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MORCEGOS NA BEIRA DA ESTRADA
ATIVIDADE, DIVERSIDADE, FORRAGEIO E ATROPELAMENTOS

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“Se não houver frutos, valeu a beleza das flores

Se não houver flores, valeu a sombra das folhas

Se não houver folhas, valeu a intenção da semente”

DANIEL DE FIGUEIREDO RAMALHO

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RESUMO GERAL

A população humana tem crescido exponencialmente nas últimas décadas, causando diversos efeitos no meio ambiente, tais como a fragmentação de habitat. A presença de estradas como um agente de fragmentação pode ter efeitos diretos e indiretos sobre os organismos que vivem nos ambientes localizados às suas margens. Por usarem extensas áreas de forrageamento, morcegos são particularmente afetados e podem levar mais tempo para se recuperarem de efeitos prejudiciais da estrada. Portanto, neste estudo, pretendemos avaliar como os morcegos são considerados em estudos de ecologia de estradas ao redor do mundo e, em um estudo de caso, avaliar os efeitos da presença de estradas na atividade e diversidade de morcegos em uma savana Neotropical. Também avaliamos quais fatores influenciam os atropelamentos de morcegos na área de estudo. Definimos transeções com detectores de ultra-som em diferentes distâncias da estrada, que registraram a atividade do morcego por 12 horas. Também realizamos buscas por carcaças de morcegos em 114 km de estradas durante cinco anos. Por meio de modelos lineares generalizados ou mistos (GLMs ou LMMs), avaliamos a influência da estação, tipo de estrada e distância da água nas taxas de atropelamentos, número de passes e atividade de forrageamento, adicionando distância da estrada nas últimas análises. Identificamos 87 indivíduos de morcegos atropelados na área, e a taxa de atropelamentos foi associada a todas as variáveis, exceto a presença de luz. Por outro lado, a atividade foi influenciada apenas pela estação e distância da estrada, sendo maior nas margens das estradas pra morcegos de áreas abertas. A sazonalidade tem forte influência na atividade de morcegos, o que também pode explicar por que há maiores taxas de atropelamentos durante a estação chuvosa, quando mais recursos estão disponíveis. A disponibilidade de recursos também pode explicar o aumento da atividade nas margens das estradas, que podem fornecer mais recursos, especialmente quando há luz artificial. O número de atropelamentos também foi relacionado ao tipo de estrada, sendo mais de 12 vezes mais alto nas rodovias duplicadas do que nas simples. As rodovias maiores têm maior volume de tráfego, o que já foi considerado um dos principais fatores influenciando o atropelamento de morcegos. A maioria dos estudos com morcegos em estradas tem sido publicada na Europa, e poucos avaliaram os efeitos diretos e indiretos da presença na estrada em morcegos. Os morcegos representam uma das mais diversas ordens de mamíferos no mundo e fornecem importantes serviços ecossistêmicos, que devem ser preservados evitando atropelamentos. Como os morcegos são mais ativos perto de estradas, eles podem estar mais expostos a colisões, portanto sugerimos a adoção de medidas mitigatórias para garantir que os morcegos consigam atravessar de maneira segura, conservando assim as espécies.

Palavras-chave: Bioacústica, Chiroptera, Ecologia de estradas, Efeito de borda

GENERAL ABSTRACT

Human population has been increasing exponentially in the last decades, leading to fragmentation, especially derived from roads, which may have direct and indirect effects on the organisms living on the environment surrounding them. Because bats use extensive foraging areas, they are particularly affected by roads and may take longer to recover from any detrimental effects from the road. Therefore, in this study, we aim to evaluate how bats have be considered in road ecology studies around the world and, in a study case, evaluate effects of road presence on bats' activity and diversity in a Neotropical savanna. We also evaluated which factors influence bat roadkill in the study area. We placed transects with ultrasound detectors in different distances from the road, which recorded bat activity for 12 hours. We also surveyed 114km of roads during five years in order to locate road-killed bats. Via generalized or mixed linear models (GLMs or LMMs), we evaluated the influence of season, road type, and distance from water in roadkill rates, in passes number and foraging activity, adding distance from road in the latter analysis. We identified 87 bat individuals as roadkill in the area, and roadkill rate was associated with all variables but light presence. On the other hand, bat activity was only influenced by season and distance from the road, being higher on road verges for open-area insectivores. Seasonality is a strong influencer for bat activity, which might also explain why there is higher roadkill rates during wet season, when more resources are available. Resource availability may also explain the increased activity on road verges, which may provide more resources, especially when artificial light is present. Roadkill was also related to the type of road, being over 12 times higher on four-lane highways than in two-lane ones. Larger highways have higher traffic volume, which has already been considered one of the main drivers for bat road casualties. Most of studies considering bat in road ecology have been conducted in Europe, and few have evaluated both direct and indirect effects of road presence on bats. Bats are one of the most diverse orders of mammals, and provide important ecological services, which should be preserved by avoiding roadkill. Because bats are more active near roads, they may be more exposed to collisions, thus we suggest application of mitigation measures in order to guarantee safe crossing and conservation of the species.

Keywords: Bioacoustics, Chiroptera, Edge effect, Road Ecology

INTRODUÇÃO GERAL

Únicos mamíferos com capacidade verdadeira de voo (Thewissen & Babcock 1992), os morcegos pertencem à ordem Chiroptera, uma das mais diversas entre a classe Mammalia, representadas por 182 espécies no Brasil (Nogueira et al. 2018). A diversidade também é observada nos hábitos alimentares, com espécies insetívoras, frugívoras, nectarívoras, hematófagas e carnívoras, com diversas especializações dentro de cada grupo (Gardner 2007).

Com uma grande variedade de hábitos alimentares, os morcegos realizam múltiplos serviços ecossistêmicos, principalmente aqueles referentes à polinização, à dispersão de sementes e ao controle de populações de insetos, inclusive de pragas agrícolas (Aguiar & Antonini 2008, Kunz et al. 2011, Kasso & Balakrishnan 2013). Estudos indicam que a presença de morcegos próximos a áreas de agricultura pode significar uma economia de mais de mais de um milhão de dólares no controle de pragas (Cleveland et al. 2006, Kasso & Balakrishnan 2013).

Outro importante serviço prestado pelos morcegos é a dispersão de sementes (Kasso & Balakrishnan 2013), principalmente de plantas pioneiras (Garcia et al. 2000, Buddenhagen 2008), como por exemplo *Cecropia* spp., importantes para a restauração de áreas degradadas (Gorchov et al. 1993, Garcia et al. 2000). Em relação à polinização, estima-se que esse serviço prestado pelos morcegos pode representar até 200 bilhões de dólares anuais (Fujita & Tuttle 1991, Gallai et al. 2009). Espécies de relevante interesse econômico (Kasso & Balakrishnan 2013), como *Agave* spp. e *Durio* spp., dependem primordialmente dos morcegos para a polinização (Fujita & Tuttle 1991, Arizaga et al. 2000). Os morcegos também são os principais polinizadores de plantas como o *Caryocar brasiliense*, o Pequi (Gribel & Hay 1993, Brobowiec & Oliveira 2012), típico do Cerrado brasileiro (Gribel & Hay 1993).

Nesse bioma, os morcegos representam a ordem de mamíferos com maior diversidade, com pelo menos 118 espécies registradas (Aguiar et al. 2016), número que pode ser superior tendo em vista o número de áreas pouco amostradas na região (Bernard et al. 2011). Toda essa diversidade está fortemente ameaçada pela exploração contínua do bioma Cerrado nas últimas décadas (Klink & Machado 2005), que já teve mais de 50% da sua área original desmatada (Machado et al. 2004, Strassburg et al. 2017). Além disso, o ritmo de perda de área no Cerrado pode chegar a 30.000 km² por ano (Machado et al. 2004, Strassburg et al. 2017). Dos mais de 200 milhões de hectares originais, sobram poucas porções intactas, principalmente nas regiões localizadas mais ao norte (Machado et al. 2004, Strassburg et al. 2017), sendo os limites meridionais ameaçados pela ocupação humana e expansão de grandes centros urbanos.

A conversão de áreas naturais para áreas urbanas e áreas de pastagens são importantes fatores de impacto na vegetação nativa (Klink & Machado 2005, Strassburg et al. 2017). Além disso, outros fatores como aumento na densidade de animais domésticos que agem como predadores, aumento de poluentes, presença de iluminação artificial e de poluição sonora (Patroneck et al. 1997, Perugini et al. 2011, Russo & Ancillotto 2014) podem afetar os organismos presentes nos remanescentes próximos a grandes centros urbanos.

Com a criação e aumento de diversos centros urbanos, surge também a necessidade de deslocamento humano entre esses centros. Esse deslocamento é realizado principalmente em grandes rodovias que cortam áreas naturais e com pouca influência dos centros urbanos (Forman et al. 2003, Rosa 2012). O aumento do número de estradas, principalmente em áreas em desenvolvimento acelerado, como o Cerrado (Klink & Machado 2005), pode aumentar o efeito dessas estruturas nos organismos, o que demonstra a necessidade de conhecermos qual é a intensidade e extensão desse efeito.

Os efeitos das estradas mais evidenciados, tanto em estudos científicos quanto no saber popular, são os atropelamentos. De fato, atropelamentos representam uma das principais causas antropogênicas da mortalidade de vertebrados, superando atividades como a caça e o tráfico, por exemplo (Forman et al. 2003, CBEE 2018). Apenas no Brasil, 473 milhões de indivíduos são mortos nas estradas em apenas um ano, o que representa uma taxa de 15 indivíduos mortos por segundo (CBEE 2018). Apesar dos morcegos representarem uma pequena fração do total desses indivíduos, esses animais estão entre os principais mamíferos atropelados em todo o mundo.

Além dos atropelamentos, as estradas alteram o ambiente em seu entorno, afetando as características da área ao longo de toda sua extensão. Essas alterações também se refletem na poluição sonora produzida por automóveis, que pode reduzir a eficiência de forrageamento em espécies de morcegos insetívoras (Schaub et al. 2008, Siemers & Schaub 2011), principalmente aquelas que dependem de ouvir os sons produzidos pela presa para encontrarem alimento (Siemers & Schaub 2011). Devido a baixa eficiência, os morcegos podem evitar forragear em áreas com elevada influência de poluição sonora (Schaub et al. 2008, Bunkley et al. 2014). Além disso, Berthinussen e Altringham (2012) observaram, no Reino Unido, que a estrada tinha forte influência no nível de atividade dos morcegos, que preferiam forragear em áreas mais distantes da mesma.

A diminuição da atividade nessas áreas é preocupante, principalmente em uma região como o Cerrado, bioma com elevada diversidade de morcegos (Aguiar et al. 2016), e que vem sofrendo forte pressão antrópica nas últimas décadas (Machado et al. 2004, Klink & Machado 2005, Strassburg et al. 2017). Assim, meu objetivo nesta tese foi fazer um estudo de ecologia de estradas de morcegos em áreas do Distrito Federal, analisando como a presença das estradas afeta a atividade e a diversidade desses organismos, bem como quais características influenciam nas taxas de atropelamentos de quirópteros na área de estudo. Portanto, minha tese está dividida em três capítulos, todos redigidos em forma de artigos científicos e no formato da revista para qual os mesmos foram submetidos, sendo que esta informação está presente na primeira página de cada capítulo.

No primeiro capítulo, fiz um apanhado do conhecimento de ecologia de estradas envolvendo morcegos. Avaliei como os morcegos são considerados neste tipo de estudo e como foi o desenvolvimento e o histórico desses estudos no Brasil e no mundo.

Para o capítulo II, avaliei o efeito de borda de estrada nos níveis de atividade de morcegos. Para isso, instalei gravadores em diferentes distâncias da estrada para medir a atividade, além de identificar quais tipos de estrada mais influenciam esses níveis. Também avaliei o impacto da estrada sobre a diversidade de espécies, a fim de identificar se algumas preferem forragear em locais mais distantes, e na razão entre *feeding buzzes* e passes, para verificar onde estes organismos preferem forragear. Testei as seguintes hipóteses: (I) a atividade dos morcegos será maior em pontos mais afastados da estrada, considerada aqui como fonte de poluição sonora e luminosa, e (II) a poluição sonora será menor em estradas de terra, que terão, consequentemente, menor efeito sobre a atividade dos morcegos.

Por fim, no terceiro capítulo, realizei uma análise dos números de atropelamentos de morcegos em estradas do Distrito Federal. Neste capítulo, consta uma lista das espécies envolvidas em acidentes nas rodovias locais além de uma análise dos fatores que influenciam o número de atropelamentos. Analisei como características da estrada e do ambiente afetam o número desses acidentes. Neste capítulo, testei as seguintes hipóteses: (I) estradas pavimentadas terão maiores taxas de atropelamentos, (II) áreas próximas a fonte de água e de iluminação artificial terão mais casos, e (III) morcegos frugívoros ou nectarívoros, que voam em alturas mais baixas se comparado a insetívoros aéreos, serão mais frequentes em colisões que os morcegos insetívoros.

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CAPÍTILO I

MORCEGOS NA ESTRADA – UMA REVISÃO DOS EFEITOS DE ESTRADAS E RODOVIAS EM MORCEGOS

Enviado para a revista: Acta Chiropterologica

Bats on the road – A review of the effects of roads and highways on bats

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Short running title: How are bats considered in road ecology studies?

ABSTRACT

The increase in human population has resulted in environmental alterations and habitat fragmentation, primarily caused by road construction. Since the late 1990s, there has been an increase in studies evaluating the effects of roads on natural populations; however, few studies have considered bats in road ecology studies. In this review we evaluated how road ecology studies focusing on bats are conducted and 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. The first studies evaluating the impact of roads on bats were published in the early 1990s. Since then, most of these studies were conducted in Europe (71.43%), followed by North and South America (11.43% each), and Australia (5.71%), but there have been no studies conducted in Asia or Africa. Of the 35 studies, 18 evaluated the impact of roads on bat activity, and 17 evaluated collisions with vehicles; however, only in Europe have both effects been studied equally. In South America, all studies focused on roadkill, whereas in North America and Australia, most studies evaluated roads as barriers to movement. A total of 106 bat species from eight families have been recorded in both types of studies, with Vespertilionidae (57 spp.) and Phyllostomidae (27 spp.) showing the most diversity. Because most studies evaluating the effects of roads affect bats have been conducted in Europe, 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.

Key words: Barrier effects, Bridges, Chiroptera, Habitat Fragmentation, 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 one 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); 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 road 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 suggested 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).

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). 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 literature reviews on the effects of roads on bats include the review by Fensome and Mathews (2016), which evaluated bat-vehicle collisions and the barrier effects of roads in European bats, and Novaes et al. (2018) recently reviewed road-killed bats in Brazil. In contrast with previous studies, in this review we evaluated how bats are considered in road ecology studies around the world 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, provided results from a literature review on mitigation methods, and suggested future research topics.

MATERIAL AND METHODS

We performed online searches 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 (“carretras” and “murciélagos” or “Chiroptera”), and French (“routes” and “chauve-sourris” 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.

RESULTS AND DISCUSSION

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 23 studies published in the last 10 years for a total of 35 publications (Fig. 1). Most of these studies were conducted in Europe (71.43%), and few papers addressing effects of roads on bats were conducted in Australia, North America, and South America (Fig. 2). To our knowledge, no road ecology studies focusing on bats have been conducted in Asia or Africa.

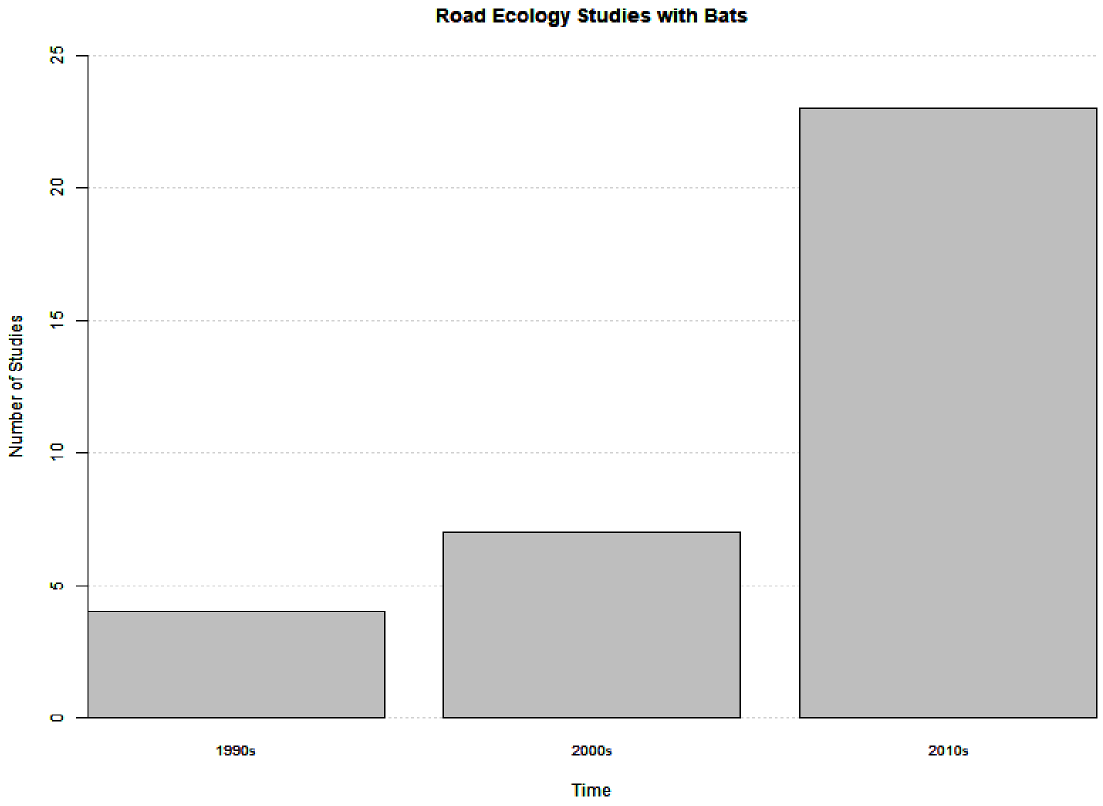

Figure 1. Temporal distribution of published studies that evaluated the effects of roads on bats.

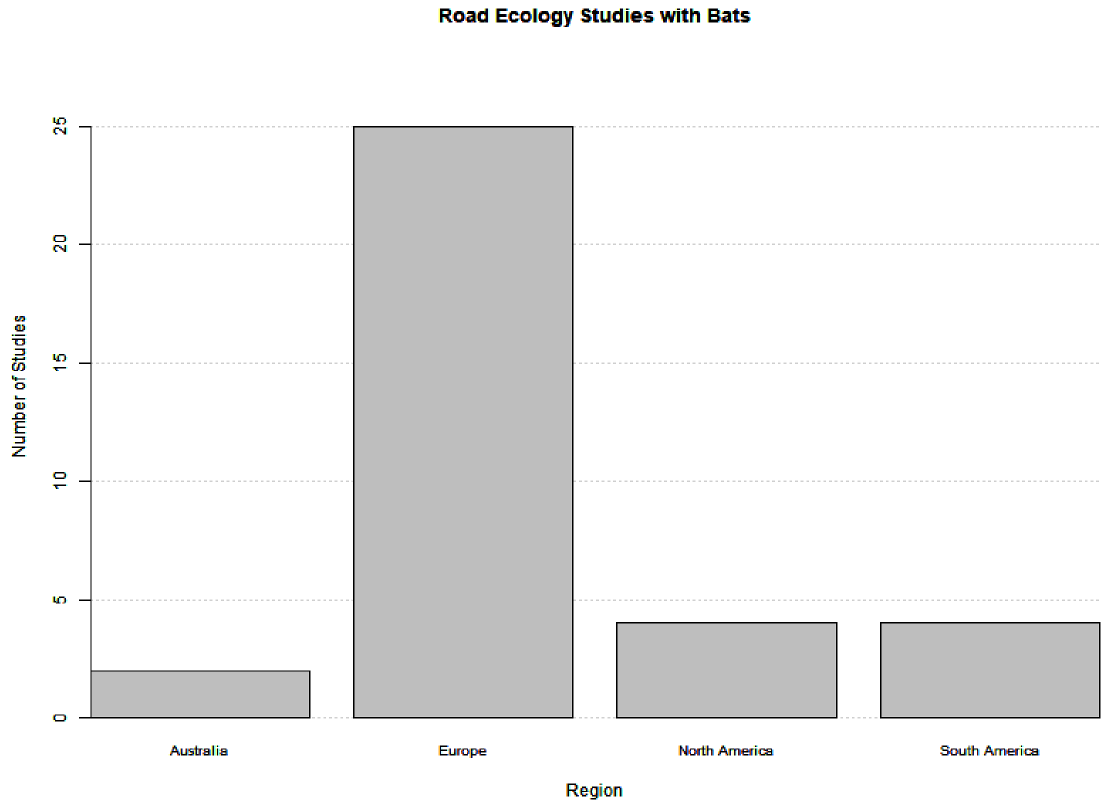

Figure 2. Geographic distribution of published studies that evaluated the effects of roads on bats.

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. 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 Jr. 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 (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. 2011b); 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 collusions: Vespertilionidae (35 species), Phyllostomidae (27 species), Molossidae (5 species), Rhinolophidae (3 species), Mormoopidae (2 species), Noctilionidae (2 species), Emballonuridae (1 species), and Miniopteridae (1 species) (Fig. 3, Table 1). 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).

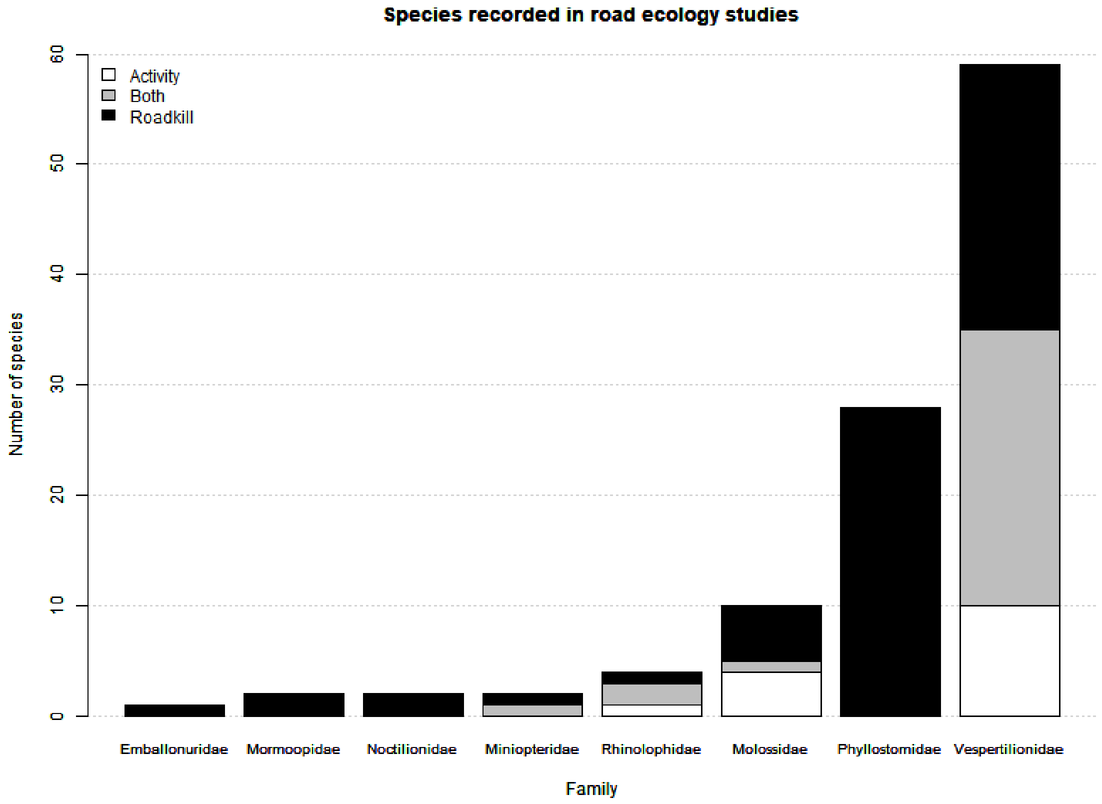

Figure 3. Number of bat species recorded in road ecology studies according to family and type of road effect (bat activity or roadkill).

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 such as *Myotis* species, which forage at 5–10 m (Schober and Grimmberger 1998), to high-flying species such as *Nyctalus* spp., 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 the same height as most cars.

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. 2011b, 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, younger bats are more naïve and could, for example, 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 (US) (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 a road section with windbreakers and bushes at its margins (Lesiński 2011).

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” forests 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).

High bat activity near roads appears to be another important factor associated with bat-vehicle collisions (Medinas et al. 2013). In Montenegro, Ikovic 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. 2013) and hibernation sites near roads increase bat activity (Capo et al. 2006), they are also associated with increased bat roadkill. In Portugal, Medinas et al. (2013) observed that areas with viaducts had more casualties, mainly because those structures are used as roosts (Keeley and Tuttle 1999). 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 (Medinas et al. 2013). 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, Ikovic 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.

Despite the large body of evidence demonstrating how species ecology and the environment surrounding roads influence bat casualties by road traffic, little is known about how road characteristics 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 (Ikovic et al. 2014). However, some researchers suggest that low-to-moderate traffic volume poses a more significant threat (Langevelde et al. 2009), because bats tend to avoid high-traffic roads while commuting or foraging (Berthinussen and Altringham 2012). Road structures may also influence roadkill, but to our knowledge, there are no data showing how road width and road types affect the risk of bat-vehicle collision.

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, especially in areas with a dense road network (Lesiński et al. 2011b), are an important threat to bats and should not be overlooked.

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, especially for birds and amphibians (Berthinussen and Altringham 2012).

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 Australia (Bonsen et al. 2015, Bhardwaj 2017), Czech Republic (Gaisler et al. 2009), England (Blake et al. 1994, Berthinussen and Altringham 2012), France (Vandevelde et al. 2014), Germany (Kerth and Melber 2009), Ireland (Abbott et al. 2012a,b), Poland (Lesiński et al. 2011a, Mycszo et al. 2017, Suchocka et al. 2019), Portugal (Medinas et al. 2019), Sweden (Sjolund 2015, Luz 2016), and the US (Zurcher et al. 2010, Bennett and Zurcher 2012, Bennett et al. 2013, Kitzes and Merenlender 2014, D'Acunto et al. 2018, Pourshoushtari et al. 2018). At least 59 species have been recorded foraging near roads, and all of them are aerial or gleaning insectivores (Kalko et al. 1996) from the families Vespertilionidae (47 species), Molossidae (7 species), Rhinolophidae (3 species), or Miniopteridae (2 species). The most common species detected near roads in European studies were *Pipistrellus pipistrellus*, *P. pygmaeus*, and *Plecotus auritus*. Approximately half of the recorded species (30 species) have not been identified as roadkill victims (Fig. 3, Table 1); however, all of them were recorded in Australia or the US, where few studies evaluating bat roadkill are available.

Distance from the road appears to be another 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, and Australia (Berthinussen and Altringham 2012, Kitzes and Merenlender 2014, Bhardwaj 2017, Claireau et al. 2019). Berthinussen and Altringham (2012) 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 1600 m. 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 *Mormopterus 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 but was highest near the road in open agricultural areas (Medinas et al. 2019).

Increased foraging activity near roads, especially in open areas, may be due to artificial lights installed in these areas (Stone et al. 2015). Fast-flying species have been observed foraging near streetlights (Stone et al. 2015), and most have also been observed in road ecology studies (Bonsen et al. 2015, Myczko et al. 2017, Suchocka et al. 2019). 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.

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, 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; this effect was especially pronounced for *Pipistrellus pygmaeus*, *Nyctalus noctula*, and *Myotis daubentonii* (Gaisler et al. 2009). In the UK, Berthinussen and Altringham (2012) 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). In Poland, Lesiński et al. (2011b) and Myczko et al. (2017) studied bat activity near forest roads in protected areas. They observed more individuals (Lesiński et al. 2011a), increased activity, more extended activity, and more feeding buzzes (Myczko et al. 2017) at roads near the forest edge compared with those in the forest interior. In France, the presence of railway verges negatively affected the activity of gleaner insectivores from the genus *Myotis* (*M. nattereri*, *M. mystacinus*, and *M. daubentonii*) (Vandevelde et al. 2014). However, for aerial-hawking species, such as *Pipistrellus pipistrellus* and *Nyctalus leisleri*, railway verges are an important habitat and used for commuting/foraging more than other areas, especially when few linear structures, which are important to bats (Lesiński et al. 2007), are present (Vandevelde et al. 2014).

The influence of traffic volume on bat activity appears to be negative. Although some authors suggest that higher traffic does not affect bat foraging (Myczko et al. 2017), most studies have reported less bat activity near highways with intense traffic (Bennett et al. 2013, Kitzes and Merenlender 2014, Pourshoushtari et al. 2018), probably because bats tend to avoid foraging in loud environments (Schaub et al. 2008, Bunkley et al. 2015). 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). Furthermore, noise may also affect acoustic characteristics of the signal, which must be altered to stand out against background noise (Brumm and Slabbekoorn 2005). 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 addition to reducing foraging efficiency, the presence of roads also reduced the foraging areas for *Myotis bechsteinii* in Germany (Kerth and Melber 2009). Roads also act as a barriers to roost switching in Bechstein's bat, which can restrict access to more suitable environments for this species or other gleaning insectivores (Kerth and Melber 2009).

Observing whether bats reverse course prior to crossing a road, i.e. fly directly towards the road but turn 180º prior to reaching it (Zurcher et al. 2010), 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

When constructing a road, building demolition and tree removal may decrease the number of roosts for several bat species (Keeley and Tuttle 1999, Limpens et al. 2005). Moreover, the presence of a road can alter the microclimate of the area (Coffin

2007), leading to roost abandonment (Limpens et al. 2005). Despite these 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, with publications dating from the 1960s to 2018 (e.g. Davis and Cockrum 1963, Keeley and Tuttle 1999, Bektas et al. 2018). The American Association of State Highway and Transportation Officials has published guidelines on bridge maintenance that take the protection of bat colonies into account (NCHRP 2005). In the US, at least 28 species have been recorded roosting in bridges, with *Tadarida brasiliensis* being the most commonly observed species (Keeley and Tuttle 1999), representing approximately 26% of the species observed. Large colonies of *T. brasiliensis* exist in states such as Texas and California, reaching over 1.5 million individuals. Other species such as the vespertilionids *Eptesicus fuscus* and *Myotis velifer* are also abundant on American bridges, representing 21.5% and 19% of the recorded species, respectively (Keeley and Tuttle 1999).

European studies investigating the bridge use by bat colonies have recorded at least 32 species with bridge roosts (Shiel 1999, Amorim et al. 2013). In most European countries, species from the genus *Myotis*, especially *Myotis daubentonii*, are the most commonly observed (Shiel 1999, Amorim et al. 2013); however, large *Nyctalus noctula* colonies with over 10,000 individuals have also been recorded in Germany (Harrje 1994, Gloza et al. 2001). A few studies have evaluated the use of bridges as day roosts by bats in other areas. 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 Brazil, Biavatti et al. (2015) observed species from the families Emballonuridae (*Rhynchonycteris naso*) and Phyllostomidae (*Desmodus rotundus* and *Carollia perspicillata*) roosting in bridges. In northwestern Peru, *Rhynchonycteris naso*, *Noctilio albiventris*, and *Myotis albescens* have been recorded roosting in bridges in the low forest (Díaz and García 2012), and in Costa Rica, 80% of the bridges surveyed were occupied as day roosts by seven species of bats (Sherwin et al. 1999). 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: *Myotis capaccinii* (in the cracks of bridge pillars), *Tadarida teniotis* (in old bridges and in aqueducts), and *Pipistrellus kuhlii* and *P. pipistrellus* (in the cracks of bridges) (Ahmin 2017). Because few studies focusing on the use of bridge as bat roosts have been conducted outside the US and Europe, research in these areas is needed.

According to Keeley and Tuttle (1999), bats also frequently use bridges as night roosts, where they rest and digest their food between nightly feedings (Anthony et al. 1981, Berthaume 2017), with 29% of the surveyed structures in America and up to 53% oin Portugal used as night roosts. 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 (1%–6.5%) (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). In the US, most bridges used by bats are located in relatively warm regions, primarily in the southern half of the country (Keeley and Tuttle 1999). Ferrara and Leberg (2005) observed that bridges used as roosts by *Corynorhinus rafinesquii* were 5ºC warmer than the outside temperature, and bat roosts were significantly warmer than the rest of the bridge. Warmer roosts reduce the metabolic costs of maintaining body temperature and provide optimal conditions for important parts of bats' annual cycle, such as hibernation and nursing (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). In in the US, Hendricks et al. (2005) observed bats using concrete bridges (75.9%) more often than steel bridges (37.5%) or wooden bridges (31.6%) in the state of Montana, and Bektas et al. (2018) reported that construction material is the primary factor influencing bridge use in the state of Iowa. 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). 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 (Hopkins 2018).

The effects of other characteristics such as height, crevice depth and width, sun exposure, and location on how bats use bridges have also been investigated (Keeley and Tuttle 1999). According to Keeley and Tuttle (1999), the ideal bridge would be at least 3 m from the ground, with crevices at least 30 cm deep and 0.25 to 3 cm wide, and located on a non-busy roadway with full sun exposure. The height is important to avoid predator access to sleeping bats (Cleveland and Jackson 2013), and these crevice characteristics are essential to protect from wind and other natural factors. Surrounding habitat is another important factor influencing bridge use (Keeley and Tuttle 1999, Bennett et al. 2008). 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 of the bridges studied provide optimal conditions for roosting, but only minor modifications are needed to provide suitable roosts for numerous bats. Regulatory agencies have published 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). In Oregon, Arnett and Hayes (2000) installed wooden bat boxes under a flat-bottom bridge, and bats used 87% of the boxes as night roosts, and 33% as day roosts. In this study, bats began using the boxes within 1 year after instalment (Arnett and Hayes 2000), which supports this approach as a way to increase bat populations under bridges, bringing more of the ecosystem services they provide.

Minimizing effects of roads on bat populations

Because of the many detrimental effects of roads, mitigation actions are being implemented around the world to avoid bat deaths by vehicle collision (Elmeros et al. 2016a, b). The two types of measures are: (i) guaranteeing safe passage across roads and (ii) preventing bats from crossing roads. Guaranteeing safe passage includes building structures that help bats avoid traffic, such as over- and underpasses (Elmeros et al. 2016b). Examples of overpasses, which allow bats to cross the roads above the vehicles, include bat gantries, hop-overs, wildlife overpasses, and modified overbridges (Elmeros et al. 2016b). Bat gantries, which are the only type of the overpass specific for bats, are simple linear structures designed to guide bats to fly above traffic (Elmeros et al. 2016b). However, Berthinussen and Altringham (2012, 2015) reported that on roads with bat gantries in England and Wales, 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. 2016b), because bats do not change their commuting routes to take advantage of overpasses (Berthinussen and Altringham 2012).

Hop-overs consist of tall trees planted on the road margins that encourage bats to fly higher over the road (Russel et al. 2009, Elmeros et al. 2016b). In the US, Russel et al. (2009) observed that bats tend to fly lower where trees do not line the road and suggested planting tall trees to prevent bat-vehicle collisions. However, this measure is more appropriate for narrow roads, whereas wildlife overpasses are more appropriate for wider highways (Elmeros et al. 2016b). Wildlife overpasses are vegetated overbridges that can be used by a range of animal taxa (Van Wieren and Worm 2001, Glista et al. 2009). If constructed correctly, wildlife overpasses are used by many bat species with different flying strategies and represent the best type of overpass mitigation measure for bats (Berthinussen and Altringham 2015).

Most of these overpass structures are expensive and require considerable structural work. A more affordable method for the creation of bat overpasses involves modifying existing structures, such as pedestrian bridges or road signs (Elmeros et al. 2016b). For example, panels that provide shelter from light and noise can be installed on overbridges (Elmeros et al. 2016b) to enhance their suitability for bats (Brinkmann et al. 2012).

Another method to guarantee safe crossing for bats is via underpasses, i.e. structures constructed under roads such as tunnels and culverts (Elmeros et al. 2016a). Culverts 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. 2016a). Viaducts and river bridges can also serve as large underpass structures for bats (Elmeros et al. 2016a). 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. 2012b).

Because commuting bats do not always use crossing structures, small habitat alterations, such as placing hedgerows, trees, or fences along the road, could guide bats to safe places to cross (Elmeros et al. 2016a) or encourage bats to fly higher. Elmeros et al. (2016a) also suggest the use of artificial lights or audible warning to induce avoidance behaviour in bats. However, these alterations, especially the use of artificial lights, may increase insect availability, thereby attracting some bat species (Stone et al. 2015) and increasing the risk of bat-vehicle collision. A simple measure to avoid collisions is lowering speed limits (Elmeros et al. 2016a, Secco et al. 2017), especially in areas with high bat activity and those considered hotspots for bat-vehicle collisions.

These studies show that there are many potential strategies to mitigate the consequences of road construction (Elmeros et al. 2016a). However, the implementation of effective mitigation measures requires more studies evaluating how highways affect bats in all areas of the world.

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 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 on 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 studies in most regions have focused on only one of these two topics (Fig. 4). 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 bats are essential to ensure conservation of the species and preserve their ecosystem services.

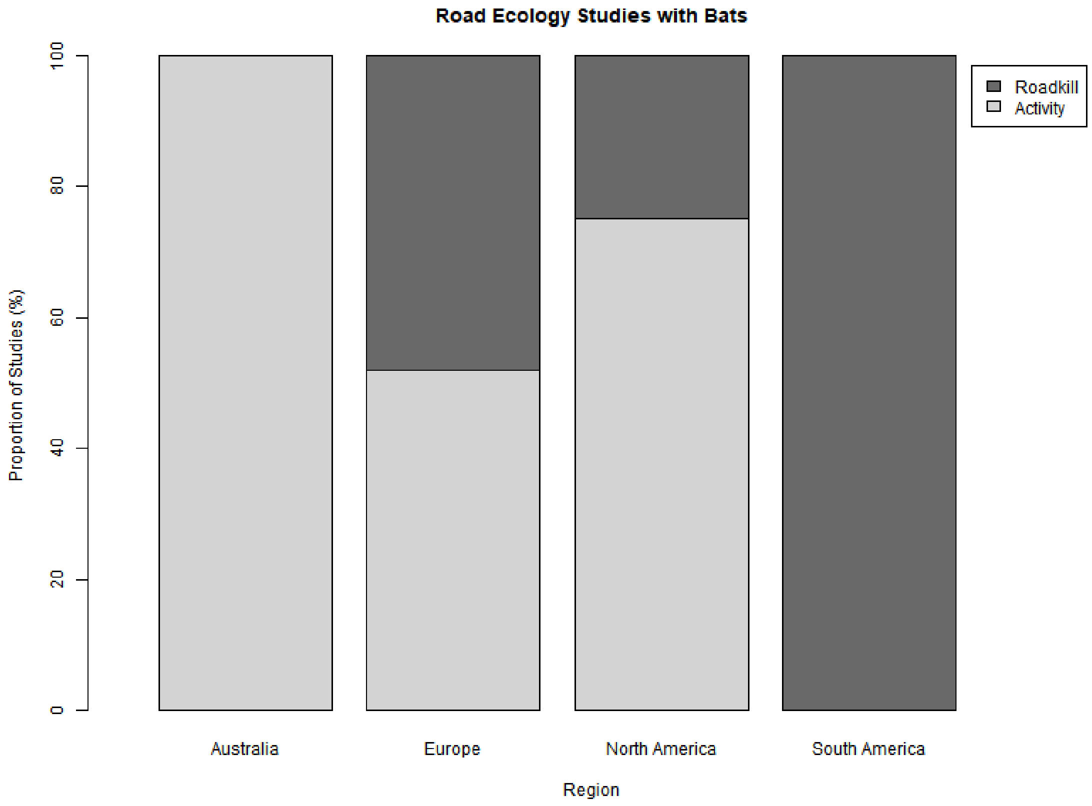

Figure 4. Proportion of study types evaluating the effects of roads on bat biology in different regions.

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Table 1. 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, CZE = Czech Republic, ENG = England, FRA = France, GER = Germany, IRE = Ireland, MON = Montenegro, POL = Poland, POR = Portugal, SPA = Spain, SWE = Sweden, USA = United States of America.

Species Grouped by Family	**Feeding Guild**	**Road-killed bats (76 species)**		**Bat activity (59 species)**	
		Country	**Reference**	**Country**	**Reference**
Emballonuridae					
Saccopteryx leptura	I	BRA	[31]	-	-
Miniopteridae					
Miniopterus australis	I	-	-	AUS	[24]
Miniopterus schreibersii	I	GER, POR, SPA	[03] [04] [05] [17]	AUS, POR	[24] [34]
Molossidae					
Austronomus australis	I	-	-	AUS	[27]
Eumops auripendulus	I	BRA	[31]	-	-
Eumops perotis	I	-	-	USA	[21]
Molossus molossus	I	BRA	[30] [31]	-	-
Molossus rufus	I	BRA	[30] [31]	-	-
Mormopterus planiceps	I	-	-	AUS	[27]
Mormopterus ridei	I	-	-	AUS	[24] [27]
Nyctinomops laticaudatus	I	BRA	[31]	-	-
Tadarida australis	I	-	-	AUS	[24]
Tadarida brasiliensis	I	BRA	[31]	USA	[21]
Tadarida teniotis	I	-	-	POR	[34]
Mormoopidae					
Pteronotus parnellii	I	BRA	[31]	-	-
Pteronotus personatus	I	BRA	[23]	-	-
Noctilionidae					
Noctilio albiventris	P	BRA	[31]	-	-
Noctilio leporinus	P	BRA	[31]	-	-
Phyllostomidae					
Anoura caudifer	N	BRA	[28] [31]	-	-
Anoura geoffroyi	N	BRA	[23] [31]	-	-
Artibeus fimbriatus	F	BRA	[28] [31]	-	-
Artibeus lituratus	F	BRA	[28] [30] [31]	-	-
Artibeus obscurus	F	BRA	[31]	-	-
Artibeus planirostris	F	BRA	[23] [31]	-	-
Carollia perspicillata	F	BRA	[30] [31]	-	-
Chiroderma doriae	F	BRA	[31]	-	-
Chiroderma villosum	F	BRA	[31]	-	-
Chrotopterus auritus	C	BRA	[31]	-	-
Dermanura cinerea	F	BRA	[31]	-	-

Desmodus rotundus	H	BRA	[31]	-	-
Diphylla ecaudata	H	BRA	[31]	-	-
Glossophaga soricina	N	BRA	[31]	-	-
Lophostoma silvicolum	I	BRA	[31]	-	-
Macrophyllum macrophyllum	I	BRA	[31]	-	-
Micronycteris minuta	I	BRA	[31]	-	-
Mimon bennettii	I	BRA	[31]	-	-
Phyllostomus hastatus	O	BRA	[30] [31]	-	-
Platyrrhinus lineatus	F	BRA	[31]	-	-
Platyrrhinus recifinus	F	BRA	[30] [31]	-	-
Sturnira lilium	F	BRA	[28] [30] [31]	-	-
Sturnira tildae	F	BRA	[31]	-	-
Tonatia bidens	I	BRA	[31]	-	-
Trachops cirrhosus	C	BRA	[31]	-	-
Uroderma bilobatum	F	BRA	[23]	-	-
Vampyressa pusilla	F	BRA	[31]	-	-
Rhinolophidae					
Rhinolophus blasii	I	MON	[20]	-	-
Rhinolophus ferrumequinum	I	FRA, GER, POR	[04] [06] [17]	FRA, POR	[33] [34]
Rhinolophus hipposideros	I	CZE, FRA, GER, MON, POL, POR, SPA	[02] [03] [04] [05] [07] [09] [17] [20] [22]	FRA, IRE	[18] [19] [33]
Rhinolophus megaphyllus	I	-	-	AUS	[24]
Vespertilionidae					
Antrozous pallidus	I	-	-	USA	[21]
Barbastella barbastellus	I	CZE, FRA, GER, POL, POR, SPA	[03] [04] [05] [06] [07] [14] [17]	CZE, FRA, GER, POL, POR	[09] [11] [13] [29] [33] [34]
Chalinolobus dwyeri	I	-	-	AUS	[24]
Chalinolobus gouldii	I	-	-	AUS	[24] [27]
Chalinolobus morio	I	-	-	AUS	[24] [27]
Corynorhinus townsendii	I	-	-	USA	[21]
Eptesicus brasiliensis	I	BRA	[31]	-	-
Eptesicus fuscus	I	-	-	USA	[12] [15] [21]
Eptesicus nilsonii	I	GER	[03] [04]	POL, SWE	[25] [32]
Eptesicus serotinus	I	CZE, GER, POL, POR, SPA	[02] [03] [04] [05] [07] [09] [14] [17]	CZE, FRA, POL	[09] [13] [32] [33]
Hypsugo savii	I	SPA	[05]	CZE	[09]
Histiotus velatus	I	BRA	[31]	-	-
Lasionycteris noctivagans	I	-	-	USA	[21]
Lasiurus blossevillii	I	BRA	[31]	USA	[21]
Lasiurus borealis	I	-	-	USA	[12] [15]
Lasiurus cinereus	I	-	-	USA	[12] [15] [21]
Lasiurus ega	I	BRA	[28] [31]	-	-
Myotis alcathoe	I	CZE	[09]	CZE	[09]
Myotis bechsteinii	I	FRA, GER	[03] [04] [06]	CZE, GER	[09] [11]

Myotis blythii	I	SPA	[05]	-	-
Myotis brandtii	I	CZE, GER, POL	[02] [03] [04] [07] [09]	CZE, POL, SWE	[09] [13] [25] [26]
Myotis californicus	I	-	-	USA	[21]
Myotis capaccinii	I	MON, SPA	[05] [20]	-	-
Myotis dasycneme	I	POL	[05]	CZE, POL	[09] [13]
Myotis daubentonii	I	CZE, FRA, GER, POL, POR, SPA	[02] [03] [04] [05] [06] [07] [09] [17]	CZE, IRE, POL	[09] [13] [19]
Myotis emarginatus	I	CZE, FRA, SPA	[05] [06] [09]	CZE	[09]
Myotis escalerai	I	POR	[17]	-	-
Myotis evotis	I	-	-	USA	[21]
Myotis izecksohni	I	BRA	[31]	-	-
Myotis lucifugus	I	USA	[20]	USA	[15] [21]
Myotis myotis	I	FRA, GER, POL	[02] [03] [04] [06] [07]	CZE, GER, POL	[09] [11] [13]
Myotis mystacinus	I	CZE, FRA, GER, MON, POL	[03] [04] [06] [07] [09] [20]	CZE, GER, SWE	[09] [11] [25] [26]
Myotis nattereri	I	CZE, FRA, GER, POL	[02] [03] [04] [06] [07] [08] [09] [14]	CZE, GER, IRE, POL	[09] [11] [13] [19]
Myotis nigricans	I	BRA	[31]	-	-
Myotis riparius	I	BRA	[31]	-	-
Myotis ruber	I	BRA	[28]	-	-
Myotis sodalis	I	USA	[10]	USA	[12]
Myotis thysanodes	I	-	-	USA	[21]
Myotis volans	I	-	-	USA	[21]
Myotis yumanensis	I	-	-	USA	[21]
Nyctalus leisleri	I	CZE, GER, POL, POR	[02] [03] [04] [07] [09] [14] [17]	CZE, FRA, IRE, POL	[09] [13] [18] [32] [33]
Nyctalus noctula	I	CZE, GER, POL	[02] [03] [04] [07] [09] [14]	CZE, FRA, POL, SWE	[09] [13] [25] [29] [32] [33]
Nycticeius humeralis	I	-	-	USA	[12]
Nyctophilus spp.	I	-	-	AUS	[24]
Parastrellus hesperus	I	-	-	USA	[21]
Perimyotis subflavus	I	-	-	USA	[12]
Pipistrellus kuhlii	I	FRA, MON, POR, SPA	[05] [06] [17] [20]	FRA, POR	[33] [34]
Pipistrellus nathusii	I	CZE, FRA, GER, MON, POL	[04] [07] [08] [09] [14] [22]	CZE, POL	[09] [29] [32]
Pipistrellus pipistrellus	I	CZE, FRA, GER, POR, SPA	[02] [04] [05] [06] [09] [17] [22]	CZE, ENG, FRA, GER, IRE, POL, POR	[01] [09] [11] [16] [18] [19] [29] [32] [33] [34]
Pipistrellus pygmaeus	I	CZE, MON, POR	[09] [14] [17]	CZE, ENG, IRE, POL, POR, SWE	[09] [13] [16] [18] [19] [25] [29] [32] [34]
Plecotus auritus	I	CZE, FRA, GER, POL	[02] [04] [06] [07] [08] [09] [14]	CZE, GER, IRE, POL, SWE	[09] [11] [13] [18] [19] [25] [32]
Plecotus austriacus	I	CZE, FRA, GER, POL, SPA	[02] [04] [05] [06] [07] [09]	CZE, POL	[09] [13]

Scotorepens balstoni	I	-	-	AUS	[27]
Vespadelus darlingtoni	I	-	-	AUS	[24]
Vespadelus regulus	I	-	-	AUS	[27]
Vespadelus vulturnus	I	-	-	AUS	[24]
Vespertilio murinus	I	GER	[02] [04]	POL	[32]

[01] Blake et al. 1994; [02] Rackow and Schlegel 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. 2011a; [14] Lesiński et al. 2011b; [15] Bennett and Zurcher 2012; [16] Berthinussen and Altringham 2012; [17] Medinas et al. 2013; [18] Abbott et al. 2012a; [19] Abbott et al. 2012b; [20] Iković et al. 2014; [21] Kitzes and Merenlender 2014; [22] Parise 2014; [23] Alves et al. 2015; [24] Bonsen et al. 2015; [25] Sjolund 2015; [26] Luz 2016; [27] Bhardwaj 2017; [28] Ceron et al. 2017; [29] Myczko et al. 2017; [30] Secco et al. 2017; [31] Novaes et al. 2018; [32] Suchocka et al. 2019; [33] Claireau et al. 2019; [34] Medinas et al. 2019.

CAPÍTULO II

EFEITO DE BORDA DE ESTRADAS SOBRE A DIVERSIDADE E A ATIVIDADE DE MORCEGOS (MAMMALIA, CHIROPTERA) EM UMA SAVANA NEOTROPICAL

Enviado para a revista: Animal Conservation

Road-induced edge effects on bat diversity and activity in a Neotropical savanna

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Short title: Road-induced edge effects on a bat community

Abstract

Roads cause direct and indirect effects on animals present in the surrounding habitat fragments. Because bats have extensive foraging ranges, they may be particularly affected by roads and may take longer to recover. This study aims to analyze road effects on bat activity and diversity, analyzed as species richness, in a Neotropical savanna and is the first to analyze road edge effects on bats in any Neotropical area. Near protected areas in Brasília, Brazil, we placed nine transects, and established sampling points at 0, 500, 1,000, and 1,500 m from the road. At each sampling point, we recorded bats for 12 hours using an ultrasound detector (Song Meter SM2). We used linear mixed-effect models to evaluate the influence of road type, distance from road, and distance from water on bat activity, species richness, and foraging effort, using season as a random effect. We identified 8,274 passes belonging to 35 species or species groups. Activity, foraging effort, and species richness were higher during the rainy season. The model including quadratic response to distance from road was the most parsimonious for bat activity, which was higher on road verges. Resource availability is lower in dry areas; thus, road verges can provide more feeding opportunities for bats as the artificial light lures insects. Moreover, individuals may be crossing roads to forage in sites located outside protected areas. More resources in the area may also affect other insectivorous taxa, such as birds and other small mammals, which may also be crossing roads. Because higher activity near roads may increase the risk of collision with vehicles, we suggest that new road construction take bat commuting and foraging paths into consideration, adding structures to guarantee safe crossing when roads meet those paths.

Keywords: Chiroptera, Highways, Insectivorous bats, Road ecology, Road verges, Urbanization.

Introduction

Brazil has one of the largest road networks in the Americas, with the federal, state, and municipal roads consisting of approximately 220,000 km of paved roads and over 1 million km of unpaved roads (DNIT 2015). Since roads are agents of habitat fragmentation, this large number of highways strongly influences the environment (Forman *et al.* 2003). In contrast to habitat fragmentation caused by agricultural crops, which is common in the Cerrado of central Brazil (Klink & Machado 2005), roads represent an uninhabitable matrix for any type of vertebrate (Pires *et al.* 2002, Rosa 2012).

Roads alter the structure and dynamics of the surrounding environment, with both direct and indirect effects on the animals present in these fragments (Forman & Alexander 1998, Forman *et al.* 2003). Indirect effects include the creation of a border on the habitat fragments, and direct effects include barriers to dispersal, population fragmentation, and roadkill (Coffin 2007).

Roadkill is often reported as the leading cause of mortality for many vertebrate species and is more important than natural causes or other anthropogenic causes such as hunting and habitat loss (Forman & Alexander 1998). Although rates of roadkill are lower for bats than other vertebrates (Lesiński 2007, Braz & França 2016), roads still have considerable effects at the bat population and community levels (Medinas, Marques & Mira 2013), primarily affecting patterns of diversity and activity (Zurcher, Sparks & Bennet 2010, Berthinussen & Altringham 2012). Those effects are mainly due to habitat degradation caused by the edge effect of the roads and the disruption of flight routes (Berthinussen & Altringham 2012).

Kerth and Melber (2009) observed a decrease in bat foraging areas near a motorway in Germany and a consequent decrease in the reproductive success of the insectivorous bat *Myotis bechsteinii*. For other insectivorous species, noise pollution caused by traffic reduces foraging efficiency (Schaub, Ostwald & Siemers 2008, Siemers & Schaub 2011), with a 10% reduction in prey-capture success compared with foraging in silence (Schaub *et al.* 2008). Moreover, street lights located near roads can hamper the foraging of some species, such as *Rhinolophus hipposideros* (Stone, Jones & Haris 2009), or attract other species that forage near light bulbs (Blake *et al.* 1994) because of the increased insect availability (Frank 1988, Barghini & Souza de Medeiros 2012).

Furthermore, roads can significantly affect bat diversity and activity (Berthinussen & Altringham 2012). In a study conducted near a major road in the United Kingdom (UK), Berthinussen and Altringham (2012) observed that the number of bat passes increased with distance from the highway. The decrease in activity may reduce the ecosystem services provided by these species (Kunz *et al.* 2011), with potential consequences for the environment and the bats themselves. Similarly, declining bat diversity, especially in a megadiverse country such as Brazil (Lewinsohn & Prado 2002) with many areas still poorly studied (Bernard, Machado & Aguiar 2011), may affect the ecological dynamics of the environment.

Because of their life history strategy, with low fecundity, high longevity, and use of extensive foraging areas, bats are particularly affected by roads and may take longer to recover lost populations (Altringham 2008). The effect of traffic noise on foraging bats has been observed mainly in experimental studies (e.g., Schaub *et al.* 2008, Siemers & Schaub 2011); thus, studies evaluating foraging behavior in natural sites are needed (Jones 2008). The objective of this study is to assess road effects on Neotropical bat diversity and activity in a savanna area and assess the effects of distance from road, different types of roads, season, and distance from water. We tested the following hypotheses: (i) species richness and activity will increase according to distance from the road, with higher levels in deeper regions of native vegetation and (ii) dirt roads will have less effect on bat activity and species richness.

Material and Methods

This study was conducted in the Brazilian Federal District, located in the central region of the country, in the Cerrado biome. The Cerrado is a tropical savanna (Aw in the Köppen climate classification) characterized by a shifting mosaic of habitats, with open savanna areas and gallery forests along streams. The local climate is typical of the biome, with two well-defined seasons: a rainy season from October to April, and a dry season from May to September (Ratter, Ribeiro & Bridgewater 1997).

Cerrado is one of the most threatened biomes in Brazil, with more than half of its original area already deforested, and a deforestation rate that can reach 30,000 km² per year (Machado *et al.* 2004). Of the more than 200 million hectares, the few portions that remain intact are located mainly in the northern region; the southern region is more threatened by human occupation and the expansion of large urban centers (Klink & Machado 2005). Cerrado is also considered a biodiversity hotspot (Myers *et al.* 2000), which reinforces the need to study human impacts in this area.

We selected nine sites on five different roads (three sites on dirt roads, three on two-lane highways, and three on four-lane highways) along the main protected areas in the study area: Brasília National Park (PNB) (42,389 ha, 15°41'42"S/48°08'10"W), Ecological Station of the Botanic Garden of Brasilia (EEJBB) (4,518 ha, 15°55'42"S/ 47°50'22"W), and Ecological Station of Águas Emendadas (ESECAE) (10,547 ha, 15°36'32"S/47°33'03"W) (Fig. 1).

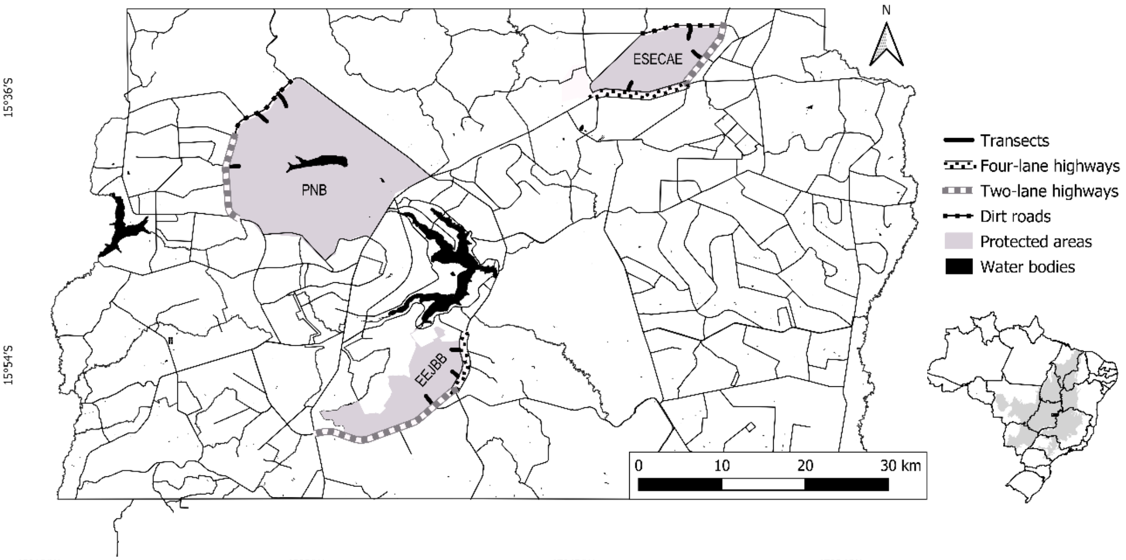

Figure 1. Study area showing the location of monitored transects and protected areas in Distrito Federal. The small map shows the location of Distrito Federal within the Cerrado.

In each selected site, we defined a 1,500-m transect with four sampling points located at different distances from the road (0, 500, 1,000, and 1,500 m). We verified potential spatial autocorrelation among sampling points using a Mantel test. At each of the 36 sampling point, we placed an ultrasound detector (Song Meter SM2) set to start recording 30 min before sunset and continue recording for 12 hours. Recordings were made every 15 min, for 3 min (3-min recording, 12-min interval). We collected activity data during 2 months of the dry season (July 2017 and August 2017) and during 2 months of the rainy season (January 2018 and February 2018).

Sound analysis was conducted using Avisoft-SASLab Pro (version 5.2.11, Avisoft Bioacoustics e.K.). The sound files were first shredded into 5-s files (with 0.1-s overlap) for better visualization and then individually inspected for the presence of bats in the Hamming window (fast fourier transformation [FFT] length: 512) with an intensity threshold of 50% to 60%. Bats were considered present when there was at least one pulse at the search phase, and passes were separated when calls had an interval ≥1 s. Activity was assessed as the number of passes per hour. Sound files containing bat passes with three or more pulses were analyzed for species identification. In this step, we constructed a spectrogram with a Hamming window (FFT length: 1,024) and temporal overlap of 93.75%, from which we determined the main characteristics of the pulses: start and end frequencies, frequency of maximum energy, call duration, and pulse interval. Species were identified based on call characteristics using the criteria of Arias-Aguilar *et al.* (2018) and classified in foraging guilds according to Kalko *et al.* (1996) and Denzinger and Schnitzler (2013).

We evaluated road effects on open-area aerial insectivores and on background-cluttered aerial insectivores by constructing two Linear Mixed-effects Models (LMMs), one for each of the aforementioned guilds, in which the dependent variables were number of passes per hour in each of the 36 sampling points for both seasons, and the independent variables were: (i) distance from the road (in m), (ii) distance from the closest water source (in m, including streams, rivers, or lakes), and (iii) interaction between distance and road type (dirt road, two-lane highway, or four-lane highway). Season (dry or rainy) was included in the model as a random factor in order to account for the temporal variation on bat activity. We evaluated the interaction between distance and road type because we assumed that this characteristic would mainly affect areas closest to the road. We tested activity response to distance from the roads for both linear and quadratic responses.

To evaluate whether these independent variables affect bat foraging, we evaluated buzz ratio (i.e., number of feeding buzzes per pass), which is a measure of foraging effort (Vaughan, Jones & Harris 1995) and can be used to identify preferred areas for feeding. We then constructed other two LMMs with the same independent variables used to evaluate activity to analyze effects on species richness and buzz ratio. We used the Akaike Information Criterion (AIC) to rank models and select the most parsimonious model for each case, with $\Delta AIC > 2$. We also performed Student's t-tests to evaluate the temporal variation between dry and rainy seasons for activity, richness, and buzz ratio.

We performed all tests on R 3.2.2 (R Core Team 2015) by using packages "lme4" (Bates *et al.* 2015) and "MuMIn" (Bartoń 2019), and considered $p < 0.05$ to be significant.

Results

After recording and file shredding, we generated 261,072 sound files, which were manually analyzed for the presence of bat passes. We recorded 8,274 individual passes, from which we identified 7,882 passes from 35 bat species or species groups from eight families. The most abundant species were vespertilionids *Myotis lavali* (2,040 individual passes), *Lasiurus blossevillii* (1,477 passes), and molossid *Molossus molossus* (748 passes), respectively (Table S1).

Overall bat activity was approximately two times higher during rainy season when compared with dry season ($t = -4.474$, $p = 1.61 \times 10^{-5}$). Richness and buzz ratio were also higher during rainy season ($t = -6.786$, $p = 3.25\times 10^{-10}$; and $t = -4.6221$, $p = 1.20 \times 10^{-5}$, respectively). The best model for activity of open-area aerial insectivores included only quadratic response to distance from the road (Table 1), whereas the model including only distance from water was the best fitted for background-cluttered aerial insectivores. Regarding species richness, both quadratic response to distance from the road and interaction between road type and distance from road were included in the most parsimonious model (Table 1). The null model had the lowest AIC values for buzz ratio values (Table 1).

Discussion

In this study, which is the first to analyze road edge effects on bats in any Neotropical area, we detected a strong relationship between distance from roads and open-area aerial insectivorous bat activity and species richness, with similar results for the three types of roads evaluated (dirt roads, two-lane highways, four-lane highways). Contrary to our hypotheses, bat passes at road margins were approximately two times that of sites located 500 m from the margins, and activity was similar among sites located in 500, 1,000, and 1,500 m from the road. However, this result was observed only for species adapted to forage in open areas, whereas activity of background-cluttered species was only influenced by distance from water. Foraging effort was related only to season, being higher during rainy season. Distance from the road and road type had no influence on foraging effort, which suggests that bats generally prefer to commute in sites near roads but don’t prefer to forage in road verges

In the present study, bat species adapted to forage in open-areas were more active near roads, indicating that they might be commuting or foraging on road verges. Similarly, in Australia, Bonsen, Law and Ramp (2015) observed more commuting (represented by bat passes) and foraging (represented by feeding buzzes) in the first 10 m from the road, especially for fast-flying species. In contrast, two studies conducted in the US and in the UK reported that bat activity increased more than two fold in sites located 300 and 1,600 m from the road, respectively (Berthinussen & Altringham 2012, Kitzes & Merenlender 2014). Moreover, in France, Claireau *et al.* (2019) observed that distance had a negative effect on activity, especially for clutter-adapted species.

A Portuguese study by Medinas *et al.* (2019) reported that the surrounding habitat influences road effects on bat activity. Consistent with this finding, the UK study (Berthinussen & Altringham 2012) showing that bat activity was lower near roads was conducted in woodland areas, whereas the Australian study (Bonsen *et al.* 2015) and our study showing the opposite results were conducted in open fields. We also observed higher species richness in areas near road verges, in contrast with previous studies, which reported higher species richness with increased distance from roads (Berthinussen & Altringham 2012). The use of roads or road verges by certain bat species as commuting routes increases the number of species and activity observed in the area.

Various factors may account for the higher bat activity observed near roads in open areas. Insect density is strongly related with forest cover (Kishimoto-Yamada & Itioka 2015, Macedo-Reis, Quesada & Neves 2019), which suggests that resource availability for insectivorous bats is greater throughout forested environments; therefore, bats avoid disturbed areas, such as road margins (Medinas *et al.* 2019). However, in open dry areas, resources are scarcer (Janzen & Schoener 1968, Macedo-Reis *et al.* 2019). Medinas *et al.* (2019) suggested that in habitats with fewer resources, road verges can provide more feeding opportunities for bats, especially for species adapted to forage in open areas. Insects may be attracted to road verges because of the change in microclimate and the presence of artificial light (Stone, Harris & Jones 2015), including light from cars. Moreover, higher temperatures and light reflection of asphalt may also attract insects to roads (Muñoz, Torres & Megías 2015), increasing resource availability to insectivores. In our study, however, foraging effort did not varied according to distance from roads, which suggests that resource availability may not be higher in these areas, as observed by Bhardwaj *et al.* (2019) in Australia, and bats may be crossing the road to forage in sites located outside the protected areas.

In our study, we observed more passes and higher buzz ratio during the rainy season both as a general pattern and for most of the species, which were indicator of rainy season. Insect abundance is higher in the rainy season (Pinheiro *et al.* 2012), thus providing more resources for insectivorous bats. Bat activity may also be influenced by the adjacent environment. In the present study, activity of background-cluttered insectivorous species decreased with distance from water, similarly to the results observed by Geisler, Řehák and Bartonička (2009), who observed higher activity at roads near two large lakes, suggesting that the lake habitats provided additional resources. In Brazilian Cerrado, areas near water are usually surrounded by forest (Ratter et al. 1997), which may increase activity of species adapted to forage in areas with higher amount of clutter.

The effects of roads on insectivorous bat species have been relatively well documented, especially in Europe (e.g., Berthinussen & Altringham 2012, Bennet, Sparks & Zollner 2013, Kitzes & Merenlender 2014, Bonsen *et al.* 2015, Claireau *et al.* 2019), however, there are no available data regarding how roads affect other guilds such as frugivorous and nectar-feeding bats. Frugivory and nectar-feeding are widespread feeding behaviors in Neotropical bats (Baker *et al.* 2003, Fleming, Muchhala & Ornelas 2005) and are present in over 50% of the Phyllostomidae family (Tamsitt 1967, Baker *et al.* 2003), the most diverse bat family in Brazil (Nogueira *et al.* 2018). Frugivorous bats are more likely to collide with vehicles in South America (Novaes *et al.* 2018), which highlights the relevance of studies investigating road effects on these species. In our study, we observed high insectivorous bat activity near roads, suggesting that roads may have similar effects on bats from other feeding guilds or even other taxa, such as birds and other small mammals; however, this requires further study.

Higher bat activity near roads may increase the likelihood of collision with vehicles, especially for species that fly at low or medium heights (Lesiński 2007, Fensome & Mathews 2016), which are abundant in our study area. Because juvenile bats usually fly at lower heights compared to adults (Kurta 1982), they are also more vulnerable to collision with vehicles. Although our results do not show a negative effect of roads on bat activity, roads may serve as barriers to bat dispersion, as suggested by previous studies, which have reported road avoidance behavior (Zurcher *et al.* 2010, Bennet & Zurcher 2012, Bennet *et al.* 2013), resulting smaller foraging areas (Kerth & Melber 2009). This avoidance behavior is especially strong for high-traffic roads (Bennet *et al.* 2013).

We observed that bats commute on road verges even though foraging effort is not increased in those areas, which indicates that they can be crossing roads to feed. Thus, we suggest that mitigation measures are needed in the study area to provide safe crossing points for bats, either with under- or overpasses (Elmeros *et al.* 2016). In addition, planting higher trees on road verges would cause bats to fly higher over roads, thus avoiding collisions with vehicles (Russel *et al.* 2009, Elmeros *et al.* 2016). Finally, improving existing structures such as road signs, by adding noise- and light-deflective screens or green verges, may increase its potential as overpasses for bats, and could be especially important along existing bat commuting routes (Elmeros *et al.* 2016). Because road construction is still a growing industry, especially in underdeveloped countries, we suggest that new installations take bat commuting and foraging paths into consideration, adding structures to guarantee safe crossing when roads meet those paths.

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Table 1. Akaike Information Criterion (AIC) and marginal and conditional R2 (mR2 and cR2) for the best-supported LMMs that explain activity of open-area and background-cluttered aerial insectivorous bats, species richness, and buzz ratio for insectivorous bat species recorded in Brasília, Brazil, from Aug/2017 to Feb/2018. Highlighted in bold are the most parsimonious models according to AIC.

Model	**Open-area Insectivorous Activity**			**Background-cluttered Insectivorous Activity**			**Species Richness**			**Buzz Ratio**		
	AIC	**mR2**	**cR2**	**AIC**	**mR2**	**cR2**	**AIC**	**mR2**	**cR2**	**AIC**	**mR2**	**cR2**
Distance+Distance^2+Distance:Type+Distance_Water	334.37	0.1391	0.3750	481.54	0.0916	0.2380	335.16	0.1526	0.6348	-156.46	0.0880	0.3678
Distance+Distance^2+Distance:Type	332.60	0.1384	0.3776	483.24	0.0543	0.2011	**333.96**	**0.1497**	**0.6337**	-157.03	0.076	0.3603
Distance+Distance^2	**330.42**	**0.1253**	**0.3689**	479.42	0.0535	0.2045	336.50	0.1164	0.6067	-155.09	0.024	0.3143
Distance	333.14	0.0839	0.3287	478.93	0.0373	0.1899	341.79	0.0755	0.5644	-156.52	0.018	0.3108
Distance:Type	335.44	0.0977	0.3378	482.75	0.0385	0.1869	339.74	0.1101	0.5920	-158.45	0.072	0.3576
Distance_Water	341.23	0.0040	0.2465	**477.96**	**0.0482**	**0.2011**	353.00	0.0010	0.4899	-154.81	0.0014	0.2920
Null	339.61	0.0000	0.2453	480.17	0.0000	0.1535	351.13	0.0000	0.4923	**-156.67**	**0.0000**	**0.2943**

Supporting material

Table S1. Bat species recorded in areas located on different distances from the road in a Neotropical savanna distributed according to the type of road and distance from road. Guilds were defined according to Kalko et al. (1996) and Denzeinger and Schnitzler (2001). OAAI = Open-area aerial insectivores; BCAI = Background-cluttered aerial insectivores; HCAI = High-cluttered aerial insectivores.

Family	**Guild**	**Dirt road**				**Two-lane highway**				**Four-lane highway**			
Species		0m	500m	1,000m	1,500m	0m	500m	1,000m	1,500m	0m	500m	1,000m	1,500m
Emballonuridae													
Peropteryx kappleri	BCAI	-	-	-	-	2	-	-	-	-	1	-	1
Peropteryx macrotis	BCAI	18	5	5	5	1	2	4	7	41	61	67	38
Peropteryx trinitatis	BCAI	5	1	-	1	-	-	11	13	3	8	7	4
Furipteridae													
Furipterus horrens	BCAI	3	-	-	-	4	1	-	1	11	2	1	3
Molossidae													
Cynomops greenhalli	OAAI	12	-	11	3	3	8	5	6	7	9	6	8
Cynomops planirostris	OAAI	3	2	-	2	3	5	7	7	3	19	6	2
Cynomops sp.	OAAI	-	1	-	-	-	-	-	-	-	-	-	-

Eumops sp.	OAAI	58	22	25	31	91	4	3	15	44	17	11	11
Molossops temminckii	BCAI	20	20	12	19	74	15	26	34	77	31	9	59
Molossus currentium	OAAI	5	1	3	-	2	4	-	1	11	2	7	12
Molossus molossus	OAAI	45	5	10	8	166	68	53	55	151	72	49	66
Molossus rufus	OAAI	3	2	5	-	7	2	1	-	3	-	-	-
Molossus sp.	OAAI	-	-	-	1	1	-	-	1	1	-	-	2
Neoplatymops mattogrossensis	OAAI	-	-	-	1	-	-	3	-	-	-	-	-
Nyctinomops laticaudatus	OAAI	12	-	4	2	-	3	1	-	2	-	3	3
Nyctinomops macrotis/*Eumops* sp.	OAAI	85	53	60	57	98	13	13	11	27	23	16	23
Promops centralis	OAAI	-	1	-	1	2	-	-	-	1	1	1	-
Promops nasutus	OAAI	23	14	5	7	7	4	27	8	19	4	6	11
Tadarida brasiliensis	OAAI	-	-	-	1	1	2	-	-	1	1	1	-
Mormoopidae													
Pteronotus cf *parnellii*	HCAI	10	10	4	5	46	5	-	7	-	9	2	2
Pteronotus gymnonotus	BCAI	44	3	7	7	104	24	21	11	26	17	20	17
Natalidae													
Natalus sp.	BCAI	-	1	-	-	1	-	-	-	-	-	-	-
Phyllostomidae													

NI	HCAI	-	1	-	-	1	-	-	-	7	-	-	1
Thyropteridae													
Thyroptera sp.	BCAI	3	2	1	5	6	2	2	-	9	9	2	3
Vespertilionidae													
Eptesicus brasiliensis	BCAI	1	1	7	1	5	-	-	-	-	-	-	-
Eptesicus furinalis	BCAI	10	-	2	-	-	3	1	3	3	1	1	-
Eptesicus sp.	BCAI	1	-	-	-	1	-	-	-	-	-	-	-
Histiotus velatus	BCAI	13	7	4	-	19	7	4	4	13	2	2	1
Lasiurus blossevillii	BCAI	97	7	34	10	269	88	283	84	255	197	47	106
Lasiurus cinereus	BCAI	3	6	-	3	-	1	-	1	-	-	-	9
Lasiurus ega/*L. egregius*	BCAI	40	4	7	2	33	59	12	5	109	16	14	64
Myotis lavali	BCAI	183	79	302	256	244	116	177	28	202	301	44	107
Myotis nigricans	BCAI	10	1	35	21	29	78	9	24	5	12	7	38
Myotis riparius	BCAI	3	3	29	13	15	6	1	57	2	1	9	36
Myotis ruber	BCAI	12	18	1	12	36	19	35	41	3	14	21	45
Rhogeessa sp.	BCAI	4	-	-	4	-	1	-	3	-	-	-	-
TOTAL		726	270	573	478	1271	540	699	427	1036	830	359	672

CAPÍTULO III

FATORES DE INFLUÊNCIA NA MORTALIDADE DE MORCEGOS (MAMMALIA, CHIROPTERA) EM ESTRADAS EM UMA SAVANA NEOTROPICAL

Enviado para a revista: Austral Ecology

Factors influencing bat road casualties in a Neotropical savanna

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Abstract

Collision with vehicles is one of the main causes of death for many vertebrates; however, little is known about bat roadkill. Thus, in this study we described bat roadkill in an area of Neotropical savanna and evaluated factors potentially affecting its occurrence. We surveyed 114 km of roads on the margins of the main protected areas in the Brazilian Federal District for 5 years. We analyzed bat roadkill rates on three types of roads (dirt roads, two-lane paved highways, and four-lane paved highways) and recorded distance from water and presence of artificial light. Bat roadkill was calculated for 2-km sections and analyzed by using a generalized linear model (GLM) with the following independent variables: season, road type, presence of artificial light, and distance from water. We identified 87 individuals from three families (Phyllostomidae, Molossidae, and Vespertilionidae). The rate of road-killed bats was related to all independent variables tested except presence of artificial light. Bat road casualties were more numerous in the rainy season, on four-lane highways, and near water. The higher roadkill rate during the rainy season may be explained by higher bat activity due to the increased availability of resources, with many plant species flowering or fruiting and higher insect abundance. Regarding the influence of road type, four-lane highways have the highest traffic volumes in the area and the highest speed limits, which are associated with higher roadkill rates. Previous studies have reported the low detectability of bat carcasses, which indicates that roadkill may be underestimated by surveys. Bats represent the most diverse order of mammals in the Cerrado, where they provide many important ecological services, which need to be preserved. We therefore suggest reducing speed limits on four-lane highways near protected areas, which may decrease bat mortality.

Key words: Chiroptera, Phyllostomidae, Roadkill, Car collision, Wildlife-Vehicle Conflict.

1. Introduction

Roadkill is the most obvious direct cause of wild vertebrate mortality related to habitat fragmentation by roads (Forman & Alexander, 1998; Prado et al., 2006). Although the number of road-killed bats is small compared with roadkill deaths of other vertebrates such as birds and amphibians (Glista et al., 2008; Russel et al., 2009), bats are more likely than most other mammalian species to be involved in vehicle collisions (González-Prieto et al., 1993). The annual mortality rate on roads near bat roosts is estimated to be 5% (Russel et al., 2009); however, the actual rate may be higher because bats look for minimum-cost paths for commuting (Pyke, 1984) and commonly use linear landscape features such as roads.

Because of their small body size, it can be challenging to detect bat carcasses on roads (Bafaluy, 2000). Moreover, small carcasses are easily removed by predators, destroyed during the vehicle collision, or thrown into the surrounding vegetation (Bafaluy, 2000; Slater, 2002, Prosser et al., 2008; Santos et al., 2011). This difficulty locating and identifying road-killed bats contributes to the underestimation of the number of individuals killed (Slater, 2002; Lesiński, 2008; Gaisler et al., 2009; Medinas et al., 2013), which hampers our understanding of the effect of vehicle collisions on bat populations (Bafaluy, 2000; Prosser et al., 2008).

Nevertheless, studies have shown that roads negatively impact bats (Shaub et al., 2008; Siemers & Shaub, 2010; Berthinussen & Altringham, 2012) and may significantly reduce their populations (Schorcht et al., 2009). Because chiropterans have low fecundity rates and later sexual maturity, the lasting effects of roadkill over bat populations makes population recovery harder (Medinas et al., 2013).

Although agile and maneuverable in flight, some bats species fly at low speeds (<20 km/h) and close to the ground (0–4 m) (Russell et al., 2009; Berthinussen & Altringham, 2012), particularly when crossing open spaces. These species, which are mainly frugivorous and nectar-feeding bats, may be more susceptible to road casualties than high-flying species (Lesiński, 2008; Gaisler et al., 2009). The risk of collision for high-flying species, which are mainly insectivores, is considered negligible because they generally fly above vehicles (Limpens et al., 2005; Zurcher et al., 2010). However, insectivorous bats can be attracted by insects around road lamps or car lights (Blake et al., 1994; Zortéa et al., 2001), leading to collision with vehicles on the road.

Other factors that may influence the risk of vehicle-bat collisions include features of the habitat surrounding the road (Lesiński, 2007; Gaisler et al., 2009;

Medinas et al., 2013; Secco et al., 2017). Roads near high-quality habitats are associated with higher bat roadkill rates (Medinas et al., 2013), whereas roads crossing open areas or suburban areas are associated with lower roadkill rates (Lesiński, 2007). Although Medinas et al. (2013) also reported that higher traffic levels were associated with bat casualties, there are no published data regarding how road type affects the bat roadkill rate.

In the biodiverse country of Brazil, previous studies have evaluated roadkill of a range of vertebrate species (e.g., Prada, 2004; Bagatini, 2006; Prado et al., 2006; Tumeleiro et al., 2006; Hengemühle & Cademartori, 2008; Braz & França, 2016), but few have evaluated bats (Alves et al., 2015; Ceron et al., 2017; Secco et al., 2017; Novaes et al., 2018), and little is known about how bat feeding habits are related to the likelihood of vehicle collision. Therefore, the objective of this study is to describe bat roadkill on roads in a Neotropical savanna in Brazil and evaluate factors potentially influencing the roadkill rate. We hypothesize that frugivorous and nectar-feeding bats are more likely than insectivorous species to be victims of vehicle collisions. We also tested the hypothesis that roadkill rates will be higher during rainy season and that four-lane highways, areas near water, and sites with artificial light have higher roadkill rates.

2. Materials and Methods

We conducted this study in the Brazilian Federal District, located in the Cerrado biome of Central Brazil (Fig. 1). The vegetation in the study area is composed primarily of savanna forest (“Cerradão” and "Mata de Galeria") and open savanna (“Cerrado sensu stricto"), with small portions of grasslands and other less representative vegetation types (Fonseca, 2008). The Cerrado is the richest savanna in the world, and bats are the most diverse order of mammals in this biome. More than 100 species have been reported, and the following species are endemic to the Cerrado: *Lonchophylla dekeyseri*, *Lonchophylla bokermanni*, *Glyphonycteris behnii*, and *Thyroptera devivoi*.

This study area is located near Brasília, the fourth most populated city in Brazil, with a population of approximately 3.1 million people. In this area, over 1 million vehicles travel every day, and most of the main roads are located near protected areas.

We conducted surveys along nine roads (total 114 km), including four-lane highways (BR-020 and DF-001; 16 km), two-lane highways (DF-001, DF-345, and DF-128; 74 km), and dirt roads (DF-205 and DF-001; 24 km) (Fig.1). The four-lane and two-lane sections were paved (with shoulders). These road sections delimit five protected areas, namely the Ecological Station of Águas Emendadas (ESECAE, 10,000 ha), Brasília National Park (PNB, 44,000 ha), Ecological Station of the Botanical Garden of Brasilia (EEJBB, 4,000 ha), Experimental Farm of the University of Brasília (FAL/UnB, 4,000 ha), and IBGE Biological Reserve (RECOR, 1,300 ha) (Fig.1). The United Nations Educational, Scientific and Cultural Organization (UNESCO) recognizes these protected areas as core areas of the Cerrado Biosphere Reserve in the Federal District.

We conducted roadkill surveys every 2 days (except for weekends) for 5 years, from April 2010 to March 2015, for a total of 484 roadkill surveys. Two observers and one driver searched for roadkill in a vehicle traveling at approximately 50 km/h. The observers identified every carcasses to the lowest possible taxonomic level and collected data on its position on the road (lane or shoulder) and geographic coordinates using a handheld GPS device with 5-m accuracy. The observers also photographed bat individuals for species identification using the criteria of Díaz et al. (2016). Road type was strongly correlated with traffic volume (four-lane road: 5,604.54 vehicles/hour; two-lane road: 2,486.21 vehicles/hour; dirt road: 621.48 vehicles/hour); therefore, only road type (not traffic volume) was used in the analysis.

Roadkill rate was calculated as the number of road-killed bats/km/day of monitoring (Rosa and Bager, 2012). This approach takes sampling effort into consideration, resulting in a more reliable analysis. To determine which factors had a greater effect on the bat roadkill rate, data regarding road characteristics and bat roadkill were collected for 2-km road section. We then constructed a generalized linear model (GLM) with the number of road-killed bats per section as the dependent variable and the following factors as independent variables: (i) season (dry or rainy), (ii) road type (dirt road, two-lane highway, or four-lane highway), (iii) artificial light (presence or absence), and (iv) linear distance between the center of the road section and the closest source of water (including streams, rivers, and lakes).

3. Results

During this 5-year study, we identified 87 individual bats from at least 3 families, 4 subfamilies, and 6 species (Table 1). Phyllostomidae bats were the most common family recorded as roadkill, representing 72.5% of the identified individuals. The overall roadkill rate was approximately 0.0016 individuals/km/day of monitoring.

Bats comprised 1.62% of the total number of individuals identified and were the second most abundant order of mammals in number of casualties, after Carnivora.

Season, road type, and distance from water were significant predictors of bat roadkill rate in the study area. More road-killed bats were observed during the rainy season (0.0022 individuals/km/day) than during the dry season (0.0010 individuals/km/day) (Table 2, Fig. 2a), and roadkill rates were over 12 times higher on four-lane highways (high traffic, 0.0081 individuals/km/day) than on two-lane highways (0.0007 individuals/km/day) (Table 2, Fig. 2b); we did not observe any road-killed bats on dirt roads. Bat roadkill decreased with distance from water (Table 2), but the presence of artificial light did not influence the number of road-killed bats in our study.

4. Discussion

In this study we recorded 87 road-killed bat individuals from at least three bat families, with Phyllostomidae bats most often involved in vehicle collisions. Significant predictors of the bat roadkill rate were season, road type, and distance from water. This is the first study reporting bat roadkill in the Brazilian Federal District and one of the few that analyzed factors potentially influencing the bat roadkill rate in Brazil. Our results supported our hypothesis that frugivorous and nectar-feeding bats were more likely to be road-killed than insectivorous bats. Our hypothesis that roadkill rates would be higher during rainy season and that four-lane highways and areas near water would have higher roadkill rates were also supported. However, we didn’t observe any relationship between presence of artificial light and road-killed bats.

Most studies of roadkill in Brazil have indicated that bats, considered as a single taxon, are not frequently involved in vehicle collisions (Fischer et al., 2003; Coelho et al., 2008; Braz & França 2016). Studies reporting bat roadkill have been conducted in all Brazilian biomes and have identified 46 species from seven bat families as casualties (Alves et al., 2015; Ceron et al., 2017; Secco et al., 2017; Novaes et al., 2018). Consistent with our results, previous studies reported that Phyllostomidae is the most affected bat family, representing over 80% of the records (Novaes et al., 2018).

Most Phyllostomidae bats fly at the height of the understory layer, which in the Cerrado is approximately 5 m (Lemos-Filho et al., 2010), and are slow-flying species (Kalko et al., 1996; Stockwell, 2001), which accounts for their greater likelihood to be involved in vehicle collisions. In our study, we also identified individuals from Molossidae and Vespertilionidae families, both of which are mainly aerial insectivores

(Kalko et al., 1996; Denzinger & Schnitzler, 2013). This feeding guild is usually recorded in roadkill surveys and represents 13.1% of the carcasses identified on Brazilian roads (Novaes et al., 2018). The typical foraging areas of aerial insectivores are open fields (Kalko et al., 1996), which may explain why these bats are active over road verges. In addition, the presence of streetlamps, or even vehicle lights, lures insects (Nabli et al., 1999), which may attract bats by increasing resource availability (Rydell, 1992; Stone et al., 2015). However, in our study area, we did not observe any relationship between the presence of artificial light and the bat roadkill rate.

According to Medinas et al. (2013), the three main factors (other than season) that influence the bat roadkill rate are bat biology (e.g., species, sex, and age), road characteristics, and land features. Regarding road characteristics, higher traffic volume has been associated with increased bat mortality (Medinas et al., 2013). In our study we also observed that bat roadkill in the Brazilian Federal District occurred most often on four-lane paved highways, which are high-traffic roads. Similarly, studies in Portugal and Montenegro have reported higher levels of bat mortality on high-traffic roads (Medinas et al., 2013; Iković et al., 2014). Bafaluy (2000) reported that areas with higher speed limits had more bat casualties in Spain. Likewise, in our study, four-lane paved highways, which had the highest bat roadkill rates, also had higher speed limits than two-lane highways and dirt roads.

Consistent with our observation that distance from water was associated with higher bat roadkill rates, previous studies have also recorded higher bat mortality due to traffic in areas near water sources (Lesiński, 2007; Gaisler et al., 2009; Medinas et al., 2013; Iković et al., 2014). Fensome and Mathews (2016) suggested that the high-quality habitat near water increases the chance of bat-vehicle collision. Other environmental characteristics that have been reported to predict the rate of bat roadkill include linear elements, which are associated with higher bat mortality (Lesiński, 2008, Iković et al., 2014) and windbreaks and bushes, which are associated with lower bat mortality (Lesiński et al., 2011). However, in our study, distance from water was the only feature of the surrounding habitat that was a significant predictor of bat mortality on roads.

In our study, we observed more bat roadkill during the rainy season (summer), especially in February and March. In most European studies, bat roadkill rates are also higher during the summer, which occurs from July to September (Bafaluy, 2000; Lesiński, 2007, 2008; Gaisler et al., 2009; Lesiński et al., 2011; Medinas et al., 2013; Iković et al., 2014; Parise 2014). In temperate areas such as Europe, most bats hibernate during the winter months (Beer & Richards, 1956; Boyles et al., 2006), which explains the higher summer roadkill rates. Similarly, climactic conditions have been suggested to influence bat activity in the Pacific Northwest (Erickson & West, 2002; Burles et al., 2009). In the Brazilian Cerrado resource availability is higher in the rainy season, when many plant species are flowering or fruiting (Pilon et al., 2015) and insect abundance is higher (Pinheiro et al., 2012). Accordingly, the activity of insectivorous bats is approximately two times higher in the rainy season (see results in chapter II), and phyllostomid bats are usually captured in higher numbers in the rainy season than in the dry season (Willig, 1985; Sousa et al., 2013). Conflicting results have been reported by other studies carried out in Brazil. For example, in the Atlantic Forest in Rio de Janeiro, no difference in roadkill rates was observed between seasons (Secco et al., 2017); however, seasonal differences in weather are smaller in this region compared with the Cerrado (Secco et al., 2017). In a Cerrado area in the state of Minas Gerais, bat roadkill rates were higher in June and July than in the other months studied (Alves et al., 2015); however, this study was conducted during the dry season only (Alves et al., 2015). Thus, the results of our study, carried out over 5 years during both wet and dry seasons, are more relevant for the Cerrado.

Bats are generally thought to be less affected by vehicle collisions compared with other vertebrates (Ashley & Robinson, 1996), especially birds and amphibians (Glista et al., 2008; Russel et al., 2009; Šemrl et al., 2012). However, bat roadkill can be strongly underestimated. For small mammals (<100g), such as rodents, carcass persistence in study area is of approximately two days (Santos et al., 2016), which is consistent with studies conducted in other areas (Santos et al., 2011; Barrientos et al., 2018). Many bats that occur in the study area are considerably smaller (weighting approximately 20g), therefore, the 2-day persistence may be a very conservative estimation for the group. Moreover, surveys are often carried out during the day (Lesińska, 2008; Gaisler et al., 2009), which also hampers roadkill localization and identification, because the bat carcasses may have been removed or destroyed during the night, when bats are active and the collisions are more likely to occur. Arnett (2006) found that the detectability of bat carcasses may be as low as 14%, further supporting the idea that bat roadkill is underestimated. Bat casualties on roads may affect up to 5% of a bat colony (Russel et al., 2009), which highlights the importance of studies evaluating bat-vehicle collisions and factors that may influence roadkill rates.

Bats are the most diverse orders of mammals in the Cerrado (Aguiar et al., 2016), where they are important pollinators of economically valuable plants such as *Caryocar brasiliense* (Gribel, 1986; Gribel & Hay, 1993; Carvalho, 2009) and play an important role in fruit dispersal, which is indispensable to the restoration of degraded areas (Kunz et al., 2011, Kuhlmann & Ribeiro, 2016). In Neotropical regions, pollination and fruit dispersal are carried out by the family Phyllostomidae (Kunz et al., 2011), which were the bats most often identified as roadkill in our study. Loss of these important ecosystem services may have adverse consequences on the environment. Measures such as the construction of overpass structures (Elmeros et al., 2016) and reduction of speed limits near protected areas in the Cerrado may be useful to promote bat conservation and protect the environment.

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Table 1. Identified bat species involved in road casualties in Distrito Federal, Brazil from April 2010 to March 2015. NI = not identified

Taxon	**Season**		**Total**
	Dry	**Wet**	
Phyllostomidae: Stenodermatinae			
Artibeus spp.	1	1	2
Platyrrhinus spp.	1	1	2
Sturnira lilium	1	-	1
Phyllostomidae: Glossophaginae			
Glossophaga soricina	3	10	13
Phyllostomidae: NI			
NI	2	9	11
Molossidae: Molossinae			
Molossops temminckii	2	0	2
Molossidae: NI			
NI	4	4	8
Vespertilionidae: NI			
NI	0	1	1
TOTAL	14	26	40

Table 2. Coefficients of the generalized linear model assessing the potential influence of variables on the rate of bat roadkill on roads in the Brazilian Federal District from April 2010 to March 2015.

	Estimate	**Std. Error**	**t**	**p**
(Intercept)	0.3630719	0.3951996	0.919	0.3603
Season	0.5789474	0.262758	2.203	0.02969*
Type (four-lane highway)	3.8068248	0.4666302	8.158	6.73×10^{-13}***
Type (two-lane highway)	0.8445007	0.4911054	1.72	0.08837
Artificial light	-0.3628641	0.3933358	-0.923	0.35831
Distance from water	-0.0009186	0.0002834	-3.241	0.00158**

*p<0.05, **p<0.01, ***p<0.0001

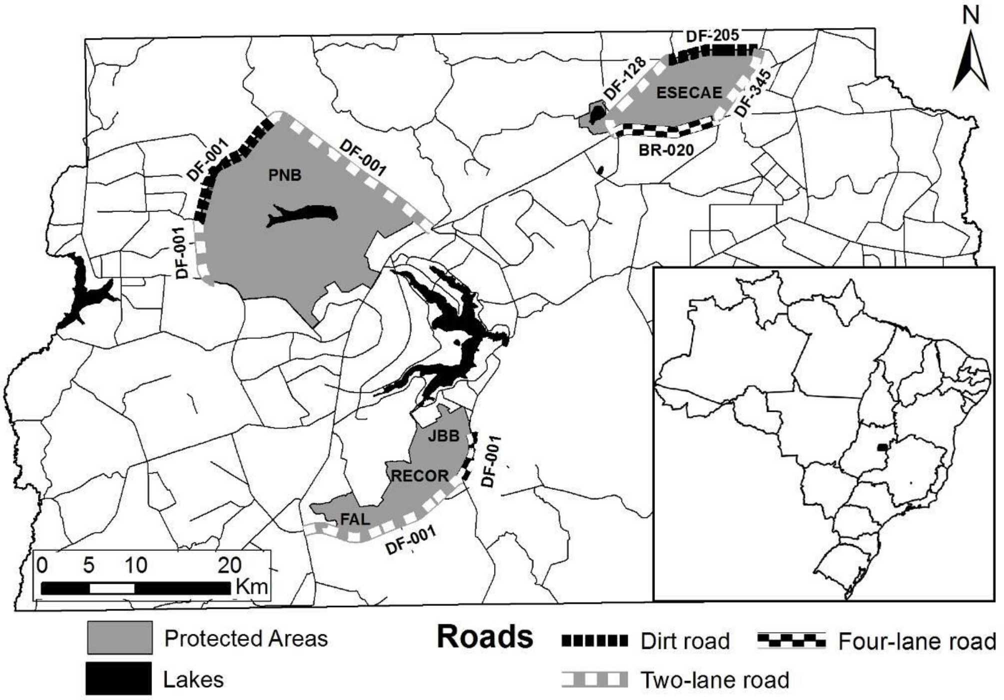

Figure 1. Study area with locations of monitored roads and protected areas. ESECAE, Ecological Station of Águas Emendadas; FAL, Experimental Farm of the University of Brasília; JBB, Botanical Garden of Brasilia; PNB, Brasília National Park; RECOR, IBGE Biological Reserve.

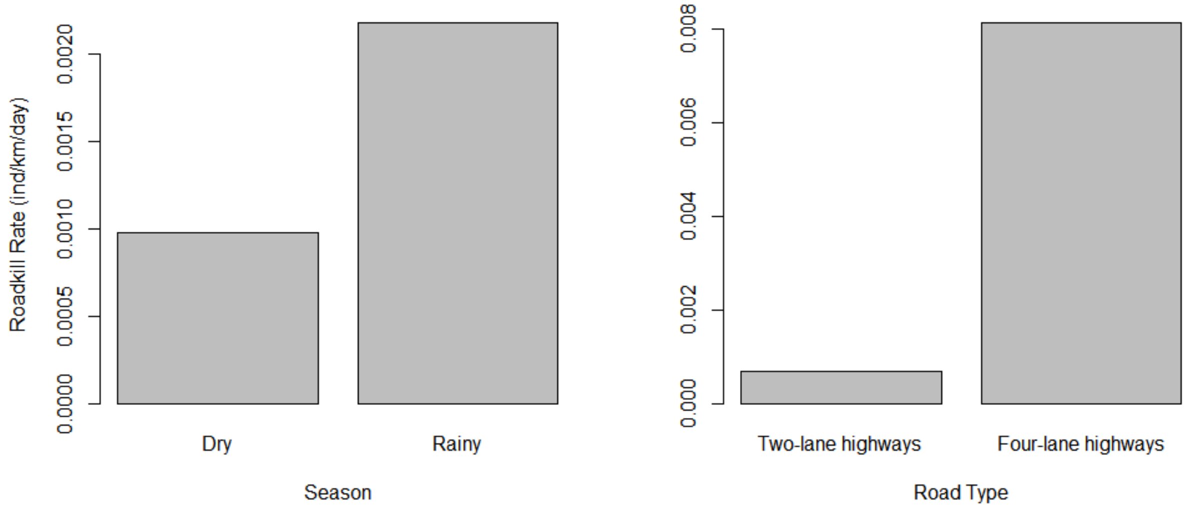

Figure 2. Comparison of bat roadkill rates between the wet and dry seasons and between two- and four-lane highways in the Brazilian Federal District from April 2010 to March 2015.

CONSIDERAÇÕES FINAIS

O estudo do efeito das estradas nos morcegos ainda é um campo pouco pesquisado, com um número reduzido de artigos publicados nas últimas décadas. Apesar do baixo número de estudos, os resultados indicam que estradas podem influenciar negativamente a população de morcegos localizadas nos fragmentos em seu entorno. A maior parte dos estudos ocorreu na Europa, com poucos estudos em outras áreas, especialmente avaliando diferentes efeitos da estrada (atropelamentos e efeito de barreira). Na América do Sul, apenas estudos avaliando a mortalidade de morcegos nas estradas tem sido realizados, sendo inexistentes estudos que avaliam o efeito das estradas nas atividades dos morcegos.

O estudo desenvolvido no capítulo II é, portanto, o primeiro a avaliar como as estradas afetam a atividade e a diversidade de morcegos neotropicais. Por meio da análise acústica, também foi possível avaliar o efeito das estradas na atividade de forrageamento dessas espécies. Apesar de haver maior número de passes nas áreas mais próximas às estradas, os morcegos não estão selecionando essas áreas para forragear, com exceção de estradas iluminadas, onde há maior esforço de forrageio nas áreas mais próximas da estrada. É possível que os morcegos estejam utilizando a estrada como um corredor para a sua rota de voo, ou ainda, que estejam atravessando as estradas para forragear em áreas fora das Unidades de Conservação.

A maior presença de morcegos nas margens da estrada pode representar uma ameaça para essas espécies, uma vez que existem estradas movimentadas em algumas áreas do entorno das UC’s. Apesar da presença de estradas, o número de morcegos atropelados na região foi baixo, quando comparado com outros animais com indivíduos de pequeno porte. Em áreas com estradas duplicadas (BR-020 e parte da DF-001), houve um maior número de morcegos atropelados quando comparado com outros tipos de estradas. Uma melhor fiscalização da velocidade nessas áreas, particularmente na BR-020, poderia diminuir o número de morcegos envolvidos nesses acidentes.

Apesar deste ser um dos poucos estudos avaliando o efeito direto (atropelamento) e indireto (atividade) das estradas sobre os morcegos, não foi possível delinear uma relação entre áreas com maior atividade de morcegos e áreas com maior numero de atropelamentos, uma vez que a maior parte das espécies atropeladas é da família Phyllostomidae, dificilmente registrada em estudos de bioacústica. Portanto, é importante que futuros estudos avaliem o efeito da presença de estradas em outras guildas tróficas de morcegos, particularmente os frugívoros e nectarívoros, já que estas espécies foram as mais representadas nos atropelamentos. Além disso, é importante que novos estudos foquem na avaliação dos efeitos de outras características da urbanização, tais como iluminação artificial e poluição sonora, na atividade destes animais.