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Bats on the road — a review of the impacts of roads and highways on bats

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The increase in human population has resulted in environmental alterations and habitat fragmentation, such as those caused by road construction. Since the late 1990s, there has been an increase in studies evaluating the effects of roads on vertebrate populations; however, few studies have considered bats in road ecology studies. In this review on road ecology studies focusing on bats, we evaluated the impacts of roads on bat mortality, commuting, and foraging. We also evaluated the use of road structures as roosts and provide suggestions for future research and mitigation methods based on available results. Road impacts on bat activity and roadkill are strongly influenced by landscape features, and areas with short trees have more impact on roadkill. Also, in open areas, bats prefer to forage near roads whereas in woodland areas activity increases with distance from the road. Most studies evaluating the effects of roads on bats have been conducted in Europe, therefore it is essential that these studies are conducted in other areas, especially in developing countries. To ensure the conservation of bat species, it is imperative that studies consider all impacts that roads have on bat populations and that mitigation measures are applied, especially when road construction meets bat commuting or foraging paths.

Key words: barrier effects, bridges, Chiroptera, roadkill

INTRODUCTION

Human populations have expanded exponentially in the last decades (Ehrlich and Ehrlich, 1990; Brandt *et al*., 2017) and environmental alterations come along with this growth (Pimentel *et al*., 1997; Brandt *et al*., 2017). One of the leading impacts of anthropogenic alteration on wildlife is increased habitat fragmentation (Fahrig, 2003; Haddad *et al*., 2015). Roads represent an extreme form of fragmentation as virtually no vertebrate organism can inhabit this matrix (Pires *et al*., 2002; Rosa, 2012). Currently, most regions around the world have at least one road and road density is likely to increase (Bennett, 2017), highlighting the importance of studies evaluating road effects on the environment.

In the late 1990s, landscape ecologist Richard Forman coined the term 'road ecology' to describe the study of the effects of roads on ecosystem structures and processes (Forman, 1998: Road ecology: a solution for the giant embracing us); since then, many studies have evaluated road effects on both biotic and abiotic components of the surrounding environments (Coffin, 2007). Those studies have described the effects of roads on a range of taxa, including birds (Rosa and Bager, 2012), amphibians (Eigenbrod *et al*., 2008), reptiles (Woltz *et al*., 2008), and mammals (Grilo *et al*., 2009; Barthelmess and Brooks, 2010). Most mammalian studies have focused on large carnivores and small non-flying mammals (e.g., Oxley *et al*., 1974; Adams and Geis, 1983; Newmark *et al*., 1996; Ascensão *et al*., 2017; Carvalho *et al*., 2018; Pinto *et al*., 2018; Santos *et al*., 2018), but some authors have shown that bats are profoundly affected by traffic casualties (Lesiński, 2008; Gaisler *et al*., 2009; Novaes *et al*., 2018) and traffic noise (Zurcher *et al*., 2010; Berthinussen and Altringham, 2012*b*).

Bats represent the second largest order of mammals, with at least 1,386 described species (Burgin *et al*., 2018) that include insectivorous, frugivorous, hematophagous, and nectar-feeding bats (Kalko *et al*., 1996; Simmons, 2005; Kunz *et al*., 2011). Because of their large repertoire of feeding habits, bats play an important ecological role by providing ecosystem services such as pollination, seed dispersal, and insect control (Kunz *et al*., 2011). Moreover, bats are of importance for conservation biology because at least 186 of the species are threatened (IUCN, 2019). Road mortality may pose additional conservation problems for bats because of their low fecundity and late maturation, which increases their local extinction risk.

Previous review papers on the effects of roads on bats include the review by Richarz (2000), who evaluated effect of traffic routes in German bats, Fensome and Mathews (2016), which evaluated bat-vehicle collisions and the barrier effects of roads in European bats, Novaes *et al*. (2018), who recently reviewed road-killed bats in Brazil, and Smith *et al*. (2017) and Jones *et al*. (2019), who reviewed impacts of roads and mitigation measures in New Zealand bats. Moreover, book chapters on bats and roads have been recently published by Abbott *et al*. (2015), who considered only small insectivorous species from temperate regions, and Altringham and Kerth (2016), who also reviewed studies conducted in temperate regions, however, including work on other animals, especially birds, to fill important knowledge gaps in tropical areas. In contrast with previous studies, in this review we evaluated how bats are considered in road ecology studies around the world, including data from North and South America, Europe, Australia, Asia, and Africa, and the impacts of roads on bat mortality, commuting, and foraging. We also evaluated studies reporting the use of road structures as roosts for bat populations and provided suggested mitigation methods and future research topics.

We performed online searches at Google Scholar database using search terms related to road ecology. We used a combination of the following key words: ‘roads’ or ‘highways’ and ‘bats’ or ‘Chiroptera’. To increase the number and geographic range of analysed papers, we also included the same words in Portuguese (‘estradas’ and ‘morcegos’ or ‘Chiroptera’), Spanish (‘carreteras’ and ‘murciélagos’ or ‘Chiroptera’), and French (‘routiers’ and ‘chauve-souris’ or ‘Chiroptera’). In addition to reviewing the articles identified through the database search, we reviewed papers cited in those articles. Only publications focusing on the effects of roads on bats were considered. Articles that only mentioned the presence of bats, especially in roadkill, but did not focus on bats, were not used to the analysis. From the resulting publications, we extracted data related to geographic location and year of publication, bat species, and factors that contributed to the effects of roads on bat populations. We performed another online search including the key words ‘bridge(s)’ or ‘culverts’ and ‘bats’ or ‘Chiroptera’ to identify studies that reported the use of road structures as roosts. We also included words in Portuguese (‘pontes’), Spanish (‘puentes’), and French (‘ponts’).

Historical and Regional Distribution of Studies

The first studies considering the impacts of roads on bats were published in the early 1990s (Blake *et al*., 1994; Rackow *et al*., 1994), and the number of studies has been increasing, with 30 studies published in the last 10 years for a total of 43 publications (Table 1). Most of these studies were conducted in Europe (67.44%), and few papers addressing effects of roads on bats were conducted in Australia, North America, and South America (Table 1). To our knowledge, no road ecology studies focusing on bats have been conducted in Asia or Africa, however, few studies have considered road presence in multiple-variable analysis (Deshpande, 2012; Azhar *et al*., 2015).

Impacts of Roads on Bats

Bats as Victims of Roadkill

Roadkill is one of the main anthropogenic causes of mortality for several vertebrate species in the wild, exceeding mortality caused by hunting or habitat loss (Forman and Alexander, 1998). Worldwide, millions of individuals are killed every year on the roads, which may ultimately result in local extinction for some species (Slater, 1994; Forman and Alexander, 1998; Coffin, 2007). Among vertebrates, mammals represent a relatively high number of road-killed individuals (Glista and DeVault, 2008; Barthelmess and Brooks, 2010); however, few studies have evaluated bat roadkill.

Many studies have reported that bats are not frequently involved in vehicle collisions (Hodson, 1960; Seibert and Conover, 1991; Ashley and Robinson, 1996; Bartoszewicz, 1997; Smith and Dodd, 2003); however, the number of casualties may be higher than previously thought. Because the small body mass of these animals facilitates carcass removal, their numbers may be underestimated

TABLE 1. Road ecology studies focusing on bat roadkill, activity, and diversity along roads in different countries with main findings in each study. Reference number as in Table 2

No.	Reference	Country	Main findings
		Activity and diversity	
[01]	Blake *et al*. (1994)	U.K.	Higher activity near illuminated roads
[09]	Gaisler *et al*. (2009)	Czech Republic	Higher activity in roads near lakes
[11]	Kerth and Melber (2009)	Germany	Smaller foraging area; Barrier to roost switch
[12]	Zurcher *et al*. (2010)	U.S.A.	Higher avoidance with car presence
[14]	Lesiński *et al*. (2011*a*)	Poland	Higher individuals in large roads
[15]	Bennett and Zurcher (2012)	U.S.A.	Higher avoidance with car presence
[16]	Berthinussen and Altringham (2012)	U.K.	Higher activity and diversity further from roads (1,600 m)
[17]	Deshpande (2012)	India	Decreased activity in areas with roads
[19]	Abbott *et al*. (2012*b*)	Ireland	Bats use underpasses more than overpasses
[20]	Abbott *et al*. (2012*a*)	Ireland	Clutter-adapted species prefer to cross on underpasses
[22]	Kitzes and Merenlender (2014)	U.S.A.	Higher activity further from roads (300 m)
[24]	Azhar *et al*. (2015)	Malaysia	Higher richness near roads
[26]	Bonsen *et al*. (2015)	Australia	Higher activity and feeding buzz near roads
[27]	Sjolund (2015)	Sweden	More crossing on underpasses
[28]	Luz (2016)	Sweden	More crossing on underpasses
[29]	Bhardwaj (2017)	Australia	Higher activity further from roads
[31]	Myczko *et al*. (2017)	Poland	Longer activity on larger roads
[34]	Suchocka *et al*. (2019)	Poland	Nine bat species were observed foraging and roosting on the road alley
[35]	Claireau *et al*. (2019)	France	Higher activity further from roads
[36]	Medinas *et al*. (2019)	Portugal	Higher activity near roads on open dry areas and far from roads on woodland areas
[37]	Davies (2019)	U.K.	Larger culverts and those located in areas with features to guide bats are more efficient as underpasses
[38]	Geipel *et al*. (2019)	Panama	Traffic noise playback doesn't affect emergence time, but increases the number of exploration flights
[40]	Bhardwaj *et al*. (2020)	Australia	Individuals avoid using lit underpasses
[41]	Bolliger *et al*. (2020)	Switzerland	Areas with traffic-regulated dimming lights had less activity
[42]	Borkin *et al*. (2020)	New Zealand	Activity decreases with higher traffic volume
[43]	Finch *et al*. (2020)	U.K.	Use of traffic noise playback decreases activity and foraging
		Roadkill	
[02]	Rackow *et al*. (1994)	Germany	More roadkill during summer months
[03]	Kiefer *et al*. (1995)	Germany	More roadkill during summer months
[04]	Haensel and Rackow (1996)	Germany	Males more roadkilled than females
[05]	Bafaluy (2000)	Spain	Higher roadkill near periurban areas
[06]	Capo *et al*. (2006)	France	Higher roadkill rates in low-flying species
[07]	Lesiński (2007)	Poland	Higher roadkill rates in youngs and low-flying species
[08]	Lesiński (2008)	Poland	Higher roadkill near linear features
[09]	Gaisler *et al*. (2009)	Czech Republic	Higher roadkill rates in low-flying species
[10]	Russel *et al*. (2009)	U.S.A.	Higher roadkill rates in open areas
[13]	Lesiński *et al*. (2011*b*)	Poland	Less roadkill near windbreaks and bushes
[18]	Medinas *et al*. (2013)	Portugal	More bats roadkilled in areas with high habitat quality, higher traffic volume, and more viaducts
[21]	Iković *et al*. (2014)	Montenegro	Higher roadkill rates in areas with higher traffic volume and near linear features
[23]	Parise (2014)	France	Few individuals
[25]	Alves *et al*. (2015)	Brazil	Individuals from four families roadkilled in areas near houses
[30]	Ceron *et al*. (2017)	Brazil	More roadkill in Phyllostomidae species
[32]	Secco *et al*. (2017)	Brazil	Higher roadkill in higher traffic volumes; Less roadkill in areas near natural forests
[33]	Novaes *et al*. (2018)	Brazil	More roadkill in Phyllostomidae species
[39]	Stoianova *et al*. (2019)	Bulgaria	Higher roadkill rates in areas near potential roosts

(Svensson, 1998; Bafaluy, 2000; Slater, 2002; Schwartz *et al*., 2018). Road impacts on bats are well studied in Central and Eastern Europe (Kiefer *et al*., 1995; Haensel and Rackow, 1996; Lesiński, 2007, 2008; Gaisler *et al*., 2009; Kerth and Melber, 2009; Lesiński *et al*., 2011*a*); however, few studies have been conducted in southern Europe (Bafaluy, 2000; Medinas *et al*., 2013; Presetnik *et al*., 2014), North America (Russel *et al*., 2009), and South America (Ceron *et al*., 2017; Secco *et al*., 2017; Novaes *et al*., 2018). To our knowledge, there are no published studies focusing on bat roadkill in Africa, Asia, or Australia.

Studies conducted in Europe and in North and South America have recorded at least 76 species from the following eight families of bats that were involved in bat-vehicle collisions: Vespertilionidae (35 species), Phyllostomidae (27 species), Molossidae (five species), Rhinolophidae (three species), Mormoopidae (two species), Noctilionidae (two species), Emballonuridae (one species), and Miniopteridae (one species) (Table 2). According to Fensome and Mathews (2016) *Pipistrellus* and *Myotis* are the bat genera most affected by vehicle collisions in Europe. In South America, frugivorous species from the Phyllostomidae family account for more than 60% of road-killed bats on Brazilian roads (Novaes *et al*., 2018).

Some species are more affected by vehicle collisions because of their hunting strategies (Fensome and Mathews, 2016; Novaes *et al*., 2018). Depending on their ecology and feeding behaviour (Kalko *et al*., 1996), bats fly in different heights, from low-flying species, which forage at 5–10 m (Schober and Grimmberger, 1998), to high-flying species, which forage at altitudes up to 50 m (Schnitzler and Kalko, 2001; Gaisler *et al*., 2009). Most *Pipistrellus* species forage near the ground, at 2–6 m (Schober and Grimmberger, 1998), as do frugivorous bats from the family Phyllostomidae, which forage below the canopy level, at under 10 m (Kalko *et al*., 1996; Stockwell, 2001). Low-flying species tend to be the most affected by vehicle collisions (Stratman, 2006; Lesiński, 2007) because they fly at traffic height.

Other characteristics, such as sex and age, may also affect the risk of bat-vehicle collision. Fensome and Mathews (2016) reported that males are more likely to be involved in collisions, and this finding is consistent with that of other studies (Lesiński *et al*., 2011*a*; Medinas *et al*., 2013; Iković *et al*., 2014). Males tend to fly longer distances and may have larger home ranges (O'Donnell, 2001; Safi *et al*., 2007), which may increase the likelihood of an encounter with a vehicle (Fensome and Mathews, 2016). Younger bats may also be more prone to collisions (Lesiński, 2007; Fensome and Mathews, 2016) because they usually fly in lower heights (Buchler, 1980; Kurta, 1982). In addition, many bats could mistake a smooth road surface after rain for a water surface (Lesiński, 2007).

The structure of the environment adjacent to the road is another important factor influencing the number of bats involved in vehicle collisions (Lesiński, 2008; Russel *et al*., 2009; Medinas *et al*., 2013; Iković *et al*., 2014). Lesiński (2008) proposed that linear elements near the roads might increase bat roadkill because bats usually commute in routes with linear features (Verboom and Huitema, 1997; Rodríguez-San Pedro *et al*., 2018). A correlation between linear features in the landscape and a higher number of casualties has been observed in Poland (Lesiński, 2008), Montenegro (Iković *et al*., 2014), and the United States (Russel *et al*., 2009). Furthermore, when the road is surrounded by deforested areas or smaller trees, bats tend to fly closer to the ground, increasing the risk of collision (Russel *et al*., 2009). In Poland, fewer bats were killed by vehicles in road sections with windbreakers and bushes at its margins (Lesiński *et al*., 2011*b*).

The risk of bat-vehicle collision is also increased by the construction of roads across existing migration or commuting routes (Lesiński, 2007) and features that improve habitat quality near roads (Russel *et al*., 2009; Medinas *et al*., 2013, 2019), because bats prefer to use high-quality habitats for foraging and roosting (Pyke, 1984). For example, in Portugal, the presence of 'montado', an extensive savanna-like system, and nearby streams increases the number of road-killed bats (Medinas *et al*., 2013). Similarly, there was also a correlation between nearby water habitats and bat mortality on roads in the Czech Republic, especially for *Pipistrellus* spp. and *Myotis* spp. (Gaisler *et al*., 2009). In Bulgaria, Stoianova *et al*. (2019) registered that bat roadkill were higher in areas near existing or potential roosts.

High bat activity near roads appears to be another important factor associated with bat-vehicle collisions (Medinas *et al*., 2013). In Montenegro, Iković *et al*. (2014) observed that *Pipistrellus kuhlii*, the most abundant species in the study area, was the species most likely to be involved in collisions. Similarly, in Spain, Bafaluy (2000) observed that road sites near urban areas were associated with higher mortality rates for *Pipistrellus kuhlii* and *P. pipistrellus,* species well adapted to the urban environment (Bogdanowicz, 2004; Wawrocka *et al*., 2012). Synanthropic bats are not typically hampered by anthropogenic alterations (Figueiredo *et al*., 2015); thus, vehicle collision may represent an essential threat to these species (Bafaluy, 2000). Because the presence of roosts (Medinas *et al*.,

TABLE 2. Bat species and feeding guilds identified in studies of road-killed bats and bat activity along roads in different countries. I = insectivorous, P = piscivorous, N = nectar-feeding, F = frugivorous, C = carnivorous, H = hematophagous, O = omnivorous, AUS = Australia, BRA = Brazil, BUL = Bulgaria, CZE = Czech Republic, FRA = France, GER = Germany, IND = India, IRE = Ireland, MAL, Malaysia, MON = Montenegro, NZL = New Zealand, PAN = Panama, POL = Poland, POR = Portugal, SPA = Spain, UK = United Kingdon, SWE = Sweden, USA = United States of America

Species grouped by family	Feeding guild	Road-killed bats (76 species)		Bat activity (80 species)	
		Country	Reference	Country	Reference
Emballonuridae					
Saccolaimus saccolaimus	I	–	–	IND	[17]
Saccopteryx leptura	I	BRA	[33]	–	–
Taphozous melanopogon	I	–	–	IND	[17]
Miniopteridae					
Miniopterus australis	I	–	–	AUS	[26]
M. pusillus	I	–	–	IND	[17]
M. schreibersii	I	BUL, GER, POR, SPA	[03] [04] [05] [18] [39]	AUS, IND, POR	[17] [26] [36]
Megadermatidae					
Megaderma lyra	O	–	–	IND	[17]
M. spasma	O	–	–	IND	[17]
Molossidae					
Austronomus australis	I	–	–	AUS	[29] [40]
Eumops auripendulus	I	BRA	[33]	–	–
E. perotis	I	–	–	USA	[22]
Molossus molossus	I	BRA	[32] [33]	–	–
M. rufus	I	BRA	[32] [33]	–	–
Nyctinomops laticaudatus	I	BRA	[33]	–	–
Ozimops planiceps	I	–	–	AUS	[29] [40]
O. ridei	I	–	–	AUS	[26] [29]
Tadarida aegyptiaca	I	–	–	IND	[17]
T. australis	I	–	–	AUS	[26]
T. brasiliensis	I	BRA	[33]	USA	[22]
T. teniotis	I	–	–	POR	[36]
Mormoopidae					
Pteronotus personatus	I	BRA	[25]	–	–
P. rubiginosus	I	BRA	[33]	–	–
Noctilionidae					
Noctilio albiventris	P	BRA	[33]	–	–
N. leporinus	P	BRA	[33]	–	–
Hipposideridae					
Hipposideros pomona	I	–	–	IND	[17]
Phyllostomidae					
Anoura caudifer	N	BRA	[30] [33]	–	–
A. geoffroyi	N	BRA	[25] [33]	–	–
Artibeus fimbriatus	F	BRA	[30] [33]	–	–
A. lituratus	F	BRA	[30] [32] [33]	–	–
A. obscurus	F	BRA	[33]	–	–
A. planirostris	F	BRA	[25] [33]	–	–
Carollia perspicillata	F	BRA	[32] [33]	–	–
Chiroderma doriae	F	BRA	[33]	–	–
C. villosum	F	BRA	[33]	–	–
Chrotopterus auritus	C	BRA	[33]	–	–
Dermanura cinerea	F	BRA	[33]	–	–
Desmodus rotundus	H	BRA	[33]	–	–
Diphylla ecaudata	H	BRA	[33]	–	–
Glossophaga soricina	N	BRA	[33]	–	–
Lophostoma silvicolum	I	BRA	[33]	–	–
Macrophyllum macrophyllum	I	BRA	[33]	–	–
Micronycteris minuta	I	BRA	[33]	PAN	[38]
Mimon bennettii	I	BRA	[33]	–	–
Phyllostomus hastatus	O	BRA	[32] [33]	–	–
Platyrrhinus lineatus	F	BRA	[33]	–	–
P. recifinus	F	BRA	[32] [33]	–	–
Sturnira lilium	F	BRA	[30] [32] [33]	–	–

TABLE 2. Continued

Species grouped by family	Feeding guild	Road-killed bats (76 species)		Bat activity (80 species)	
		Country	Reference	Country	Reference
Phyllostomidae					
S. tildae	F	BRA	[33]	–	–
Tonatia bidens	I	BRA	[33]	–	–
Trachops cirrhosus	C	BRA	[33]	–	–
Uroderma bilobatum	F	BRA	[25]	–	–
Vampyressa pusilla	F	BRA	[33]	–	–
Pteropodidae					
Cynopterus brachyotis	F	–	–	MAL	[24]
C. sphinx	F	–	–	IND	[17]
Eonycteris spelaea	F	–	–	MAL	[24]
Pteropus giganteus	F	–	–	IND	[17]
Rousettus leschenaultii	F	–	–	IND	[17]
Rhinolophidae					
Rhinolophus beddomei	I	–	–	IND	[17]
R. blasii	I	MON	[21]	–	–
R. ferrumequinum	I	FRA, GER, POR	[04] [06] [18]	FRA, POR, UK	[35] [36] [37] [43]
R. hipposideros	I	CZE, FRA, GER, MON, POL, POR, SPA	[02] [03] [04] [05] [07] [09] [18] [21] [23]	FRA, IRE	[19] [20] [35]
R. lepidus	I	–	–	IND	[17]
R. megaphyllus	I	–	–	AUS	[26]
R. rouxii	I	–	–	IND	[17]
Vespertilionidae					
Antrozous pallidus	I	–	–	USA	[22]
Barbastella barbastellus	I	CZE, FRA, GER, POL, POR, SPA	[03] [04] [05] [06] [07] [14] [18]	CZE, FRA, GER, POL, POR	[09] [11] [13] [31] [35] [36]
Chalinolobus dwyeri	I	–	–	AUS	[26]
C. gouldii	I	–	–	AUS	[26] [29] [40]
C. morio	I	–	–	AUS	[26] [29] [40]
C. tuberculatus	I	–	–	NZL	[42]
Corynorhinus townsendii	I	–	–	USA	[22]
Eptesicus brasiliensis	I	BRA	[33]	–	–
E. fuscus	I	–	–	USA	[12] [15] [22]
E. nilsonii	I	GER	[03] [04]	POL, SWE	[27] [34]
E. serotinus	I	CZE, GER, POL, POR, SPA	[02] [03] [04] [05] [07] [09] [14] [18]	CZE, FRA, POL	[09] [13] [34] [35]
Hypsugo savii	I	SPA	[05]	CZE	[09]
Histiotus velatus	I	BRA	[33]	–	–
Lasionycteris noctivagans	I	–	–	USA	[22]
Lasiurus blossevillii	I	BRA	[33]	USA	[22]
L. borealis	I	–	–	USA	[12] [15]
L. cinereus	I	–	–	USA	[12] [15] [22]
L. ega	I	BRA	[30] [33]	–	–
Myotis alcathoe	I	CZE	[09]	CZE	[09]
M. bechsteinii	I	FRA, GER	[03] [04] [06]	CZE, GER	[09] [11]
M. blythii	I	SPA	[05]	–	–
M. brandtii	I	BUL, CZE, GER, POL	[02] [03] [04] [07] [09] [39]	CZE, POL, SWE	[09] [13] [27] [28]
M. californicus	I	–	–	USA	[22]
M. capaccinii	I	MON, SPA	[05] [21]	–	–
M. dasycneme	I	POL	[05]	CZE, POL	[09] [13]
M. daubentonii	I	CZE, FRA, GER, POL, POR, SPA	[02] [03] [04] [05] [06] [07] [09] [18]	CZE, IRE, POL	[09] [13] [20]
M. emarginatus	I	CZE, FRA, SPA	[05] [06] [09]	CZE	[09]
M. escalerai	I	POR	[18]	–	–
M. evotis	I	–	–	USA	[22]
M. horsfieldii	I	–	–	IND	[17]
M. izecksohni	I	BRA	[33]	–	–

TABLE 2. Continued

Species grouped by family	Feeding guild	Road-killed bats (76 species)		Bat activity (80 species)	
		Country	Reference	Country	Reference
Vespertilionidae					
M. lucifugus	I	USA	[21]	USA	[15] [22]
M. myotis	I	FRA, GER, POL	[02] [03] [04] [06] [07]	CZE, GER, POL	[09] [11] [13]
M. mystacinus	I	CZE, FRA, GER, MON, POL	[03] [04] [06] [07] [09] [21]	CZE, GER, SWE	[09] [11] [27] [28]
M. nattereri	I	CZE, FRA, GER, POL	[02] [03] [04] [06] [07] [08] [09] [14]	CZE, GER, IRE, POL	[09] [11] [13] [20]
M. nigricans	I	BRA	[33]	–	–
M. riparius	I	BRA	[33]	–	–
M. ruber	I	BRA	[30]	–	–
M. sodalis	I	USA	[10]	USA	[12]
M. thysanodes	I	–	–	USA	[22]
M. volans	I	–	–	USA	[22]
M. yumanensis	I	–	–	USA	[22]
Nyctalus leisleri	I	BUL, CZE, GER, POL, POR	[02] [03] [04] [07] [09] [14] [18] [39]	CZE, FRA, IRE, POL	[09] [13] [19] [34] [35]
N. noctula	I	CZE, GER, POL	[02] [03] [04] [07] [09] [14]	CZE, FRA, POL, SWE	[09] [13] [27] [31] [34] [35]
Nycticeius humeralis	I	–	–	USA	[12]
Nyctophilus spp.	I	–	–	AUS	[26]
Parastrellus hesperus	I	–	–	USA	[22]
Perimyotis subflavus	I	–	–	USA	[12]
Pipistrellus ceylonicus	I	–	–	IND	[17]
P. coromandra	I	–	–	IND	[17]
P. kuhlii	I	FRA, MON, POR, SPA	[05] [06] [18] [21]	FRA, POR	[35] [36]
P. nathusii	I	CZE, FRA, GER, MON, POL	[04] [07] [08] [09] [14] [23]	CZE, POL	[09] [31] [34]
P. pipistrellus	I	CZE, FRA, GER, POR, SPA	[02] [04] [05] [06] [09] [18] [23]	CZE, FRA, GER, IRE, POL, POR, UK	[01] [09] [11] [16] [19] [20] [31] [34] [35] [36] [43]
P. pygmaeus	I	CZE, MON, POR	[09] [14] [18]	CZE, IRE, POL, POR, SWE, UK	[09] [13] [16] [19] [20] [27] [31] [34] [36]
P. tenuis	I	–	–	IND	[17]
Plecotus auritus	I	CZE, FRA, GER, POL	[02] [04] [06] [07] [08] [09] [14]	CZE, GER, IRE, POL, SWE	[09] [11] [13] [19] [20] [27] [34]
P. austriacus	I	CZE, FRA, GER, POL, SPA	[02] [04] [05] [06] [07] [09]	CZE, POL	[09] [13]
Scotophilus heathii	I	–	–	IND	[17]
Scotorepens balstoni	I	–	–	AUS	[29] [40]
Scotozous dormeri	I	–	–	IND	[17]
Vespadelus darlingtoni	I	–	–	AUS	[26] [40]
V. regulus	I	–	–	AUS	[29] [40]
V. vulturnus	I	–	–	AUS	[26] [40]
Vespertilio murinus	I	GER	[02] [04]	POL	[34]

[01] Blake *et al.* (1994); [02] Rackow *et al.* (1994); [03] Kiefer *et al.* (1995); [04] Haensel and Rackow (1996); [05] Bafaluy (2000); [06] Capo *et al.* (2006); [07] Lesiński (2007); [08] Lesiński (2008); [09] Gaisler *et al.* (2009); [10] Russel *et al.* (2009); [11] Kerth and Melber (2009); [12] Zurcher *et al.* (2010); [13] Lesiński *et al.* (2011*b*); [14] Lesiński *et al.* (2011*a*); [15] Bennett and Zurcher (2012); [16] Berthinussen and Altringham (2012); [17] Deshpande (2012); [18] Medinas *et al.* (2013); [19] Abbott *et al.* (2012*b*); [20] Abbott *et al.* (2012*a*); [21] Iković *et al.* (2014); [22] Kitzes and Merenlender (2014); [23] Parise (2014); [24] Azhar *et al.* (2015); [25] Alves *et al.* (2015); [26] Bonsen *et al.* (2015); [27] Sjolund (2015); [28] Luz (2016); [29] Bhardwaj (2017); [30] Ceron *et al.* (2017); [31] Myczko *et al.* (2017); [32] Secco *et al.* (2017); [33] Novaes *et al.* (2018); [34] Suchocka *et al.* (2019); [35] Claireau *et al.* (2019); [36] Medinas *et al.* (2019); [37] Davies (2019); [38] Geipel *et al.* (2019); [39] Stoianova *et al.* (2019); [40] Bhardwaj *et al.* (2020); [41] Bolliger *et al.* (2020); [42] Borkin *et al.* (2020); [43] Finch *et al.* (2020)

2013) and hibernation sites near roads increase bat activity (Capo *et al.*, 2006), they are also associated with increased bat roadkill (Satoianova *et al.*, 2019). Because many bats roost in human-made structures, such as houses and bridges (Keeley and Tuttle, 1999; Alves *et al*., 2015), their presence near roads also appears to increase bat roadkill, as observed by Medinas *et al*. (2013) in Portugal, where areas with viaducts had more casualties. The presence of artificial lights along roads may be another factor influencing bat abundance (Rydell, 1992; Stone *et al*., 2015); however, no study has evaluated whether the presence of artificial lights affects roadkill.

Likewise, seasonal patterns of activity may influence the number of bats killed on the roads. Most studies conducted in Europe reported increased bat roadkill during the summer months (August and September) (Bafaluy, 2000; Lesiński, 2007, 2008; Gaisler *et al*., 2009; Medinas *et al*., 2013; Iković *et al*., 2014; Parise, 2014), and in Brazil, Alves *et al*. (2015) recorded more road-killed bats in June and July (during the dry season). In contrast, Secco *et al*. (2017) reported that roadkill numbers were similar throughout the year in southeastern Brazil.

There is a large body of evidence demonstrating how species ecology and the environment surrounding roads influence bat casualties by road traffic, however, little is known about how road characteristics, except for traffic volume, affect this risk. Several studies have demonstrated that higher traffic volume is associated with increased bats casualties in Spain (Bafaluy, 2000), Portugal (Medinas *et al*., 2013), and Montenegro (Iković *et al*., 2014). Some authors suggest that road characteristics may also influence roadkill, but to our knowledge, there are no data showing how road width and different road types, such as paved highways or dirt roads, affect the risk of bat-vehicle collision, for example.

As previously mentioned, the number of road-killed bats may be underestimated (Slater, 2002; Lesiński, 2008; Gaisler *et al*., 2009; Medinas *et al*., 2013). Bats are easily removed from the road and often undetected because of their small size (Fischer, 1997; Slater, 2002), especially when searches are conducted by car. According to Russel *et al*. (2009), highway mortality may affect approximately 5% of a colony, indicating that collisions with vehicles are an important threat to bats and should not be overlooked, especially in areas with a dense road network (Lesiński *et al*., 2011*a*).

Bat Activity near Roads

Traffic noise is an important element of the soundscape (Botteldooren *et al*., 2006) and has been shown to cause physiological and behavioural stress in animals (Halfwerk *et al*., 2011; Morgan *et al*., 2012). For example, traffic noise may result in acoustic masking, impairing communication between individuals (Halfwerk *et al*., 2011) and avoidance behaviour in the presence of a predator (Chan *et al*., 2010). Higher levels of traffic noise have been described as detrimental for most species (Berthinussen and Altringham, 2012*b*). For bats, it has been observed that presence of roads may reduce foraging efficiency (Siemers and Schaub, 2011; Bunkley and Barber, 2015) and foraging areas (Kerth and Melber, 2009), as well as act as barriers to roost switching, which can restrict access to more suitable environments (Kerth and Melber, 2009).

The effects of traffic on the habitat use of bats varies, mainly because species with different foraging ecologies show different responses to road-related habitat alteration (Kerth and Melber, 2009). Studies evaluating road effects on bat activity have been conducted in different regions (Table 1), some of them considering road presence as one of many variables. At least 81 species from the families Vespertilionidae (54 species), Molossidae (eigtt species), Rhinolophidae (six species), Pteropodidae (five species), Miniopteridae (three species), Emballonuridae (two species), Megadermatidae (two species), and Hipposideridae (one species) (Table 2) have been recorded foraging near roads, and most of them are aerial or gleaning insectivores (Kalko *et al*., 1996).

Distance from the road appears to be an important factor influencing bat activity. Many species avoid foraging in sites near roads, as has been observed in the United Kingdom (UK), the US, France, India, and Australia (Berthinussen and Altringham, 2012*b*; Deshpande, 2012; Kitzes and Merenlender, 2014; Bhardwaj, 2017; Claireau *et al*., 2019; Finch *et al*., 2020). Berthinussen and Altringham (2012*b*) observed that proximity to a major highway in England negatively affected both activity and species richness, with a 3.5-fold increase in bat passes and 2.5-fold increase in species richness as distance from the road increased from 0 to 1,600 m. In India, Deshpande (2012) observed that activity of Rhinolophidae, Molossidae, and Miniopteridae (Vespertilionidae) was hampered by the presence of highways. Similarly, in the US the activity of bats from the families Molossidae and Vespertilionidae (*Tadarida brasiliensis*, *Eptesicus fuscus*, and *Lasiurus cinereus*) was twice as high at 300 m from the road than at its margin (Kitzes and Merenlender, 2014), and for the vespertilionid *Lasionycteris noctivagans*, bat passes were three times higher in sites located further from the road. In France, Claireau *et al*. (2019) observed a significant negative effect of roads on bat activity, especially for clutter-adapted species. In Australia, the activity of most bat species also decreased with distance from the road, with the exception of the molossid *Ozimops ridei* (Bhardwaj, 2017).

However, another Australian study conducted by Bonsen *et al*. (2015) reported higher bat activity in the first 10 m from the road, especially for the fast-flying species *Chalinolobus gouldii*, *Miniopterus schreibersii*, and *Tadarida australis*. In this study, foraging activity was also higher near roads, with 53.6% of feeding buzzes recorded within 10 m of the road (Bonsen *et al*., 2015). This discrepancy may be explained by an observation by Medinas *et al*. (2019), who observed that the effect of distance from the road on bat activity depends on the surrounding environment. In this Portuguese study, researchers observed that bat activity increased with distance from the road in woodland areas, whereas the opposite was observed in open agricultural areas, where activity decreased with distance from the road (Medinas *et al*., 2019). Moreover, Azhar *et al*. (2015) observed increased bat richness near roads in Malaysia, possibly because of the presence of banana crops planted in those areas, which increases food and roost availability for fruit bats.

The presence of artificial lights installed near roads may also affect species that choose to forage in these areas (Stone *et al*., 2015). Fast-flying species are usually benefited from artificial lighting as it lures insects, thus providing more resources (Stone *et al*., 2015). In England, Blake *et al*. (1994) reported that orange street lamps were associated with a two-fold increase in bat activity compared with unlit roads, and white street lamps were associated with a five-fold increase. On the other hand, slow-flying species tend to avoid foraging near light bulbs (Stone *et al*., 2015), and can therefore avoid road verges. Bolliger *et al*. (2020) suggested that traffic-regulated lights have less effect on bat activity and that dimming of street lights could become an important tool for mitigating the negative effects of artificial lighting on organisms.

Other environmental attributes that appear to influence bat activity include proximity to water, tree cover, and structures or vegetation along the roads (Gaisler *et al*., 2009; Berthinussen and Altringham, 2012*b*; Medinas *et al*., 2013, 2019). For example, in the Czech Republic, road sites with two large artificial lakes on both sides had twice as many bat passes compared with road sites near a stream running under two bridges (Gaisler *et al*., 2009). In the U.K., Berthinussen and Altringham (2012*b*) observed that sites with continuous tall tree cover lining the roads showed increased bat activity. In contrast, sites with fences, walls, or hedges lining the road had significantly lower bat activity (Berthinussen and Altringham, 2012*b*). In Poland, Lesiński *et al*. (2011*b*) and Myczko *et al*. (2017) observed increased and longer activity at asphalt roads on the forest edge compared with unsurfaced forest roads with no vehicle traffic.

When comparing roads with different traffic volume, most studies have reported less bat activity near highways with intense traffic (Bennett *et al*., 2013; Kitzes and Merenlender, 2014; Pourshoushtari *et al*., 2018, Borkin *et al*., 2020), probably because bats tend to avoid foraging in loud environments (Schaub *et al*., 2008; Bunkley *et al*., 2015), therefore roads with low-to-moderate traffic volume could pose a more significant threat for roadkill (Langevelde *et al*., 2009). This conclusion is supported by a study conducted in Germany by Schaub *et al*. (2008), who observed that 81% of the time, *Myotis myotis* bats chose to forage in quiet environments. In fact, for this species, the impact of traffic noise on prey detection and capture success is clear, with 54.6% success in noisy areas compared to approximately 100% success in quiet areas (Siemers and Schaub, 2011). In US, Bunkley and Barber (2015) observed that during noisy treatments, *Antrozous pallidus* would take longer to locate food when compared to silence. Both *M. myotis* and *A. pallidus* are gleaning insectivores, which locate arthropods using prey-generated sounds (Audet, 1990; Fuzessery *et al*., 1993), therefore results may be different for aerial insectivores, which locate prey by echolocation. In UK, Finch *et al*. (2020) observed that the use of traffic noise playback reduces both activity and foraging behaviour in individuals of *Pipistrellus pipistrellus* and *P. pygmeaus*.

Furthermore, noise may also affect acoustic characteristics of the signal, which must be altered to stand out against background noise (Brumm and Slabbekoorn, 2005; Bunkley *et al*., 2015). For example, Song *et al*. (2019) reported that *Vespertilio sinensis* adjusts the temporal features of its echolocation calls in response to traffic noise. Bats exposed to noise increased the number of daily echolocation sequences and single-call sequences and decreased the number of multiple-call sequences (Song *et al*., 2019), which may impair foraging efficiency, because the bats may receive less information via echolocation. In Panama, Geipel *et al*. (2019) used rain and traffic noise playbacks and registered that bats can differentiate from those stimuli. The presence of traffic noise increases the number of exploration flights, which suggests that bats can perceive traffic noise as novel acoustic cues (Geipel *et al*. 2019) and it's important to evaluate how the presence of road and traffic noise will affect bats in a long term.

Observing whether bats reverse course prior to crossing a road, i.e. fly directly towards the road but turn 180º prior to reaching it, provides useful information regarding how bats react to roads and how some species avoid crossing them (Zurcher *et al*., 2010). The presence of cars increased this road avoidance behaviour from 32% when cars were absent to 60% when cars were present (Zurcher *et al*., 2010), and both traffic volume and road length were associated with increased avoidance behaviour (Bennett *et al*., 2013). When areas near roads have shorter trees or no trees at all, the effects of vehicle noise are more evident, and bats are more likely to turn away from the road (Bennett and Zurcher, 2012).

The discrepant study results are primarily due to the different methods used to assess road effects on bat activity. D'Acunto *et al*. (2018) evaluated how different techniques affect bat detection and suggested that, for mobile acoustic surveys, the start-stop method (i.e. when the vehicle stops for 1 min at different sites along a given route) is the most reliable for call identification. However, stationary acoustic monitoring is able to detect rare species better than mobile surveys (Tonos *et al*., 2014; de Torrez *et al*., 2017). Furthermore, species have distinct responses to the presence of roads and highways (Bonsen *et al*., 2015; Myczko *et al*., 2017); therefore, studies need to take feeding ecology into account when evaluating the effects of anthropogenic environmental alteration on bat behaviour.

Road Structures Used as Roosts

Despite the negative consequences of road construction, certain road structures such as bridges and culverts can be used as roosts for some bat species (Keeley and Tuttle, 1999) as they may offer appropriate microclimate conditions and protection from predators (Keeley and Tuttle, 1999; Russo *et al*., 2007; Amorim *et al*., 2013). Most studies investigating the use of bridges as bat roosts have been conducted in the US (e.g. Davis and Cockrum, 1963; Keeley and Tuttle, 1999; Bektas *et al*., 2018), where at least 28 species have been recorded roosting in bridges, with *Tadarida brasiliensis* being the most commonly observed species, with large colonies reaching over 1.5 million individuals (Keeley and Tuttle, 1999). European studies investigating bridge use by bat colonies have recorded at least 32 species with bridge roosts (C. Shiel, unpublished data). In most European countries, species from the genus *Myotis* are the most commonly observed (Amorim *et al*., 2013; C. Shiel, unpublished data); however, large *Nyctalus noctula* colonies have also been recorded (Harrje, 1994; Gloza *et al*., 2001). In northern Japan, Akasaka *et al*. (2007) recorded six species from two genera of Vespertilionidae roosting in bridges in Obihiro City, Hokkaido: *Myotis macrodactylus*, *M. daubentonii*, *M. gracilis*, *M. ikonnikovi*, *M. frater*, and *Murina hilgendorfi*.

To our knowledge, no published studies have focused on the use of bridges by bats in South America, Australia, or Africa, however, some data have been published in species inventories conducted in some countries. In Central and South America, species from families Emballonuridae, Phyllostomidae, Noctilionidae, and Vespertilionidae have been observed (Díaz and García, 2012; Biavatti *et al*., 2015; R. E. Sherwin, S. Haymond, M. S. Burt, and G. R. Horst, unpublished data). In New Zealand, Daniel and Williams (1984) observed *Mystacina tuberculata* and *Chalinolobus tuberculatus*, the only two extant bat species living in the country and both endemic to New Zealand (Dwyer, 1960), roosting in bridges. In Algeria, four species have been observed roosting in bridges cracks or in aqueducts (Ahmin, 2017). Because few studies focusing on the use of bridge as bat roosts have been conducted outside the U.S. and Europe, research in these areas is needed. According to Keeley and Tuttle (1999), bats frequently use bridges as night roosts, where they rest and digest their food between nightly feedings (Anthony *et al*., 1981; Berthaume, 2017). Bridges provide protection from wind and predators and usually remain warmer at night (Ferrara and Leberg, 2005), which makes them attractive for this use (Keeley and Tuttle, 1999). In contrast, the percentage of bridges used as day roosts, when bats are not active, is significantly smaller (Keeley and Tuttle, 1999; Feldhamer *et al*., 2003). Studies investigating bridge characteristics that encourage their use as day roosts have identified a variety of factors including construction material, location, and height (Keeley and Tuttle, 1999; Ferrara and Leberg, 2005; Bektas *et al*., 2018), however, microclimate, especially temperature, is one of the most important factors (Kerth *et al*., 2001; Lourenço and Palmerim, 2004; Ferrara and Leberg, 2005). Warmer roosts reduce the metabolic costs of maintaining body temperature and provide optimal conditions for hibernation and nursing, for example (Kunz, 1980).

Construction material is also an important factor influencing the use of bridges as bat roosts (Keeley and Tuttle, 1999; Hendricks *et al*., 2005; Bektas *et al*., 2018; Hopkins, 2018). Concrete bridges appear to be preferred by bats when roosting under a bridge, likely because they retain a substantial amount of the heat absorbed from the sun (Adam and Hayes, 2000), and temperatures can reach up to 15ºC higher than the ambient air (Perlmeter, 1996). However, Hopkins (2018) observed that the use of concrete bridges as night roosts in Montana was over 7-times higher than that of steel structures and over 18-times higher than that of wooden bridges; however, wooden structures were preferred for day roosts. Surrounding habitat is also an important factor influencing bridge use (Keeley and Tuttle, 1999; Bennett *et al*., 2008) and bridges located in areas with more forest cover (Feldhamer *et al*., 2003; Hendricks *et al*., 2005) or near watercourses (Smith and Stevenson, 2014) are more likely to be used as bat roosts.

Because the availability of bat roosts is a crucial factor for population survival and growth, this issue has become increasingly relevant for bat conservation in recent decades (Hutson *et al*., 2001). Keeley and Tuttle (1999) report that few bridges provide optimal conditions for roosting, but only minor modifications are needed to provide suitable roosts for numerous bats, which led regulatory agencies to publish guidelines on bridge maintenance to facilitate their use by bat colonies (Limpens *et al*., 2005; NCHRP, 2005; NRA, 2006, 2019). For bridges under construction, the easiest way to provide a bat roost is by incorporating characteristics that favour colony settlement. For existing bridges, authors suggest retrofitting with bat boxes (Keeley and Tuttle, 1999; Arnett and Hayes, 2000), which has been proven to increase its use by bats (Arnett and Hayes, 2000).

Mitigation Measures

Because of the many detrimental effects of roads, some mitigation actions can be implemented to avoid bat deaths by vehicle collision (Elmeros *et al*., 2016*a*, 2016*b*). The two types of measures are guaranteeing safe passage across roads, by under- or overpasses, and preventing bats from crossing roads (Elmeros *et al*., 2016*b*). Examples of overpasses, which allow bats to cross the roads above the vehicles, include bat gantries, hop-overs, wildlife overpasses, and modified overbridges (Brinkmann *et al*., 2012; Elmeros *et al*., 2016*b*). Bat gantries are overpasses specific for bats and consist of simple linear structures designed to guide bats to fly above traffic, however, Berthinussen and Altringham (2012*a*, 2015) reported that bats flew equally in places with or without such structures. When installing bat gantries, it is important to consider the bats' existing flight paths (Elmeros *et al*. 2016*b*), because bats do not change their commuting routes to take advantage of overpasses (Berthinussen and Altringham, 2012*a*). However, according to Bach *et al*. (2005), the use of bat gantries was not significantly higher than green bridges, which were used more intensively as they were also used as hunting ground. The use of green bridges is advantageous because they can be used by a range of animal taxa (Van Wieren and Worm, 2001; Glista *et al*., 2009), including bat species with different flying strategies and represent the best type of overpass mitigation measure for bats (Berthinussen and Altringham, 2015).

Another method to guarantee safe crossing for bats is via structures constructed under roads such as tunnels and culverts, which should be constructed as wide as possible to enable their use by more individuals, especially low-flying species (Elmeros *et al*., 2016a). In Germany, Kerth and Melber (2009) observed the species *Barbastella barbastellus* and *Myotis natererii* flying more frequently in underpasses than in other areas. Similar to overpasses, underpasses are more effective when existing commuting routes are taken into account (Elmeros *et al*., 2016*a*, Davies 2019). In Ireland, low-flying species adapted to foraging in cluttered habitats, such as *Myotis* spp. and *Plecotus auritus*, are more likely to use river bridges as under-road passageways than to cross directly over the road (Abbott *et al*., 2012*a*). According to Laforge *et al*. (2019), the use of those structures as crossing points by bats is dependent on the landscape features and are more attractive in areas with higher forest cover. Davies (2019) observed that the presence of features to guide bats into underpasses increases the use of those structures by individuals of *R. ferrumequinum* in UK. Moreover, Bhardwaj *et al*. (2020) observed that the use of artificial lighting in underpasses reduces it use by insectivorous bats in Australia.

Because commuting bats do not always use crossing structures, small habitat alterations, such as placing trees or fences along the road, could guide bats to safe places to cross or encourage them to fly higher (Russel *et al*., 2009; Elmeros *et al*., 2016*a*). Furthermore, a simple measure to avoid collisions is lowering speed limits (Secco *et al*., 2017), especially in areas with high bat activity and those considered hotspots for bat-vehicle collisions. There are many potential strategies to mitigate the effects of road construction on bats, however, effectiveness of mitigation measures still needs to be tested in many areas in order to guarantee bat preservation.

Conclusions and Future Research

Most of the studies investigating road effects on bats have been conducted in the US and Europe. However, to achieve global conservation of bats it is essential that we better understand how bats are affected in all parts of the world; this work is especially needed to protect migrating species. To date, there is insufficient evidence regarding how different species are affected by road casualties and the factors that affect the risk of bat-vehicle collisions in different habitats, especially regarding feeding habits.

To date, the effects of traffic noise on foraging success have been evaluated only in laboratory experiments. To provide effective conservation and mitigation strategies, it is necessary to study how traffic noise affects bats foraging in the wild. In particular, it is important to better understand how species might alter their echolocation signals in the presence of traffic and if traffic noise affects communication between individuals.

No studies exist regarding the effect of roads on most of the bat's annual cycle, with no data indicating whether reproduction or hibernation are affected. Furthermore, few studies have assessed the effectiveness of mitigation initiatives, such as under- and overpasses and the addition of bat boxes under bridges, especially in tropical areas.

Despite the number of studies evaluating the impacts of roads and highways on bats, it is not possible to generalize the relationship between bat activity near roads and road casualties, because of the few number of simultaneous research on mortality and space use around roads by bats. Only in Europe have similar numbers of studies focusing on bat activity or road casualties been conducted. Studies conducted in North America and Australia have focused mainly on road as barriers and their impact on activity, whereas studies conducted in South America have focused on bat roadkill. Studies that consider all direct and indirect road impacts on different bat species, including evolutionarily distant groups, are essential to ensure conservation of the species and preserve their ecosystem services.

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