn (Antilocapra Americana) [46]. Of the studies included in this review, nine identified the characteristics of road that influenced permeability, such as traffic volume [46-48], road width or the number of lanes [47, 49], and road surface type. For the latter, five studies determined that paved roads impeded the movement of wildlife more than unpaved roads (including a number of species of reptiles and chimpanzees, Pan troglodytes) [47, 50-53]. In contrast, another study found that gopher tortoises (Gopherus Polyphemus) could not physically cross a sand road with deep vehicle ruts [54].

Such research studies further demonstrated that not only can the barrier-effects of roads be species-specific across multiple taxa [47, 49, 55], they can influence some individuals within a species more than others [48, 54]. Such differences were related to gender [48, 50], age and/or body size (with smaller individuals being more restricted; [54]), and life history stage (such as the breeding season; [48, 50]). For example, in Kibale National Park in Uganda female chimpanzees with dependent young were less likely to cross a high-traffic asphalt road than other troop members [50].

But roads do not just influence landscape permeability for wildlife. A road can also affect the abundance and distribution of individuals within habitats adjacent to it (known as the road-effect zone; [4]). A total of 19 studies confirmed that a wide variety of birds, mammals, reptiles, and invertebrates could be displaced from habitats in proximity to roads. Nevertheless, only three of these studies determined the extent of the road-effect zone [56–58]. This low number was surprising considering the increasing popularity of tools, such a simulation models (see Consequences of Road Networks on Wildlife Populations section below) that are used to explore the impact of road networks on wildlife populations. The accuracy of such models depends on the inclusion of the roadeffect zone as it is a more realistic representation of the potential habitat loss associated with roads. For example, a study on Tawny owls (*Strix aluco*) in rural Portugal found that owl density could be impacted up to 2 km from a major road [56]. Even for a common and widespread species such an impact has the potential to influence population numbers and persistence in the area.

Instead, more studies focused on determining whether certain characteristics of a road influenced the extent to which wildlife avoided roadside habitats. Nine studies confirmed that species diversity and abundance near roads decreased with increasing traffic volume and three of these studies further attempted to quantify traffic volume thresholds at which species density began to decrease [57, 59, 60]. For example, a study in Canada revealed that grizzly bears (*Ursus arctos*) were more likely to use areas near roads with fewer than 20 vehicles per day [59]. It is studies like these that are essential for informing effective mitigation, such as traffic calming strategies (see Survey Design and Mitigation section).

The road effect zone can also be influenced by the degradation of air, land and water due to pollution from salt, sediment, chemical run-off, dust, noise, and light. Such roadrelated pollution can cause loss of habitat by making the area within the road effect zone unsuitable for wildlife. In this review, 23 studies explored the impact of road-related pollution on birds, mammals, amphibians, and invertebrates. Six of these studies determined that pollution caused the displacement of wildlife from roadside habitat, while the remaining 17 studies investigated the fitness consequences of polluted roadside habitats to wildlife. Among these 23 studies, 70% considered the impacts of noise pollution. For species that use vocalizations to undertaken crucial life history stages (such as song birds and amphibians; [61, 62]) or reply on sound to avoid predators, navigate and forage (such as bats and amphibians; [63, 64]), any noise that can mask sound can have a detrimental impact. For example, three studies demonstrated that bird diversity decreased as a result of road-related noise [65-67]. Another study showed that the foraging efficiency of Daubenton's bats (Myotis daubentonii) decreased when vehicle noise masked their echolocation calls, which in turn lead to the avoidance of roadside habitat [64]. A further three studies confirmed that road-related noise influenced the survival and breeding success of wildlife. Among birds, such noise led to smaller clutch sizes [68] and reduced longevity [69], and among amphibians, it induced a stress response and impaired the wood frog's (Lithobates sylvaticus) ability to

attract mates [62]. Similarly, a study on Stephen's kangeroo rat (*Dipodomys stephensi*) found that the sound of passing vehicles induced foot drumming and thus raised concerns that engaging in such false responses could potentially be energetically and biologically costly [70]. It is studies like these that emphasize the importance of the soundscape and mitigation should take noise pollution from roads into account, although it should be noted that certain species are more sensitive to noise pollution than other. For example, six studies found that road-related noise did not appear influence their study species, including arboreal rainforest mammals [71], a large ungulate [72], a bird of prey [73], certain song birds [74, 75], and some amphibian species [76].

Of the remaining studies to explore the impact of road pollution on wildlife, one explored light pollution [77], one considered heavy metals and five investigated the fitness consequences of deicing salt. The latter studies all demonstrated that amphibian larval survival was reduced by increases in salinity [78–81]. In fact, one study showed that for *Rana temporaria*, even the smallest increase in the salt concentration (500 mg/L) could cause tadpole mortality [81].

#### **Consequences of Road Networks on Wildlife Populations**

Only 10% of the studies included in this review considered the implications of road networks on wildlife. As road networks have the ability to isolate populations, disconnect resource networks, and cause the irreversible degradation of habitat at a landscape scale, it is essential that we understand how existing road networks impact wildlife and how increasing road density may influence local and regional population persistence. The lack of current research is likely due to the logistical and economic limitations associated with such landscape-scale field studies. Yet, there is an increasing trend toward the use of predictive models to estimate and explore the impacts of road networks. For example, six studies presented models that were developed specifically to provide insights into the implications of road networks. Four of these studies focused on landscape connectivity, including a model that explored how road networks could influence pronghorn migration [82] and one that was developed to predict where black bears (Ursus americanus) were likely to encounter roads [83]. Another study created a predictive model that estimated the persistence of populations in a road-fragmented landscape [84], and finally a study simulated the genetic consequences created by the barrier-effects of roads across the road network [85]. For those species that have distinct movement corridors to access resources, disperse to maintain their social structure, or seasonally migrate, the presence of a road network within the landscape may have two, not necessarily exclusive, consequences. The first being, if roads act as barriers to movement, individuals may not be able to access critical food resources, breeding grounds, hibernacula, or avoid inbreeding. Predictive models may, therefore, be essential in identifying and providing insights into such issues. These insights can then be used to inform road planning and potentially identify alternative routes, incorporate targeted mitigation measures into the road construction stage (such as crossing structures and balancing ponds), and identify critical locations for the restoration and creation of new habitats.

Of the remaining studies relating to road networks, five studies were able to explore how road density impacted large mammals, primarily by using GPS collars that enabled them to map movement patterns across landscapes (e.g., caribou, moose, and lynx were among the species studied). These research studies demonstrated that for species that are well-adapted to moving through a heterogeneous landscape, road networks can still impede their movement [86], alter their behavior and activity patterns [87, 88], and influence their habitat use [89]. But even without any changes in habitat use and/or behavior, the more roads an individual has to cross within its home range, the greater the probability of a wildlifevehicle collision [90, 91].

A number of studies also highlighted that road networks can augment the negative implications of roads. For example, one study on caribou showed that calf survival in proximity to roads decreased because predators habitually used roads as movement corridors [92]. Another emerging issue is that roads bring humans more readily into contact with wildlife. Three studies demonstrated that as road networks develop and increase accessibility of the landscape, the opportunities for hunting also increased [93-95]. Essentially, road networks increased the proportion of the landscape that could be accessed by humans and in so doing decreased the amount of available wildlife refuge [93]. For example, a notable increase in the bushmeat trade is threatening the population persistence of game species [95]. Studies included in this review showed that this increase was found to be associated with the presence of roads and not population growth in the local communities [94, 95]. Thus, as road development continues to fragment the remaining tracts of natural habitat, there is likely to be an initial and evident loss of species. One study also raised concerns that the development of road networks will impact protected areas [94]. Despite being afforded protection, the presence of roads can give humans better access to such areas and surrounding habitats and, therefore, access to species of conservation concern. Thus, poaching and the illegal pet trade are effectively made easier where roads are present and can potentially impede and jeopardize conservation efforts for many threatened and endangered species.

## Survey Design and Mitigation

Among the 215 studies reviewed, 27% were focused on survey design and mitigation, not including the six studies that presented innovative predictive models referred to in the

section above. The majority of these studies (38 of 58) involved the evaluation of proposed mitigation. One commonly used practice is the implementation of wildlife crossing structures, which are designed to allow focal species to move across roads safely. Nevertheless, despite many structures being constructed along roads all over the world, up until recently there has been a lot of uncertainty surrounding their effectiveness. Thus, it is not surprising that there has been a sudden influx of research studies that specifically evaluate such crossing structures (i.e., 26 studies included in this review). Nineteen studies evaluated the effectiveness of underpasses (culverts and tunnels) and seven evaluated overpasses ("green" bridges and tree canopy linkages or gantries). These studies demonstrated that there was a considerable amount of variation in the effectiveness of crossing structures. For example, while one study reported a 79% decline in roadrelated mortality of amphibians with crossing structures present [96], another study found that amphibian mortality remained the same with or without structures [97].

Overall, many studies agreed that crossing structures alone where not as effective as expected [98–102], and those studies that reported road mortality rates more often saw reductions ranging from 10 to 20% [103, 104]. Nevertheless, two studies speculated that crossing structures were still biologically effective as low crossing frequencies may be enough to maintain functional connectivity [105, 106]. A study on bear species in Canada supported this theory by revealing that while structures were not frequently used, overall use was sufficient to ensure gene flow between populations [107]. It is this level of connectivity that potentially justifies the continued implementation of crossing structures as mitigation, particularly where rare and endangered species are concerned [108].

Another commonly used mitigation strategy is to put up fencing along roadsides, which can either prevent wildlife from crossing a road or funnel them towards crossing structures. A total of five studies explored how effective fencing was, and among these studies, reductions in road-related mortality still varied considerably, ranging from 50 to 98% [109, 110]. They identified factors that may have influenced the effectiveness of the fencing to be species-specific use, length of fencing, and presence of intersections [109, 111, 112]. Two studies even cautioned that fencing was ineffective unless it was continually maintained and breaches in the fencing were repaired in a timely manner [111, 113]. Furthermore, many studies suggested that road-related mortality could be further reduced when crossing structures were combined with fencing [97, 114, 115]. Moreover, one study on koalas (Phascolarctos cinereus) in Australia emphasized that selecting a single mitigation option was not economically viable [114].

A third mitigation strategy is to implement traffic calming measures, such as speed bumps, lowing speed limits or using warning signs. Three studies included in this review reported that reducing speed limits effectively decreased wildlifevehicle collisions [116], but two further studies cautioned that traffic calming devices, such a roundabouts, chicanes and speed bumps, were more effective than signage alone [117, 118]. Another study suggested that warning signs were more effective when used sparingly, in other words, only when the risk of wildlife-vehicle collisions was high (i.e., during migration or the breeding season, or when visibility was poor) [119].

Finally, three studies evaluated alternative or innovative mitigation strategies. One study explored whether having a vegetative medium facilitated the movement of small mammals, reptiles, and amphibians across roads; however, the results suggested this strategy was ineffective [120]. Another study tested an odor repellent intended to deter wildlife from crossing roads. They found that the repellent successfully reduced the crossing activity of larger mammals commonly reported in wildlife-vehicle collisions [121]. The third study evaluated the effectiveness of pole barriers at preventing birds from crossing roads at vehicle height. This study reported that 94% of birds, including a wide variety of species, shifted their flight paths as a result of the pole barrier being present [122]. The development and evaluation of mitigation measures such as these remains one of the most crucial components of road ecology, as there is still a lot of scope to devise and modify more effective strategies [123, 124]. It is, therefore, important that such research and development continues and is encouraged.

Overall, many studies were in agreement that the effectiveness of crossing structures, fencing, deterrents, and traffic calming measures, was species-specific [96, 98, 105, 121]. A generic "one-size fits all" crossing structure or deterrent does not exist. These findings reiterate that transportation authorities and conservation practitioners will have to implement multiple forms of mitigation if they are to reduce wildlifevehicle collisions and maintain landscape connectivity for a range of species.

Of the remaining studies included in this review and category, 20 focused on evaluating, modifying, and developing survey techniques to better estimate road-related mortality, displacement, and road crossing activity. For example, four studies postulated that the way crossing structures are currently selected and even evaluated is biased and called for more effective mitigation selection and surveillance protocols [104, 125–127]. Similarly, a study conducted in a conservation area in South Africa revealed that the way roadkill surveys are undertaken can strongly influence road mortality estimates [128]. They identified that survey speed, time of day, and number of observers were all important factors to consider and highly recommended the use of standardized protocols. Another study determined that variations in carcass persistence could also bias survey results, as persistence was much lower in small animals and easily influenced weather conditions [129]. Other studies flagged up survey interval [130], scavenger removal [131] and species detectability [132, 133] as factors that would influence survey results. Such biased surveys are particularly concerning if mortality estimates are used to determine the impact of roads and road networks on a species, and particularly when species of concern are involved. Furthermore, the implementation of mitigation measures, and certainly the placement of crossing structures, is often based on the identification of mortality hotspots or distinct patterns of mortality along a road. Thus, if the surveys used to inform mitigation are inaccurate, then it is likely that any mitigation implemented will be ineffective.

Finally, the development and use of models continues to gain popularity with a further nine studies presenting models that could be used to estimate road-related mortality [134, 135] and identify potential mortality hotspots based on surrounding habitat and landscape features [40, 136–139]. For example, one model was constructed specifically to identify ideal locations for crossing structures for the endangered Florida panther (*Puma concolor coryi*) using GPS collar data and wildlife-vehicle collision reports [140]. Another model was developed to identify habitat patches that could be restored and define wildlife corridor locations that would have the best chance of increasing landscape connectivity [141]. Again predictive models may prove to be an essential tool in the road planning and mitigation stages of future road development.

# Conclusions

One very clear trend that was evident from this review was that while many studies speculate that the negative impacts of roads can have consequences for wildlife populations due to increased mortality rates, displacement, habitat degradation, and loss of landscape connectivity, very few studies explored the population-level consequences. Moreover, the majority of studies investigated the impact of individual road-associated factors, such as road mortality or road avoidance, but only a handful of studies considered the impact of more than one factor combined. Based on the research conducted, it is likely that most species will not be impacted by a single factor. For example, among the studies to research freshwater turtles, two studies found that roads were a source of mortality due to wildlife-vehicle collisions [120, 142] and two studies determined that the movement of turtles was physically hindered by the roads themselves [52, 143]. Yet, it is the combination of both direct and indirect factors that will provide us with a better understanding of the barrier effects of roads on freshwater turtles. Furthermore, if we are to effectively mitigate the impacts of roads, we need to understand the full extent of the impact. For example, using fencing may effectively reduce the number of pronghorns killed by vehicles on roads, but it may also reduce landscape permeability by hindering their ability to migrate across the landscape [46, 82]. Considering the large amount of research studies that has been conducted in the last three decades on a wide range of road-related factors and across a diverse array of species, there is certainly an opportunity to use the data to explore the cumulative impacts of roads on wildlife.

One emerging aspect of road ecology that warrants encouragement is the continued development of predictive landscape-scale models. Such models have great potential to be used as tools for the assessment, prevention, and mitigation of road networks. By having such models in their toolbox, transportation authorities and conservation practitioners may be better equipped to address the ecological implications of roads and proposed road development.

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#### **Compliance with Ethical Standards**

**Conflict of Interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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