

ON A COLLISION COURSE: THE VULNERABILITY OF BATS TO ROADKILLS IN BRAZIL

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ABSTRACT. In Brazil, studies on roadkills are recent and usually restricted to lists of species found at some road stretch. Among mammals, medium- and large-sized species have received greater attention. The present study aimed at presenting the first list of bat roadkills in Brazil, including comments on the traits that may cause roadkills. We recorded 415 deaths from 44 species of seven families in all Brazilian biomes. We did not observe a relationship between body size or type of flight with the number of bat-vehicle collisions. Frugivore was the trophic guild most victimized, possibly due to greater natural abundance, foraging in low height airspace, and capacity to make long-distance movements. The elevated number of species recorded indicates that these roads may exert a negative effect on bat fauna. We encourage road ecologists and environmental agencies to include bats in their fauna monitoring of road infrastructure and request to make more accurate estimates of this impact.

RESUMO. Em rota de colisão: a vulnerabilidade de morcegos à atropelamentos no Brasil. No Brasil os estudos sobre atropelamentos de fauna são recentes e, na maioria dos casos, restritos a lista de espécies encontradas em alguns trechos de rodovias. Dentre os mamíferos, espécies de médio e grande porte têm recebido maior atenção. O presente estudo apresenta a primeira lista de morcegos atropelados no Brasil, incluindo comentários sobre os fatores que podem causar os atropelamentos. Nós registramos 415 óbitos de 44 espécies e sete famílias em todos os biomas brasileiros. Nós não observamos relação entre o tamanho corporal e o tipo de voo com o número de colisões entre veículos e morcegos. Morcegos frugívoros foram os mais vitimados, possivelmente, em virtude de sua maior abundância natural, por forragear em baixas alturas e pela elevada capacidade de movimentação. O alto número de espécies indica que as estradas podem exercer um viés negativo sobre a quiropterofauna. Nós incentivamos que pesquisadores e agências ambientais incluam morcegos no monitoramento de fauna em infraestruturas viárias e solicitem estimativas mais precisas desse impacto.

Key words: Conservation. Road ecology. Urbanization impact. Vehicle collisions.

Palavras-chave: Colisão com veículos. Conservação. Ecologia de estradas. Urbanização.

INTRODUCTION

Impacts generated by roads are a significant threat to biodiversity conservation, and the main consequences for wildlife are the barriers to movements and fragmentation of populations, an increase of the edge effect, and roadkills (Laurance et al. 2009). Recent estimates indicate more than 450 million wild vertebrates are killed in Brazilian highways each year (Bager et al. 2016). Also, fatalities by collision with vehicles represent a significant threat to wildlife worldwide, with hundreds of millions of animals killed annually, resulting in severe population reduction (Eigenbrod et al. 2009; Benítez-López et al. 2010; Kociolek et al. 2011; Brown & Brown 2013; Torres et al. 2016). Moreover, the effects of these fatalities on the long-term persistence are still uncertain for the majority of species (Roger et al. 2011; Loss et al. 2015; Santos et al. 2016).

Among mammals, medium and large-sized species have received greater attention from ecologists studying roads (Barthelmeß & Brooks 2010; Cáceres 2011). Although smaller species are suggested to be less impacted by roadkills, collisions with vehicles are known to be an important cause of death of bats (Lesiński 2007, 2008; Gaisler et al. 2009; Russell et al. 2009; Lesiński et al. 2010; Berthinussen & Altringham 2012; Abbott et al. 2012; Medinas et al. 2013; Fensome & Mathews 2016). Nevertheless, few studies have investigated the biological traits that influence bat-vehicle collisions, and none of them have focused in tropical areas.

Researchers frequently relate bat mortality on roads with landscape configurations (Lesiński 2008; Lesiński et al. 2010; Medinas et al. 2013). However, to assess the impact of roads on bats, it is relevant to know which species are most affected and whether there is a relationship between vulnerability and biological characteristics of the species. This is fundamental for the management of biodiversity since impact assessment and mitigation should be based on knowledge of the species most vulnerable to road fatality, which is very limited, especially for bats (Kociolek et al. 2011; Altringham & Kerth 2016; Fensome & Mathews 2016).

Herein, we present a compilation of bat roadkills in Brazil, including a test on the biological traits that may cause bat-vehicle collisions. We hypothesized that some biological characteristics of species (e.g., trophic guild, body size, flight type) could drive the vulnerability of bats to roadkills.

MATERIAL AND METHODS

Data search, compilation and extraction

We used two sources to make a species list compilation of roadkill of bat species in Brazil. The first was literature, including articles, books and book chapters, Masters and Doctoral theses, published between January 2014 and December 2016, and identified in the following databases: Web of Science (<https://webofknowledge.com/>), SciELO (<http://www.scielo.org/>), Science Direct (<http://www.sciencedirect.com/>), Scopus (<https://www.scopus.com/home.uri>), SpringerLink (<http://link.springer.com/>), Wiley Online Library (<http://onlinelibrary.wiley.com/>), and Google Scholar (<https://scholar.google.com/>).

The search was made using multiple combinations of the words (in English and Portuguese): road, roads, roadkill, road kill, roadkills, animal-vehicle collisions, wildlife-vehicle collisions, road-effect, traffic, disturbance, impact, bat, bats, Chiroptera, mammals, Mammalia, biodiversity, Brazil, Neotropics, and Neotropical. The published works found were filtered to exclude duplications and those that did not have information on bat roadkills in Brazil.

The second source of records was the consultation of the following institutional scientific collections: Museu Nacional, Universidade Federal do Rio de Janeiro (MN, Rio de Janeiro, Brazil), Collection Adriano Lúcio Peracchi, Universidade Federal Rural do Rio de Janeiro (ALP, Seropédica, Brazil), and Collection of Laboratório de Diversidade de Morcegos, Universidade Federal Rural do Rio de Janeiro (LADIM, Seropédica, Brazil).

Categorization of bats

We hypothesized that some biological characteristics may direct the vulnerability of bats to roadkills. To test this hypothesis, we considered the following biological traits: trophic guild, body size, and type of flight. We chose these traits because they are directly related to spatial behavior and landscape use (Norberg & Rayner 1987; Kalko et al. 1996), which can provide evidence of vulnerability to roadkill.

We classified the species into trophic guilds according to Kalko et al. (1996). Species that were

not mentioned in this classification were allocated to one of the 10 trophic guilds recognized by these authors, using information about diet and space usage available in the literature.

To evaluate the effect of body size and type of flight on the vulnerability to roadkills, we used only the bat species of the family Phyllostomidae. Phyllostomid species represented more than 80% of our sample, and constitute the family that presents greater diversity in size and diet in the Neotropics (Gardner 1977; Reis et al. 2007).

We obtained mean body size and mean forearm length for each species from the literature (e.g., Reis et al. 2007). We then grouped species into the following classes: small-sized (body mass < 10 g), medium-sized (body mass ranging from 10 to 40 g) and large-sized (body mass > 40 g).

To understand the relationship between the type of flight and the vulnerability to bat-vehicle collisions, we used two measures of the wing separately: relative wing loading (WL) and aspect ratio (AR). These two metrics are directly related to bat flight and foraging behavior, including maneuverability, speed flight, flight height and space usage (Norberg & Rayner 1987; Marinello & Bernard 2014). Species with higher values of wing loading and aspect ratio have fast flights and forage preferentially in open environments (Marinello & Bernard 2014). On the other hand, species with smaller wing loading and aspect ratio have slower flights and greater maneuverability and are found more frequently in the interior of forests (Norberg & Rayner 1987; Norberg & Fenton 1988; Marinello & Bernard 2014). The values of WL and AR for phyllostomid bats were obtained through Tavares (2013) and Marinello & Bernard (2014). Even though there is a roadkill record for *Macrophyllum macrophyllum*, we excluded this species from the analysis due to the scarcity of morphological data.

Data analysis

To verify if the trophic guild directly influences the vulnerability to roadkills, we performed Kruskal-Wallis test, testing whether the means of bat-vehicle collisions records are statistically different between each category of the trophic guild. We grouped the species of carnivorous, omnivorous and piscivorous bats, in a single group hereafter called 'animalivore' due to the low number of samples. The Kruskal-Wallis test was carried out using R software (R Development Core Team 2009).

Before performing the statistical analyses to test the relationship between body size, type of flight and the vulnerability of bats to roadkills, the data were

evaluated regarding the normality of the response variable and the collinearity of the explanatory variables, following the procedures and decision making described in Zuur et al. (2010). Subsequently, we performed an analysis of Generalized Linear Models (GLM), using the Negative Binomial distribution with log link functions, which showed no bias in terms of data overdispersion.

GLM was used to evaluate the relationship between the variable "roadkills" and the explanatory variables (body mass, length of forearm, relative wing loading, and aspect ratio). Through the Spearman's rank correlation coefficient it was found collinearity ($r_s \geq 0.6$) between the variables body mass and the length of forearm. Variables with correlation above $r_s \geq 0.6$ were not used together in the same model, following Matos et al. (2017). To determine which variables were the most decisive to explain the vulnerability of bat species to roadkill, we used a theoretical approach based in second-order Akaike Information Criterion (AICc), which is indicated for small samples (Burnham et al. 2011). All models with $\Delta AICc \leq 2$ were selected as best models. After selecting the best models, we used a multi-model inference, with standardized data (Burnham et al. 2011) to calculate the independent contribution of each variable through the sum of the weight of all the models that included the variable. These analyses were calculated with R software (R Development Core Team 2009) using the packages "glmmADMB", "MuMIn" and "ggplot2".

RESULTS

Bat roadkills were recorded in all Brazilian biomes and geographic regions (**Fig. 1**), though most records were in southeastern Brazil (**Table 1**). Probably, the high number of records in that region is related to three non-mutually exclusive factors: (i) higher concentration of roads and road flow (DNIT 2004); (ii) increased road monitoring (Dornas et al. 2012), and (iii) higher concentration of bat researchers (Esbérard & Bergallo 2005).

We recorded 44 species, representing seven bat families in a total of 415 roadkill records (**Table 2**). Phyllostomidae were the most recorded, with 348 records (83.8%); of these, bats of the genus *Artibeus* were the most abundant, with 93 records (22.4% of the total). Frugivorous bats comprised 250 records (60.2%) belonging to 14 species (**Table 3**). Aerial insectivorous bats represented the second most

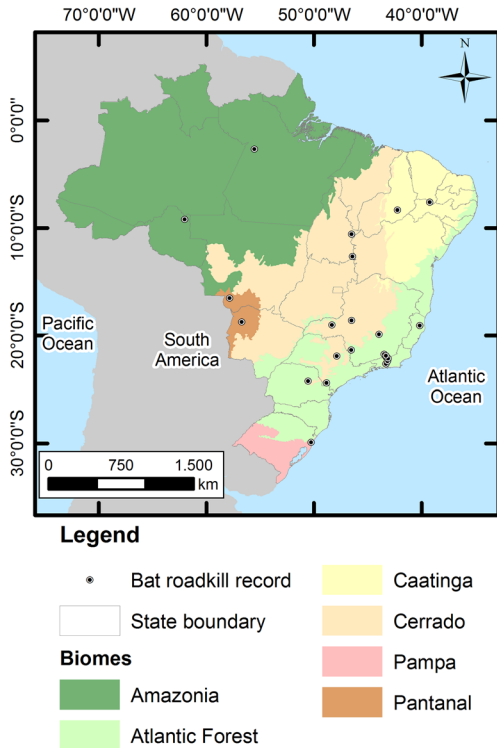


Fig. 1. Localities with occurrences of bat roadkills in Brazil.

frequent trophic guild (54 records, 13.0%), and nectarivorous bats had 49 records (11.8%). We found a statistically significant difference in the number of roadkills between the bat's trophic guilds (Kruskal-Wallis = 16.692, $p < 0.01$), being the frugivorous bats most represented to vehicle collisions (Fig. 2).

Regarding the relationship between body size, type of flight, and vulnerability to roadkills, four models were selected with $\Delta AICc < 2$, and the wing loading and body mass were the best variables to explain bat-vehicle collisions. Those variables were present in three of the four models (Table 4). The best model was the null ($\Delta AICc = 0$), demonstrating that bat roadkills are not related to the body size or type of flight since none of the biological attributes tested is influencing the number of individuals victimized (Table 5). Nevertheless, there is a positive and weak relationship between WL, BM, and roadkills (Fig. 3). Therefore, it is possible that roadkills are random events to phyllostomid bats or may be related to other traits not tested in this study.

DISCUSSION

We recorded the roadkills of species included in seven of the nine families of bats known to occur in Brazil. Forty-four species have been victims of roadkills, that is, 25% of bat species with occurrence in Brazil (see Nogueira et al. 2014). This number is a strong indicator of the bat fauna susceptibility to the impact generated by roads.

Frugivorous bats were the most common roadkills. Species of this trophic guild are highly abundant in forests and human-altered areas. They forage in low height airspace, and commonly use forest edges and open areas (Kalko et al. 1996; Cosson et al. 1999; Bernard 2001), which can make them more vulnerable to vehicle collisions. The predominance of *Artibeus* species is not surprising, as this genus is very abundant (Kalko et al. 1996; Bernard & Fenton 2002; Esbérard et al. 2014), frequently flies between forest fragments and urban areas, and makes long-distance movements (Morrison 1978; Menezes-Jr. et al. 2008; Arnone et al. 2016).

Aerial insectivorous bats were the second most common victims of roadkills. Species of this trophic guild mostly use open areas (Kalko et al. 1996) and frequently capture insects attracted by the light of road lampposts (Laurance et al. 2009). Therefore, the use of airspace above roads as a foraging area may be a risk factor, which turns the species of this trophic guild more susceptible to vehicle collisions. In a recent review about roadkills of aerial insectivores in Europe, low-flying species were more prone to collisions than high-flying species (Fensome & Mathews 2016). We found a similar result in Brazil, where insectivore species of the family Vespertilionidae, that in general fly in lower strata (see Marques et al. 2016), were 66% more frequent than aerial insectivores that fly at higher strata, especially molossid bats.

The lack of a relationship between body size, type of flight and the roadkills within Phyllostomidae indicates that the collisions with vehicles could affect all species that use the space occupied by roads. However, it is important to emphasize that other traits—such

Table 1
Roads with records of bat-vehicle collision in Brazil.

Highway	Municipality	State	Author
BR-163	Santarém	Pará	Present study
RO-133	Machadinho D'Oeste	Rondônia	Present study
CE-060	Jardim	Ceará	Novae & Laurindo (2014)
BR-020	São João do Piauí	Piauí	Present study
Urban way	Mateiros	Tocantins	Gregorin et al. (2011)
Urban way	Aurora do Tocantins	Tocantins	Present study
BR-070	Cáceres	Mato Grosso	Melo & Santos-Filho (2007)
BR-359	Corumbá	Mato Grosso do Sul	Present study
BR-101	Sooretama	Espírito Santo	Hoppe et al. (2014)
Undetermined	Mocambinho	Minas Gerais	Nogueira & Pol (1998)
MGC-354	Patos de Minas	Minas Gerais	Alves et al. (2015)
Urban way	Belo Horizonte	Minas Gerais	Present study
BR-491	Muzambinho	Minas Gerais	Present study
BR-040	Simão Pereira	Minas Gerais	Present study
BR-040	Juiz de Fora	Minas Gerais	Present study
BR-040	Matias Barbosa	Minas Gerais	Present study
BR-040	Petrópolis	Rio de Janeiro	Present study
BR-040	Duque de Caxias	Rio de Janeiro	Present study
BR-040	Com. Levy Gasparian	Rio de Janeiro	Present study
BR-040	Três Rios	Rio de Janeiro	Present study
BR-040	Areal	Rio de Janeiro	Present study
Undetermined	São Carlos nearby	São Paulo	Prada (2004)
BR-373	Apiáí	São Paulo	Present study
PR-160	Telêmaco Borba	Paraná	Zaleski et al. (2009)
BR-101	Not mentioned	Rio Grande do Sul	Dornelles et al. (2012)
BR-101	Osório	Rio Grande do Sul	Coelho et al. (2008)

as species abundance, level of activity, landscape characteristics and proximity to roosts or foraging sites—although not addressed in this study, can also influence roadkills (Lesiński 2008; Russel et al. 2009; Medinas et al. 2013; Fensome & Mathews 2016).

In fact, all the species that had 20 or more records in our study were those considered to be the most abundant in practically all Brazilian biomes (Reis et al. 2007). Abundance is one of the most important traits for flying animals (e.g., bats, birds, and butterflies) killed

on roads (Medinas et al. 2013; Skórka et al. 2013; Santos et al. 2016)

We also gathered information of the rare species *Macrophyllum macrophyllum* and *Thyroptera wynneae*, victims of vehicle collisions, although with a single record each. Fensome and Mathews (2016, p. 320) argue that “the presence of casualties from rare species on roads is of particular concern, as relatively low levels of additional mortality could potentially have an impact on the long-term sustainability of local populations.”

Table 2

Roadkills of bats in Brazil, including trophic guild, average of body mass (in grams), average of length of forearm (in millimeters), relative wing loading, aspect ratio, number of records (N), and authors: [1] present study, [2] Zaleski et al. (2009), [3] Dornelles et al. (2012), [4] Gregorin et al. (2011), [5] Prada (2004), [6] Coelho et al. (2008), [7] Melo and Santos-Filho (2007), [8] Bagatini (2006), [9] Nogueira and Pol (1998), [10] Hoppe et al. (2014).

Taxa	Trophic guild	Body mass	Length of Forearm	Wing loading	Aspect ratio	N	Author
EMBALLONURIDAE							
<i>Saccopteryx leptura</i>	Aerial insectivore	-	-	-	-	1	[1]
PHYLLOSTOMIDAE							
MICRONYCTERINAE							
<i>Micronycteris minuta</i>	Gleaning insectivore	7.5	33.5	40.7	5.8	1	[1]
<i>Micronycteris</i> sp.	Gleaning insectivore	-	-	-	-	1	[3]
DESMODONTINAE							
<i>Desmodus rotundus</i>	Sanguivore	35.0	58.5	41.7	6.7	6	[1]
<i>Diphylla ecaudata</i>	Sanguivore	30.0	53.2	38.5	6.1	2	[1]
PHYLLOSTOMINAE							
<i>Chrotopterus auritus</i>	Carnivore	75.0	81.8	27.3	6.3	5	[1] [2]
<i>Gardnerycteris crenulatum</i>	Gleaning insectivore	12.0	49.9	27.3	6.8	1	[4]
<i>Lophostoma silvicola</i>	Gleaning insectivore	34.0	54.8	33.5	5.2	1	[1]
<i>Macrophyllum macrophyllum</i>	Gleaning insectivore	-	-	-	-	1	[1]
<i>Mimon bennettii</i>	Gleaning insectivore	23.0	54.3	27.8	7.0	4	[1]
<i>Phyllostomus hastatus</i>	Omnivore	85.0	88.8	36.6	7.1	22	[1]
<i>Tonatia bidens</i>	Omnivore	30.0	51.7	29.6	5.7	3	[1]
<i>Trachops cirrhosus</i>	Carnivore	35.0	62.3	36.1	5.8	2	[1]
GLOSSOPHAGINAE							
<i>Anoura caudifer</i>	Nectarivore	10.0	36.0	43.3	6.6	24	[1]
<i>Anoura geoffroyi</i>	Nectarivore	15.0	43.5	51.0	7.7	6	[1]
<i>Glossophaga soricina</i>	Nectarivore	11.0	34.6	42.5	6.4	19	[1]

(Table 2 cont.)

Taxa	Trophic guild	Body mass	Length of Forearm	Wing loading	Aspect ratio	N	Author
CAROLLIINAE							
<i>Carollia perspicillata</i>	Frugivore	18.0	40.2	38.8	6.2	42	[1]
STENODERMATINAE							
<i>Artibeus fimbriatus</i>	Frugivore	55.0	66.8	39.0	6.3	5	[1]
<i>Artibeus lituratus</i>	Frugivore	70.0	71.8	38.1	6.2	69	[1]
<i>Artibeus obscurus</i>	Frugivore	48.0	60.0	38.6	6.4	4	[1]
<i>Artibeus planirostris</i>	Frugivore	50.0	65.4	40.1	6.3	3	[1]
<i>Artibeus</i> sp.	Frugivore	-	-	-	-	12	[1] [3] [5] [6]
<i>Chiroderma doriae</i>	Frugivore	34.0	53.2	45.0	7.1	1	[1]
<i>Chiroderma villosum</i>	Frugivore	24.0	47.1	40.3	6.3	2	[1]
<i>Chiroderma</i> sp.	Frugivore	-	-	-	-	1	[3]
<i>Dermanura cinerea</i>	Frugivore	15.0	40.2	34.3	5.4	4	[1]
<i>Platyrrhinus lineatus</i>	Frugivore	24.0	45.7	54.8	8.0	20	[1]
<i>Platyrrhinus recifinus</i>	Frugivore	20.0	42.8	50.7	7.4	11	[1]
<i>Pygoderma bilabiatum</i>	Frugivore	24.0	42.5	45.2	6.3	10	[3]
<i>Sturnira lilium</i>	Frugivore	20.0	42.4	45.0	6.2	27	[1]
<i>Sturnira tildae</i>	Frugivore	25.0	46.0	50.7	7.0	1	[1]
<i>Vampyressa pusilla</i>	Frugivore	10.0	34.8	41.9	6.1	8	[1]
Unidentified	Frugivore	-	-	-	-	30	[1] [6] [7] [8]
MORMOOPIDAE							
<i>Pteronotus parnelli</i>	Aerial insectivore	-	-	-	-	1	[1]
NOCTILIONIDAE							
<i>Noctilio albiventris</i>	Aerial insectivore	-	-	-	-	2	[1] [9]
<i>Noctilio leporinus</i>	Piscivore	-	-	-	-	2	[1]

(Table 2 cont.)

Taxa	Trophic guild	Body mass	Length of Forearm	Wing loading	Aspect ratio	N	Author
THYROPTERIDAE							
<i>Thyroptera wynneae</i>	Aerial insectivore	-	-	-	-	1	[10]
MOLOSSIDAE							
<i>Eumops auripendulus</i>	Aerial insectivore	-	-	-	-	1	[11]
<i>Molossus molossus</i>	Aerial insectivore	-	-	-	-	5	[1]
<i>Molossus rufus</i>	Aerial insectivore	-	-	-	-	2	[1]
<i>Nyctinomops laticaudatus</i>	Aerial insectivore	-	-	-	-	11	[1]
VESPERTILIONIDAE							
Unidentified	Aerial insectivore	-	-	-	-	5	[1]
VESPERTILIONINAE							
<i>Eptesicus brasiliensis</i>	Aerial insectivore	-	-	-	-	2	[1]
<i>Histiotus velatus</i>	Aerial insectivore	-	-	-	-	1	[1]
<i>Lasiurus blossevilli</i>	Aerial insectivore	-	-	-	-	1	[1]
<i>Lasiurus ega</i>	Aerial insectivore	-	-	-	-	5	[1]
MYOTINAE							
<i>Myotis izecksoni</i>	Aerial insectivore	-	-	-	-	1	[1]
<i>Myotis nigricans</i>	Aerial insectivore	-	-	-	-	2	[1]
<i>Myotis riparius</i>	Aerial insectivore	-	-	-	-	3	[1]
<i>Myotis</i> sp.	Aerial insectivore	-	-	-	-	10	[1] [3]
Unidentified	-	-	-	-	-	11	[1] [7]

Table 3
 Number of records (N) and percentage (%) of bat roadkills according to trophic guilds.

Trophic guilds	N	%
Frugivore	250	60.2
Aerial insectivore	54	13.1
Nectarivore	49	12.8
Omnivore	25	5.0
Gleaning insectivore	9	2.2
Sanguivore	8	1.9
Carnivore	7	1.7
Piscivore	2	0.5
Indeterminate	11	2.7

Fig. 2. Box-plot graph representing the bat roadkill abundance in each trophic guild. The black points represent extreme values (outliers).

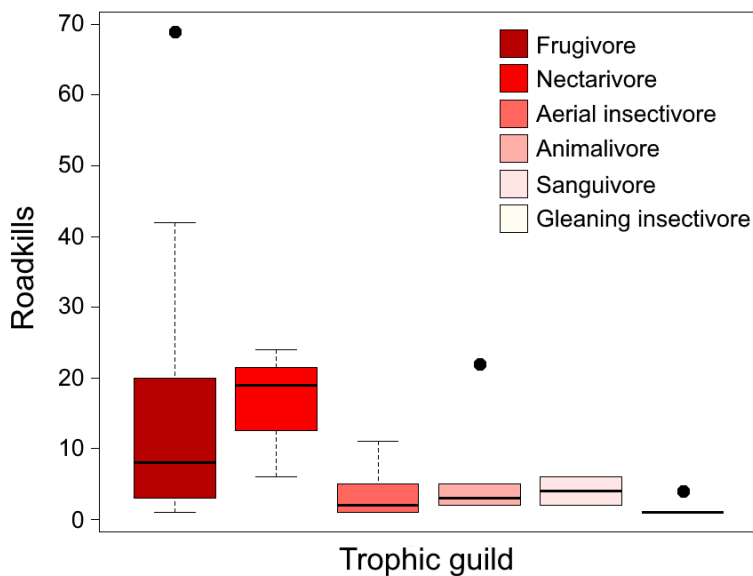


Table 4
 Ranking of the best linear models to predict bat roadkill as a function of species attributes in Brazil. Models were selected according to the second-order Akaike Information Criterion (AICc) corrected for small samples.

Models	AICc	$\Delta AICc$	W_i
Null Model	191.0	0.000	0.259
Wing loading + body mass	192.1	1.130	0.142
Body mass	192.3	1.260	0.134
Wing loading	192.5	1.470	0.129

Table 5

Model selection using the theoretical approach based in second-order Akaike Information Criterion for biological attributes influencing bat roadkills in Brazil. Biological attributes analyzed were AA = Aspect ratio, FA = length of forearm, WL = relative wing loading, BM = body mass.

Models	Intrc	AA	FA	WL	BM	Family	Init.theta	df	logLik	AICc	delta	weight
12	2.4180	-	-	-	-	NB (0.8499)	0.850	2	-93.260	191.0	0.00	0.250
5	-0.7863	-	-	0.06556	0.015840	NB (0.9733)	0.973	4	-91.165	192.1	1.13	0.142
7	2.0800	-	-	-	0.009913	NB (0.8876)	0.888	3	-92.616	192.3	1.26	0.134
10	0.8425	-	-	0.03883	-	NB (0.8789)	0.879	3	-92.724	192.5	1.47	0.129
3	2.1030	-	0.005974	-	-	NB (0.8560)	0.856	3	-93.154	193.4	2.33	0.078
11	1.2690	0.17710	-	-	-	NB (0.8555)	0.855	3	-93.157	193.4	2.34	0.078
2	-0.8411	-	0.015470	0.06019	-	NB (0.9133)	0.913	4	-92.121	194.1	3.04	0.055
6	0.8167	0.19360	-	-	0.010130	NB (0.8952)	0.895	4	-92.483	194.8	3.76	0.038
4	0.4582	-0.28350	-	0.07909	0.017020	NB (0.9870)	0.987	5	-90.968	194.8	3.77	0.038
9	1.1770	-0.07276	-	0.04220	-	NB (0.8796)	0.880	4	-92.712	195.2	4.22	0.030
8	0.9822	0.17320	0.005918	-	-	NB (0.8614)	0.861	4	-93.054	195.9	4.91	0.022
1	0.2964	-0.31870	0.019000	0.07841	-	NB (0.9257)	0.926	5	-91.913	196.7	5.66	0.015

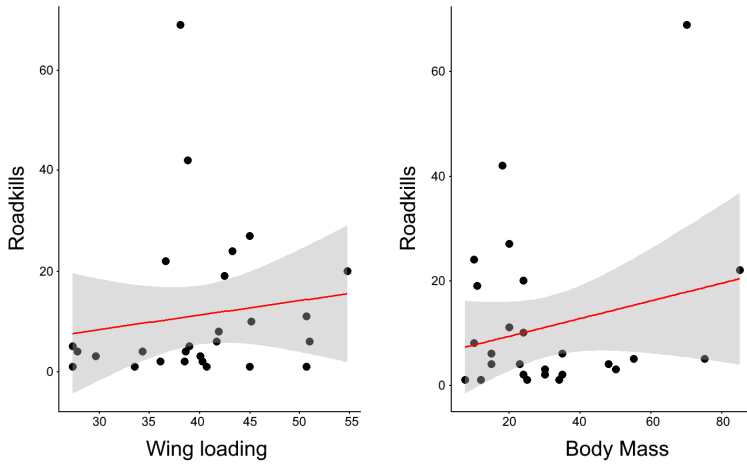


Fig. 3. Predicted response and 95% confidence bands (gray-shaded areas) of bat species roadkills to two biological attributes (wing loading and body mass).

Our observations corroborate the hypothesis that proximity to roosts may facilitate bat-vehicle collisions. At least two specimens of *Molossus molossus* recorded in the present study were part of a colony located in the roof lining of a house near a road. When bats leave their roost, they fly at low altitude, which makes them more susceptible to roadkill. It is likely that bat-vehicle collisions occur more frequently close to roosts, as observed for *Myotis lucifugus* in the United States (Russell et al. 2009). According to these authors, roadkills represent 0.6% of the fatalities of a colony with over 20 000 individual bats.

Recent estimates indicate that bats represent a small part of mammal roadkills, corresponding to approximately 2% of the cases recorded in Portugal (Santos et al. 2011), 2.4% in Mid-Western Brazil (Melo & Santos-Filho 2007), and 1.7% in Southern Brazil (Dornelles et al. 2012). The highest mortality by roadkills found for bats was reported for the Brazilian Amazon, reaching 22.3% of roadkilled mammals (Silva & Silva 2009). However, these numbers may be underestimates, as the carcasses of small animals are more easily removed by scavengers (Russell et al. 2009; Santos et al. 2011; Teixeira et al. 2013) and could be thrown at larger distances, which hinders their finding by researchers.

The difficulty in finding bat roadkill records can also be related to the method used in monitoring, frequently made by car. For small-sized

animals monitoring on foot or by bicycle is more effective, as it facilitates the visualization of carcasses (Hartmann et al. 2009; Dornas et al. 2012; Teixeira et al. 2013), but it requires many more hours of work (Santos et al. 2011). The small number

of registered bat roadkills, when compared to terrestrial mammals, may suggest that the impact of roads on bat populations is not as high as on other mammals (Cunha et al. 2010). We believe that these studies show a negative bias caused by the sampling method (Dornas et al. 2012).

In Brazil, most of the transportation of humans and goods is done on over 1.7 million kilometers of roads, not all paved (DNIT 2004). Every year more roads are paved, which results in an increase in traffic and average speed, and in fragmentation and degradation of the surrounding landscape. Also, paving is followed by greater road illumination, increasing the roadkill risk of bats that forage behind insects attracted by the lampposts (Blake et al. 1994; Mathews et al. 2015). This scenario leads to an augmentation in the number of wildlife roadkills (Coffin 2007). Nevertheless, the Brazilian law concerning the fauna and environmental licensing of roads and railroads is oblivious to this issue (IBAMA 2013). Bats have been neglected in the monitoring of wildlife roadkills in Brazil, impeding assessment to the real impact generated by roads. One way to reduce this problem is to adopt compulsory monitoring of bats in road licensing and to evaluate the type of light that will be implanted in road lighting. Studies indicate that orange light attracts fewer insects than white light, providing a potential way to mitigate impacts on insectivorous bats (Blake et al. 1994). However, light intensity

and spectral composition appears to have a differentiated effect between insectivorous bat species in Europe (Mathews et al. 2015), and studies should be conducted in Brazil to better understand this issue.

Roads can generate other negative effects on bat fauna, beyond vehicle collision, including (i) damage or destruction of roosts and habitats, (ii) disturbance of foraging flights, and (iii) barriers to large-scale movements or migration (Kerth & Melber 2009; Berthinussen & Altringham 2012). However, more accurate estimates of the impacts of roads on bats should be obtained with suitable methods (e.g., radio-tracking, GPS and acoustic monitoring) and with more careful road monitoring.

CONCLUSIONS

Forty-four bat species have already been victims of roadkills, representing approximately 25% of the Brazilian bat fauna. Frugivorous species are the most vulnerable to collisions with vehicles, which is possibly linked to their greater abundance, lower flight, and capacity to make long-distance movements.

The vulnerability to roadkills had no relation to the body size and type of flight of phyllostomid bats, indicating that collisions with vehicles affects all species that use the airspace occupied by roads. Roads act as a generalist predator, causing the death of species of all the trophic guilds, sizes and behaviors, including the rarest ones.

We show that roadkills are a significant cause of bat fatality. Therefore, road ecology researchers should include bats in their monitoring. This inclusion will give more precise estimates of the magnitude of this impact on bats and a scientific base for Brazilian laws, that should comprise bats in environmental impact assessments concerning the expansion or establishment of new roads.

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LITERATURE CITED

- ABBOTT, I. M., S. HARRISON, & F. BUTLER. 2012. Clutter-adaptation of bat species predicts their use of under-motorway passageways of contrasting sizes – a natural experiment. *Journal of Zoology* 287:124-132.
- ALTRINGHAM, J., & G. KERTH. 2016. Bats and roads. Bats in the Anthropocene: conservation of bats in a changing world (C. C. Voigt & T. Kingston, eds.). Springer International Publishing, London.
- ALVES, D. M. D., R. F. BARROS, & C. NEPOMUCENO. 2015. Levantamento de vertebrados silvestres atropelados com enfoque em indivíduos da ordem Chiroptera: estudo de caso da rodovia MGC-354, Minas Gerais, Brasil. *Perquirere* 12:176-193.
- ARNONE, I. S., E. TRAJANO, A. PULCHÉRIO-LEITE, & F. C. PASSOS. 2016. Long-distance movement by a great fruit-eating bat, *Artibeus lituratus* (Olfers, 1818), in southeastern Brazil (Chiroptera, Phyllostomidae): evidence for migration in Neotropical bats? *Biota Neotropica* 16:e0026.
- BAGATINI, T. 2006. Evolução dos índices de atropelamento de vertebrados silvestres nas rodovias do entorno da estação ecológica Águas Emendadas, DF, Brasil, e eficácia de medidas mitigadoras. MSc. Thesis, Universidade de Brasília, Brazil.
- BAGER, A., P. S. LUCAS, A. BOURSCHIEIT, A. KUCZACH, & B. MAIA. 2016. Os caminhos da conservação da biodiversidade brasileira frente aos impactos da infraestrutura viária. *Biodiversidade Brasileira* 6:75-86.
- BARTHELMESS, E. L., & M. S. BROOKS. 2010. The influence of body-size and diet on road-kill trends in mammals. *Biodiversity and Conservation* 19:1611-1629.
- BENÍTEZ-LÓPEZ, A., R. ALKEMADE, & P. A. VERWEIJ. 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation* 143:1307-1316.
- BERNARD, E., & M. B. FENTON. 2002. Species diversity of bats (Mammalia: Chiroptera) in forest fragments, primary forests, and savannas in central Amazonia, Brazil. *Canadian Journal of Zoology* 80:1124-1140.
- BERNARD, E. 2001. Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. *Journal of Tropical Ecology* 17:115-126.
- BERTHINUSSEN, A., & J. ALTRINGHAM. 2012. The effect of a major road on bat activity and diversity. *Journal of Applied Ecology* 49:82-89.
- BLAKE, D., A. M. HUTSON, P. A. RACEY, J. RYDELL, & J. R. SPEAKMAN. 1994. Use of lamplit roads by foraging bats in southern England. *Journal of Zoology* 234:453-462.
- BROWN, C. R., & M. B. BROWN. 2013. Where has all the road kill gone? *Current Biology* 23:233-234.
- BURNHAM, K. P., D. R. ANDERSON, & J. P. HUYVAERT. 2011. AIC model selection and multimodel inference in

- behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23-35.
- CÁCERES, N. C. 2011. Biological characteristics influence mammal road kill in an Atlantic Forest-Cerrado interface in South-Western Brazil. *Italian Journal of Zoology* 78:379-389.
- COELHO, I. P., A. KINDEL, & A. V. P. COELHO. 2008. Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. *European Journal of Wildlife Research* 54:689-699.
- COFFIN, A. W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography* 15:396-406.
- COSSON, J. F., J. M. PONS, & D. MASSON. 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. *Journal of Tropical Ecology* 15:515-534.
- CUNHA, H. F., F. G. A. MOREIRA, & S. D. S. SILVA. 2010. Roadkill of wild vertebrates along the GO-060 road between Goiânia and Iporá, Goiás State, Brazil. *Acta Scientiarum* 32:257-263.
- DNIT. 2004. Projeto de ampliação da capacidade rodoviária das ligações com os países do MERCOSUL: BR-101 Florianópolis-Osório. Projeto Básico Ambiental do Subprograma Proteção à Fauna, Departamento Nacional de Infraestrutura de Transportes.
- DORNAS, R. A. P., A. KINDEL, A. BAGER, & S. R. FREITAS. 2012. Avaliação da mortalidade de vertebrados em rodovias no Brasil. *Ecologia de Estradas: tendências e pesquisas* (A. Bager, ed.). Universidade Federal de Lavras, Lavras.
- DORNELLES, S. S., A. SCHLICKMANN, M. J. CREMER, & A. BAGER. 2012. Mortalidade de vertebrados na rodovia BR-101, no sul do Brasil. *Ecologia de Estradas: tendências e pesquisas* (A. Bager, ed.). Universidade Federal de Lavras, Lavras.
- EIGENBROD, F., S. J. HECNAR, & L. FAHRIG. 2009. Quantifying the road-effect zone: threshold effects of a motorway on anuran population in Ontario, Canada. *Ecology and Society* 14:a24.
- ESBÉRARD, C. E. L., & H. G. BERGALLO. 2005. Research on bats in the state of Rio de Janeiro, southeastern Brazil. *Mastozoologia Neotropical* 12:237-243.
- ESBÉRARD, C. E. L., J. L. LUZ, L. M. COSTA, & H. G. BERGALLO. 2014. Bats (Mammalia, Chiroptera) of an urban park in the metropolitan area of Rio de Janeiro, southeastern Brazil. *Iheringia, Série Zoologia* 104:59-69.
- FENSOME, A. G., & F. MATHEWS. 2016. Roads and bats: a meta-analysis and review of the evidence on vehicles collisions and barrier effects. *Mammal Review* 46:311-323.
- GAISLER, J., Z. ŘEHÁK, & T. BARTONIČKA. 2009. Bat casualties by road traffic (Brno-Vienna). *Acta Theriologica* 54:147-155.
- GARDNER A. L. 1977. Feeding habits. *Biology of bats of the New World family Phyllostomidae, Part II* (R. J. Baker, J. K. Jones Jr. & D. C. Carter, eds.). Special Publications, Texas Tech University, Lubbock.
- GREGORIN, R., E. GONÇALVES, C. C. AIRES, & A. P. CARMIGNOTTO. 2011. Morcegos (Mammalia: Chiroptera) da Estação Ecológica Serra Geral do Tocantins: composição específica e considerações taxonômicas. *Biota Neotropica* 11:299-311.
- HARTMANN, P. A., M. T. HARTMANN, & M. MARTINS. 2009. Ecology of a snake assemblage in the Atlantic Forest of southeastern Brazil. *Papéis Avulsos de Zoologia* 49:343-360.
- HOPPE, J. P. M., V. T. PIMENTA, & A. D. DITCHFIELD. 2014. First occurrence of the recently described Patricia's Diskwinged bat *Thyroptera wynneae* (Chiroptera: Thyropteridae) in Espírito Santo, southeastern Brazil. *Check List* 10:645-647.
- IBAMA. 2013. Instrução Normativa Nº 13, de 19 de julho de 2013, Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis.
- KALKO, E. K. V., C. O. HANDLEY, & D. HANDLEY. 1996. Structure, diversity, and long-term dynamics of a Neotropical bat community. Long-Term studies of vertebrate communities (M. L. Cody & J. A. Smallwood, eds.). Academic Press, New York.
- KERTH, G., & M. MELBER. 2009. Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. *Biological Conservation* 142:270-279.
- KOCIOLEK, A. V., A. P. CLEVINGER, C. C. CLAIR, & D. S. PROPPE. 2011. Effects of road networks on bird populations. *Conservation Biology* 25:241-249.
- LAURANCE, W., M. GOOSEM, & S. LAURANCE. 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution* 24:659-669.
- LESIŃSKI, G. 2007. Bat road casualties and factors determining their number. *Mammalia* 71:138-142.
- LESIŃSKI, G. 2008. Linear landscape elements and bat casualties on roads—an example. *Annales Zoologici Fennici* 45:277-280.
- LESIŃSKI, G., A. SIKORA, & A. OLSZEWSKI. 2010. Bat casualties on a road crossing a mosaic landscape. *European Journal of Wildlife Research* 57:217-223.
- LOSS, S. R., T. WILL, & P. P. MARRA. 2015. Direct mortality of birds from anthropogenic causes. *Annual Review of Ecology, Evolution and Systematics* 46:99-120.
- MARINELLO, M. M., & E. BERNARD. 2014. Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. *Canadian Journal of Zoology* 92:141-147.
- MARQUES, J. T., M. J. RAMOS-PEREIRA, & J. M. PALMEIRIM. 2016. Patterns in the use of rainforest vertical space by Neotropical aerial insectivorous bats: all the action is up in the canopy. *Ecography* 39:476-486.
- MATHEWS, F. ET AL. 2015. Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Philosophical Transactions of the Royal Society B* 370:a20140124.
- MATOS, F. A. R. ET AL. 2017. Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. *Journal of Ecology* 105:265-276.
- MEDINAS, D., J. T. MARQUES, & A. MIRA. 2013. Assessing road effects on bats: the role of landscape, road

- features, and bat activity on road-kills. *Ecological Research* 28:227-237.
- MELO, E. S., & M. SANTOS-FILHO. 2007. Efeitos da BR-070 na Província Serrana de Cáceres, Mato Grosso, sobre a comunidade de vertebrados silvestres. *Revista Brasileira de Zociências* 9:185-192.
- MENEZES-JR., L. F. ET AL. 2008. Deslocamento de *Artibeus lituratus* (Olfers, 1818) (Mammalia, Chiroptera) entre ilha e continente no Estado do Rio de Janeiro, Brasil. *Biota Neotropica* 8:243-245.
- MORRISON, D. W. 1978. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* 59:716-723.
- NOGUEIRA, M. R., & A. POL. 1998. Observações sobre os hábitos de *Rhynchonycteris naso* (Wied-Neuwied, 1820) e *Noctilio albiventris* (Desmarest, 1818) (Mammalia, Chiroptera). *Revista Brasileira de Biologia* 58:473-480.
- NOGUEIRA, M. R., I. P. LIMA, R. MORATELLI, V. C. TAVARES, R. GREGORIN, & A. L. PERACCHI. 2014. Checklist of Brazilian bats, with comments on original records. *Check List* 10:808-821.
- NORBERG, U. M., & M. B. FENTON. 1988. Carnivorous bats? *Biological Journal of the Linnean Society* 33:383-394.
- NORBERG, U. M., & J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society B, Biological Sciences* 316:335-427.
- NOVAES, R. L. M., & R. S. LAURINDO. 2014. Morcegos da Chapada do Araripe, nordeste do Brasil. *Papéis Avulsos de Zoologia* 54:315-328.
- PRADA, C. S. 2004. Atropelamento de vertebrados silvestres em uma região fragmentada do nordeste do estado de São Paulo: quantificação do impacto e análise de fatores envolvidos. MSc. thesis. Universidade Federal de São Carlos, Brazil.
- R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/. Accessed 12 March 2017.
- REIS, N. R., A. L. PERACCHI, W. A. PEDRO, & I. P. LIMA (Eds.). 2007. *Morcegos do Brasil*. Universidade Estadual de Londrina, Londrina.
- ROGER, E., S. W. LAFFAN, & D. RAMP. 2011. Road impacts a tipping point for wildlife populations in threatened landscapes. *Population Ecology* 53:215-227.
- RUSSELL, A., C. BUTCHKOSKI, L. SAIDAK, & G. MCCracken. 2009. Road-killed bats, highway design, and the commuting ecology of bats. *Endangered Species Research* 8:49-60.
- SANTOS, S. M., F. CARVALHO, & A. MIRA. 2011. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE* 6:e25383.
- SANTOS, S. M., A. MIRA, P. A. SALGUEIRO, O. COSTA, D. MEDINAS, & P. BEJA. 2016. Avian trait-mediated vulnerability to road traffic collisions. *Biological Conservation* 200:122-130.
- SILVA, S. G., & M. O. SILVA. 2009. Vertebrados mortos por atropelamentos na BR-364 entre os municípios de Pimenta Bueno e Cacoal, Rondônia. *Anais do IX Congresso de Ecologia do Brasil* (W. Delitti, ed.). Sociedade de Ecologia do Brasil, São Lourenço.
- SKÓRKA, P., M. LENDA, D. MORON, R. MARTYKA, P. TRYJANOWKI, & W. J. SUTHERLAND. 2013. Biodiversity collision blackspots in Poland: separation causality from stochasticity in roadkills of butterflies. *Biological Conservation* 187:154-163.
- TAVARES, V. C. 2013. Phyllostomid bat wings from Atlantic Forest bat ensembles: an ecomorphological study. *Chiroptera Neotropical* 19:57-70.
- TEIXEIRA, F. Z. ET AL. 2013. Are road-kill hotspots coincident among different vertebrate groups? *Oecologia Australis* 17:36-47.
- TORRES, A., J. A. G. JAEGER, & J. C. ALONSO. 2016. Assessing large-scale wildlife responses to human infrastructure development. *Proceedings of the National Academy of Sciences* 113:8472-8477.
- ZALESKI, T., V. ROCHA, A. S. FILIPAKI, & E. L. A. MONTEIRO-FILHO. 2009. Atropelamentos de mamíferos silvestres na região do município de Telêmaco Borba, Paraná, Brasil. *Natureza & Conservação* 7: 81-94.
- ZUUR, A. F., E. N. IENO, & C. S. ELPHICK. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3-14.