

ROAD AND LANDSCAPE FEATURES THAT AFFECT BAT ROADKILLS IN SOUTHEASTERN BRAZIL

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ABSTRACT

The most studied impact on road ecology is roadkill, however, there is little information about the relations between highways and specific groups like bats. This study intended to identify the species of bats roadkilled and to evaluate the existence of temporal fluctuation between the roadkill rates, specific stretches of the road with higher rates, and characteristics of the road/landscape that may influence those rates. We encountered at least nine bat species among 65 roadkills (most Phyllostomidae), which comprise a subgroup of the local fauna that presents ecologic features that make them susceptible to being hit, especially *Artibeus lituratus*. The medium roadkill rate was of 0.01 individuals/km/day of monitoring, and there was no significant temporal variation. We identified five hotspots through special 2D HotSpot Identification Analysis. The selection of theoretical models through Generalized Linear Models showed that roadkill occurrence has a positive relation with vehicular traffic and negative relation with presence of marginal pasture and forests. As the major part of records was of species that are tolerant to human-disturbances, the increase in traffic consequently affected a higher number of bats capable to explore the area occupied by the road. The presence of native forest close to the road can lead to a decrease of animals hit by vehicles, once it offers more resources and favorable habitats, which reduces the need for bats to cross the roads for foraging. On the other hand, many species that necessarily depend on areas sheltered by trees for shelter, and do not possess the ability to fly long distances do not occur in open areas such as pastures. In this context, we suggest that the main measure of mitigation regard bat species would be the traffic control through speed limit, especially on the roadkill hotspots areas.

Keywords: Atlantic Forest; BR-101/RJ Norte; Chiroptera; conservation; Road Ecology.

INTRODUCTION

Highways are an extensively used model of transportation in constant expansion especially in the last decades (Forman *et al.* 2003), particularly in developing countries like Brazil, being associated with social and economic development of a region (Coffin 2007, Bager *et al.* 2015). Road construction results in several ecological effects over wild fauna, including positive and negative effects on population density (Fahrig & Ritwinski 2009). Among the most relevant negative impacts to species conservation are habitat fragmentation (Goosem 2007, Laurance *et al.* 2009)

and direct mortality resulted from collisions of animals against vehicles (Forman & Alexander 1998, Trombulak & Frissell 2000).

Those deaths by roadkills may compromise viability of populations and alter the richness and diversity of species from the region accordingly to pre-existing circumstances (Gibbs & Shriver 2005, Barthelme & Brooks 2010, Jackson & Fahrig 2011). Among all impacts caused by highways, the most studied is represented by the death of mammals hit by vehicles (Dussault *et al.* 2006, Orlowski & Nowak 2006, Grilo *et al.* 2009, Cáceres 2011, Cserkesz *et al.* 2013, Huijser *et al.* 2013, D'Amico *et al.* 2015, van

der Ree *et al.* 2015). Nevertheless, the magnitude of this kind of impact on bats remains incipient, and the majority of studies are limited to Europe (*e.g.*, Kiefer *et al.* 1995, Wray *et al.* 2005, Lesiński 2008, Lesiński *et al.* 2011).

Bats are the only active flying mammals and one of the most diverse groups of animals (18 families, and approximately 202 genera and 1120 species; Simmons 2005). Most of bats are small-sized animals with various trophic strategies, although the majority of them eat insects and fruits (Nowak 1994, Jones & Rydell 2003). Bats have a high longevity, parental care, and complex social behaviors, including mixed colonies with different species (Wilkinson & South 2002, Reis *et al.* 2007). As they present peculiar biological features, it is difficult to evaluate precisely the degree of the threat from roadkill over their populations, even though specific methodologies (*e.g.*, marking-and-recapture, genetic markers) and more complex sampling designs (*e.g.*, before-after-control-impact) it is possible to achieve better inference capacity. In this sense, Bernard *et al.* (2012) elaborated an initiative to value the anthropogenic impacts (including the ones from roads), and the hiatus of knowledge about Brazilian bats fauna through a horizon analysis. Ten types of impact were evaluated; the one that referred to roads was the last on the list, which expresses the little knowledge available and the need to carry out studies that evaluate the mortality rates, and the extension, and the magnitude of those effects on bats.

Some bat species are capable of moving for long distances, crossing and exploring areas modified by human activities such as roads and cities (Bredt & Uieda 1996, Bernard & Fenton 2003, Bianconi *et al.* 2006, Albrecht *et al.* 2007, Bennet *et al.* 2013). Their pattern of movement and foraging alter according to climate seasons and spatial availability of resources along the year (Heithaus *et al.* 1975, Dinerstein 1986, Fleming & Heithaus 1986). The movement between shelters and feeding areas frequently occurs through systematic routes created from linear corridors of open areas such as transport routes with tree lines on the borders (Stone 2013). This strategy intends to prevent the action of eventual predators and optimizes the energetic cost, avoiding

changes on the way to deviate from obstacles or gusts of wind (Verboom *et al.* 1999, Stone 2013).

Studies show that some insectivore species are specialized in prey during the flight in open areas with high concentration of insects and no obstacles, or in areas where insects are attracted by artificial light in urban regions (Rydell 2006, Lacoecilhe *et al.* 2014). Bats can detect the sound of motors and avoid to use the ways of higher traffic (Zurcher *et al.* 2010), and consequently, use those places as part of their route of daily foraging area (Frank 1988, Blake *et al.* 1994, Svensson & Rydell 1998). Due to facilitated access to some food resources (*e.g.* insects and fruits) in human-occupied areas, some bat species have their colonies in urban constructions such as bridges, tunnels, fissures in buildings, chimneys, and rooftops (Kunz 1982, Everette *et al.* 2001, Nogueira *et al.* 2007, Pacheco *et al.* 2010). The shelter's choice is related to the particularities of each species, such as flight characteristics, social behavior, diet, size of the colonies, and reproductive strategies (Kunz & Pierson 1994). It is common that bats use bridges over rivers and culverts as shelter, which turns the road and its surrounding into intensively used areas for those individuals that may cross it through drainage structures or over the lanes (Berthinussen *et al.* 2014).

Recent studies showed that the stretches with a higher concentration of roadkilled bats tend to be associated with landscape elements such as water bodies or a canopy structure of the trees on the wayside (Gaisler *et al.* 2009, Russel *et al.* 2009, Medinas *et al.* 2013). The factors associated with the amplitude of this negative effect vary according to each road features such as traffic intensity, total area occupied by the lanes, and characteristics of use and cover of the road verges (Medinas *et al.* 2013, Kitzes & Merenlender 2014). According to these factors, species may develop distinct behaviors as avoiding or attraction to the road (Jaeger *et al.* 2005, Fahrig & Rytwinski 2009, Jacobson *et al.* 2016).

Despite the high diversity of bats (nine families, 65 genera, and 178 species; Nogueira *et al.* 2014) and the wide extension of highway network (1.7 million km; DNIT 2014) in Brazil, studies describing patterns of mortality of bats in Brazilian roads and relating the possible causes or the factors that contribute to the

intensity of roadkill are absent. In this context, this study aims to: i) characterize the mortality of bats identifying the diversity of species roadkilled and test the hypothesis that there is a seasonal and inter-annual variation in the rates; ii) test the hypothesis – based on the assumption that bats have preferential areas along the road – that there are specific stretches with a higher concentration of collisions of vehicles and bats; iii) test – after confirming the existence of hotspots – which characteristics of the road and of the landscape that influence the sites of bat roadkills.

MATERIAL AND METHODS

Study area

Study area comprehends the stretch between kilometers 190 and 261 of BR-101/RJ Norte in southeastern Brazil. It is an undivided two-way road that is in process of being duplicated into a four-lane highway. The road is inside the Environmental Protection Area of the drainage basin of São João River (22° 25' S; 42° 15' W) and landscape presents different land uses and covers such as urban areas, plantation, and pasture mixed with Atlantic rainforest fragments and a continuous forest protected by Poço das Antas Biological Reserve (from km 214 to km 218) (Figure 1). This stretch crosses the municipalities of Rio Bonito, Silva Jardim, and Casimiro de Abreu, on the lowland region of state of Rio de Janeiro offering access to the touristic regions named Região dos Lagos, which has a high activity especially during summer time and recess period (December to February). According to the highway concessionaire, the current traffic characterization indicates that 75% of the vehicles are small-sized and rapid passenger cars, and 25% are heavy vehicles (Autopista Fluminense 2016).

The drainage basin of São João River is predominantly a coastal plain, formed mostly by mountain ranges, plateaus, and hills, and less often by alluvial plains subject to permanent or periodic inundation, and *restingas* (Primo & Volker 2003). It has a tropical savanna climate with dry winters and wet summers, and the average temperatures are high during most of the year (Köppen 1948). The average precipitation varies from 1500 to 2000mm; the period

from June to August has the driest months and the lowest temperatures; the period from November to March has the rainiest months and the highest temperatures (Primo & Völker 2003). Presently 25 bat species were formally recorded to Poço das Antas Biological Reserve (Baptista & Mello 2001, Brito *et al.* 2004).

Roadkill data

We collected data in 74 sampling sessions along 71 kilometers of road (both ways) in a vehicle at 40 km/h with a frequency of 2.2 monitoring per month from May 2013 to January 2016. It is also worth noting that the road was monitored before the first campaign in May 2013, in order to remove any previous carcasses exposed on the lane. Dead animals were photographed and georeferenced. The taxa were identified based on specialized literature (Gregorin & Taddei 2002, Peracchi *et al.* 2006, Tavares *et al.* 2008, Reis *et al.* 2013). We also registered complementary information as date and time of record, sex, and reproductive stage. Some bats were collected and sent to the mammal collection of Núcleo em Ecologia e Desenvolvimento Sócio-Ambiental de Macaé, Universidade Federal do Rio de Janeiro (NUPEM/UFRJ) as a specimen-witness and to corroborate the taxonomic identification done in field (Table 1). Some individuals could not be identified due to the high level of damage suffered or to their decomposition state.

Data analysis

The representativeness of each taxon among roadkill was calculated using relative frequency (RF), dividing the number of individuals from each taxon by the amount of records. The species richness that may be hit by vehicles was estimated based on our database through bootstrap, a non-parametric estimator, using the “Quadrat richness” function in PAST 3.12 software (Hammer *et al.* 2001). Through program EstimateS 9.1 (Colwell 2004) we generate an accumulation curve of bat species to evaluate the sampling sufficiency. The records were distributed graphically along the road kilometers marks according to the distance between the point of roadkill and the closest kilometer.

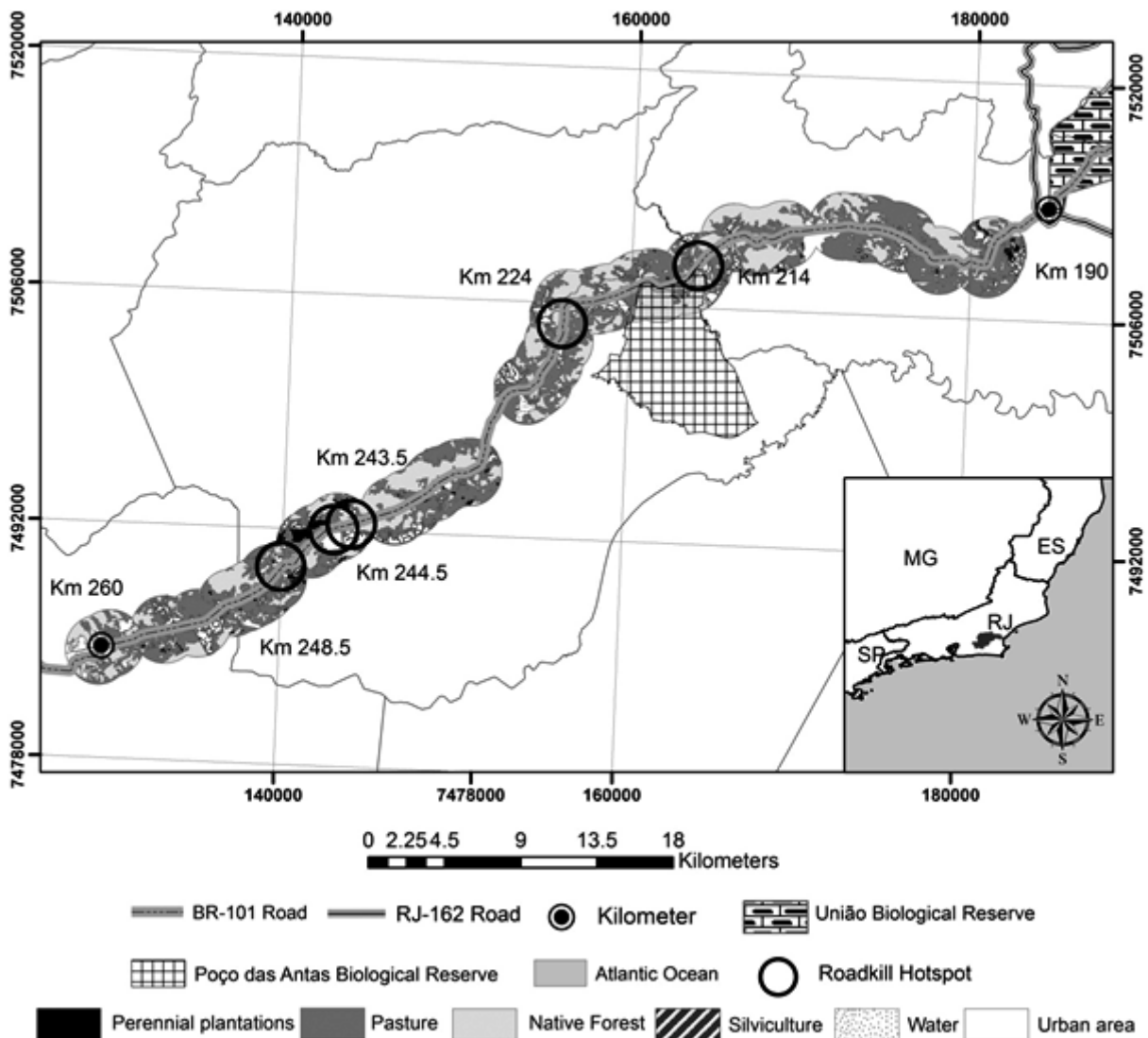


Figure 1. Map of middle-north State of Rio de Janeiro, southeastern Brazil, where is the stretch between km 190 and km 261, including the contact points with the protected areas, and the bat roadkill hotspots with land use circular buffers surrounding each roadkill record along the road BR-101 RJ/Norte.

The roadkill rate was calculated according to Rosa & Bager (2012): number of roadkill/kilometers/day of monitoring. This approach considers the influence of the sampling effort variation, which allows the development of more reliable space-time analysis among different periods and stretches of the road. The roadkill rate was estimated monthly and the time variation was evaluated through graphic construction and Kruskal-Wallis test to check the annual and seasonal differences.

In order to map the points of higher incidence of roadkill we used the statistic software SIRIEMA v1.1 (Coelho *et al.* 2011), using cumulative records of bats that were roadkilled between May 2013 and

January 2016, between kilometers 190 and 261 of BR-101/RJ Norte. We identified a lower radius of significant distance to the identification of those areas of roadkill concentration through the 2D Ripley K-Statistics Test (Coelho *et al.* 2008). We used an initial radius of 50 meters, an increment radius of 50 meters, a confidence limit of 95%, and 1000 simulations intending to refine the spatial scale of analysis. In this context, Teixeira *et al.* (2013a) recommended to evaluate hotspots in small scales in order to enable the application of mitigation measures to specific target-groups to increase the probability of correctly identifying the places of higher priority on the road.

In the second step of analysis, 2D HotSpot Identification Test was used to identify the hotspots of bat roadkill (Coelho *et al.* 2012). The Nevents-Nsimulated values were above the confidence limit and indicate stretches with high intensity of significant aggregation (Levine 2000). To perform this test, we analyzed each subdivision of 100 meters of the highway in order to identify the hotspots. We also used a radius of 50 meters, as the 2D Ripley K-Statistics test performed earlier presented this value as the smallest significant radius to the incidence of roadkill concentration areas (Coelho *et al.* 2008). Furthermore, the spatial scale of 50 meters on the highway is appropriate to receive eventual mitigation measures. The established confidence limit was 95% of 1000 simulations.

For the identification of which features of the road and landscape are more favorable to bat roadkill occurrence we used the Generalized Linear Model (GLM; McCullagh & Nelder 1989). We used the records of bat on the studied period and added the same number of records for other faunal groups extracted from our database with the purpose of randomly select of non-bat roadkill points on the road, making it possible to contrast with the spatial pattern of bat mortality. The models were constructed through response variable (dependent) with binomial distribution represented by the presence or absence of dead bats among the total of records, and logit as a link-function (adapted from Freitas *et al.* 2015). The characteristics of road and landscape were added as predictor variables (independent). Variables related to the road that were included in the modeling were the (1) linear distance between the roadkill and the closest underpass culvert or bridge under a river (potentially used as shelter), (2) linear distance between the roadkill and the closest artificial light source (a potentially attractive to insectivore bats), and (3) the traffic intensity (potentially repulsive to bats) represented by the daily average number of vehicles estimated at the closest tollbooth at the same day of the bat record.

To map the different types of use, initially we acquired the satellite images of Landsat 7 and 8, specifically of the orbit-points 217-76 and 216-76, adjusted to the periods of the data collection, faithful to land use and cover at the time. We established a

datum reference (Universal Transverse Mercator coordinate system) and the geodetic datum (Sirgas 2000) to the cartographic base, the reference points, and the images. After that, we used the supervised by maximum likelihood classification, using the thermal bands 3, 4, and 5, RGB composite, to elaborate a terrestrial map of land use and cover of the studied areas through ArcGis 10.3 (ESRI 2012). To aid the visual interpretation of the areas with vegetation cover, we used Google Earth[®] as a support tool, allowing us to delimit with more details the land cover where we identified the categories of land use and cover through satellite image. Through supervised by maximum likelihood classification, we defined the samples for training set through polygons that represented the types of land use and cover according to the tonality and texture of identified targets.

Different types of mapped land use and cover were represented by (a) water, (b) perennial plantations, (c) silviculture, (d) pasture, and (e) native forest, which are the factors that more influence the abundance of bats in tropical regions (Ávila-Cabadilla *et al.* 2012, Bolívar-Cimé *et al.* 2013). Based on these studies that confirmed the influence of land use and cover over the composition and abundance of bat species (Lesiński *et al.* 2011, Ávila-Cabadilla *et al.* 2012, Bolívar-Cimé *et al.* 2013), we chose (1) 50, (2) 250, and (3) 1000 meters as different values of radius to analyze. Each variable of land use and cover was expressed through the area (m²) it occupies in the used buffers. Studies performed close to turbines on wind farms in south Mexico used circular buffers with radius of 100 meters to analysis (Bolívar-Cimé *et al.* 2016). We chose to use radius both shorter and longer than 100 meters in order to find the scale with the best predictive power.

A total of 92 models were sorted through Akaike information criterion (AIC; Burnham & Anderson 2002), categorized initially in eight groups of predictive variables based in hypothesis about the factors that could explain the occurrence of bat roadkills: (1) road characteristics; (2) landscape variables in a 50 meters scale; (3) landscape variables in a 250 meters scale; (4) landscape variables in a 1000 meters scale; (5) road + landscape in a 50 meters scale; (6) road + landscape in a 250 meters scale; (7) road + landscape

in a 1000 meters scale; (8) none of the variables (null model). The models of hypotheses 1, 2, 3 and 4 were formulated from the possible combinations between exclusive variables of the same group, while the models representing hypotheses 5, 6 and 7 were composed by combining variables of the best models ranked in each group.

The multicollinearity of predictable variables was evaluated using Variance Inflation Factor (VIF) through “car” package in R (R Development Core Team 2015) environment. The VIF value among variables that form the same model was lower than three, which indicates that the variables are not correlated (Zuur *et al.* 2009, 2010). We considered the most robust models those that presented $\Delta AIC < 2$. All models were elaborated using the function “glm” of package “stats” from statistic software R. The most robust models accuracy was confirmed through the calculation of the area under the curve (AUC) and adjusted R^2 (Fielding & Bell 1997). The best model was considered the one that presented the highest values of these parameters.

RESULTS

We registered 65 roadkilled individuals in the span of time of the study, contemplating at least three

families, five subfamilies and nine species (Table 1). According to Jackknife 1, total estimate richness of bat was 11.96 (Figure 2).

The general rate of bats roadkill during the period was of 0.01 individuals/kilometer/day of monitoring, with a minimal monthly value of zero and maximum of 0.056 (Figure 3). We did not identified a difference on the monthly roadkill rate compared seasonally ($p = 0.708$; $H = 1.387$) and annually ($p = 0.117$; $H = 4.285$). The distribution of roadkill bats presented records spatially concentrated in some areas of the road (hotspots). Spatial analysis pointed to the existence of five hotspots (Figure 4) near the markers km 214, 224, 243.5, 244.5 and 248.5 (Figure 1).

As for the preferences of the road and landscape, we highlight two robust models that explain the occurrence of bats roadkill along several locations along the road. The traffic and land cover of native forest were variables present on both models. In one model, the presence of pasture as land cover close to the roadkill point was also present. Landscape scales of 50 and 250 meters were the only ones that presented sufficiently robust models to explain the occurrence of roadkill, but it was always combined with traffic as the only structural preponderant feature of the road (Table 2).

Table 1. Registered bat species among roadkills on BR-101/RJ Norte road between kilometers 190 and 261, from May 2013 to January 2016. RA: relative abundance of each taxon; RF: relative frequency of each taxon; Code Collection: codes of roadkilled specimen-witness from each taxon listed in the taxonomic collection of NUPEM/UFRJ.

Taxon	RA	RF	Code Collection
Phyllostomidae: Stenodermatinae			
<i>Artibeus lituratus</i>	30	0.462	NPM1466
<i>Platyrrhinus</i> sp.	4	0.062	NPM1467
<i>Artibeus</i> sp.	3	0.046	NPM1410
<i>Sturnira lilium</i>	2	0.031	
<i>Platyrrhinus recifinus</i>	1	0.015	NPM1468
Phyllostomidae: Carolliinae			
<i>Carollia perspicillata</i>	4	0.062	
Phyllostomidae: Phyllostominae			
<i>Phyllostomus hastatus</i>	3	0.046	
Molossidae: Molossinae			
<i>Molossus molossus</i>	3	0.046	NPM1465
<i>Molossus rufus</i>	1	0.015	NPM1373
<i>Tadarida brasiliensis</i>	1	0.015	
Vespertilionidae: Myotinae			
<i>Myotis</i> sp.	1	0.015	
Unidentified	12	0.185	

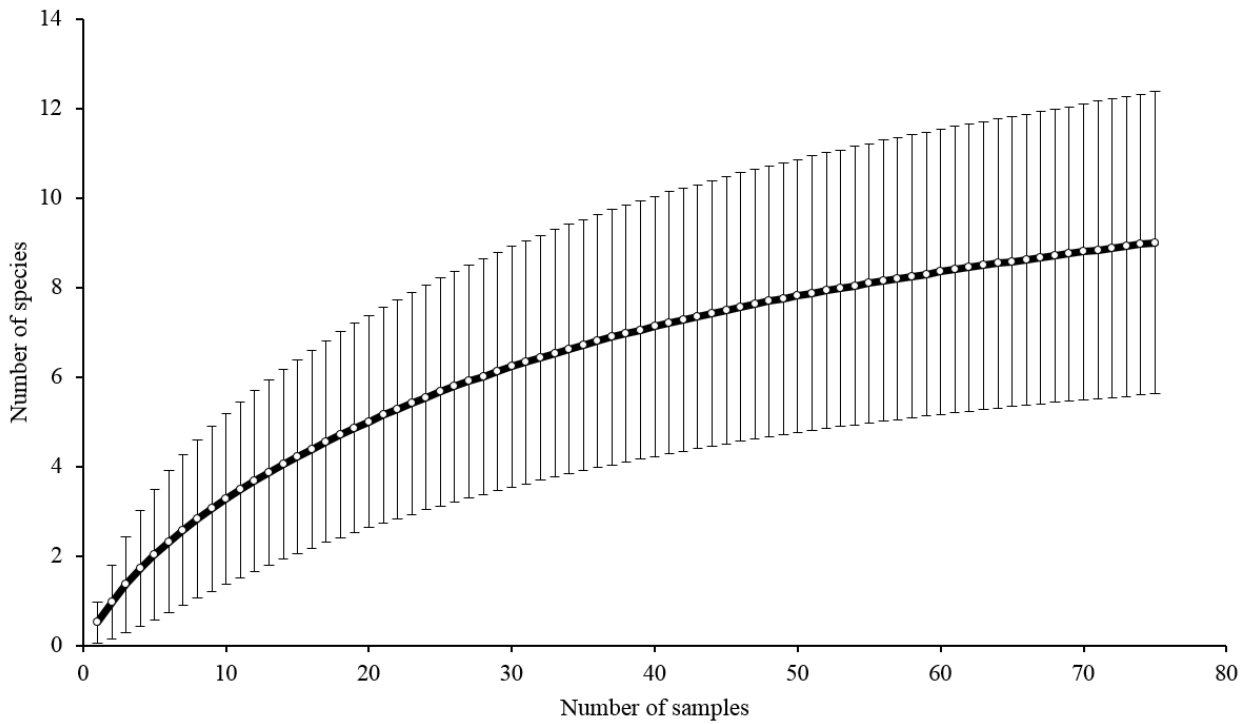


Figure 2. Cumulative curve of bat richness along sampling days in BR-101/RJ Norte road. Bars represent the confidence interval of 95%.

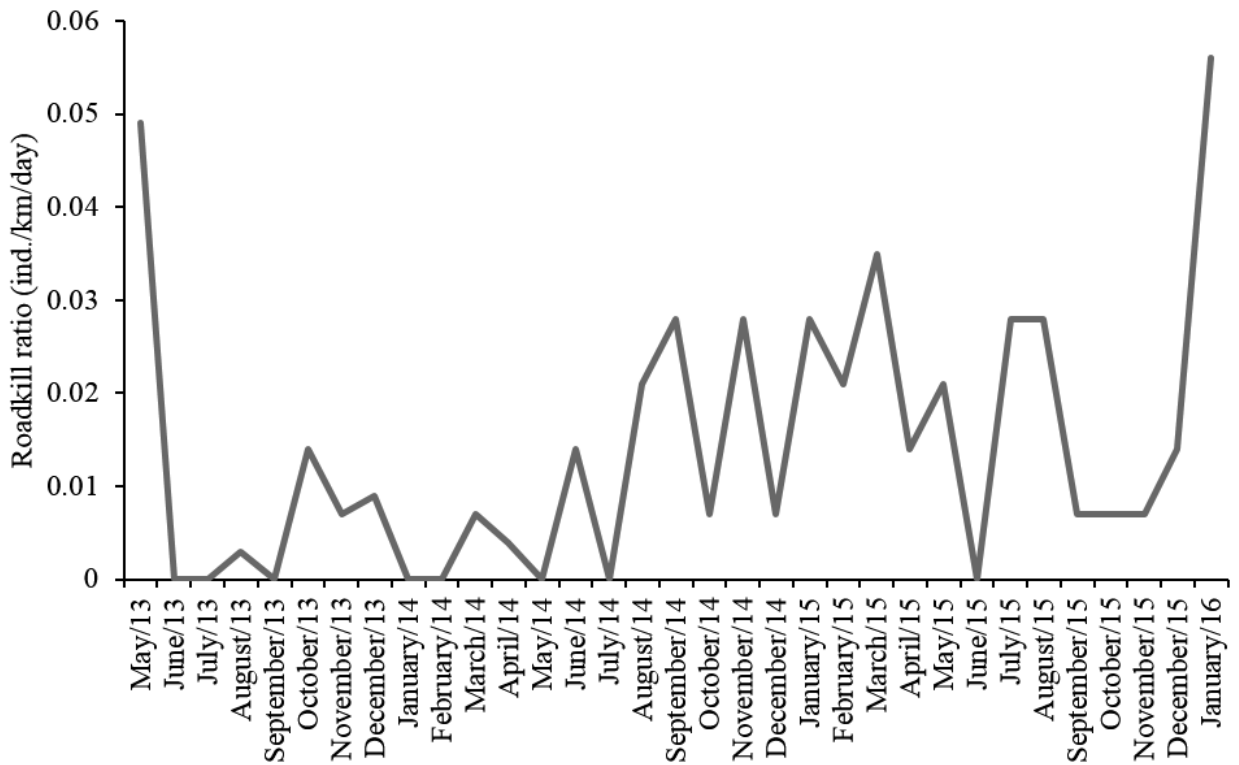


Figure 3. Temporal variation of bats roadkill rate on BR-101/RJ Norte road.

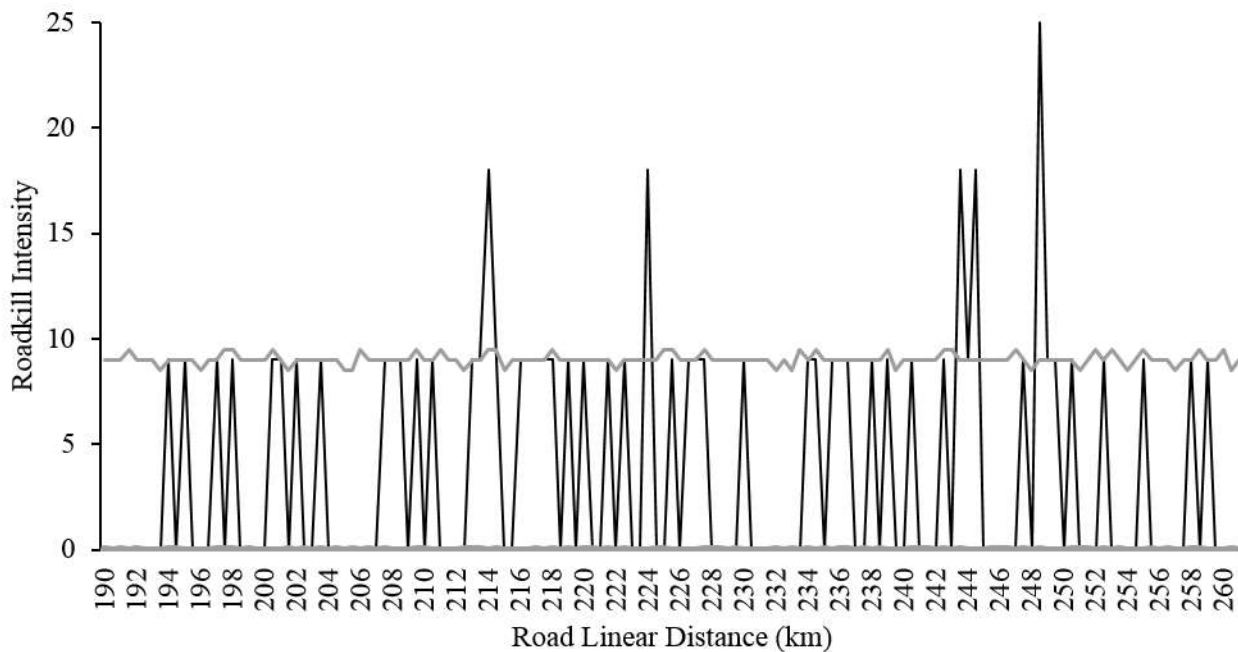


Figure 4. The result of 2D Hotspot Identification (50 meters scale and 95% confidence limit) that takes into account all records of roadkill bats between May 2013 and January 2016 on BR-101/RJ Norte road between kilometers 190 and 261 (0 - 71). Y-axis shows the values of function N events - N simulated, whereas x-axis represents the location of roadkill aggregations on the highway. The black line shows the function value, and the gray lines show the superior and inferior confidence limits. Values above the confidence limit confirm the existence of roadkill hotspots (km 214, 224, 243.5, 244.5 e 248.5).

Table 2. Generalized Linear Models parameters relative to candidate models that explain the occurrence of bats roadkill on the BR-101/RJ Norte road. AIC = Akaike information criterion, $\Delta AIC = AIC_i - AIC_{min}$, $AIC\omega$ = Akaike weight, AUC = Area under curve, R^2c = R-squared measure. We listed only the model with the lowest ΔAIC among each group of variables.

Type of candidate model	Candidate model	AIC Parameter			AUC	R^2c
		AIC	ΔAIC	$AIC\omega$		
Road	traffic	178.54	3.20	0.035	-	-
Landscape_50	pasture_50+native_forest_50	178.68	3.34	0.033	-	-
Landscape_250	native_forest_250	179.07	3.73	0.027	-	-
Landscape_1000	plantations_1000+pasture_1000	180.62	5.28	0.012	-	-
Road + Landscape_50	traffic+pasture_50+native_forest_50	175.34	0	0.175	0.615	0.914
Road + Landscape_250	traffic+native_forest_250	175.78	0.44	0.140	0.577	0.387
Road + Landscape_1000	traffic+plantations_1000+pasture_1000	178.38	3.04	0.038	-	-
Null	—	182.22	6.88	0.006	-	-

The classification parameters of "traffic+pasture_50+native_forest_50" were AUC = 0.615 and R^2c = 0.914, whereas of "traffic+ native_forest_250" were AUC = 0.577 and R^2c = 0.387. Therefore, the first model was considered more appropriate. It showed

significant positive correlation between traffic and bats roadkill (Table 3). Landscape variables on 50 meters scale, represented only by pasture and native forest, had a not-significant negative correlation with roadkill (Table 3).

Table 3. Parameters of the variables included on the best explicative model about the occurrence of bats roadkill on BR-101/RJ Norte road: β = regression coefficient; SE = standard error; Z-value = Z test; p-value = significance on Z test.

Variable	β	SE	Z-value	p-value
Intercept	-1.8	1.2	-1.551	0.121
traffic	5.6×10^{-5}	2.5×10^{-5}	2.207	0.027
pasture_50	-3.8×10^{-5}	8.8×10^{-5}	-0.435	0.663
native_forest_50	-1.8×10^{-4}	1.3×10^{-4}	-1.456	0.145

DISCUSSION

The richness of bats is close to what was projected from the continuity of sampling effort and only part of recorded species on previous studies in the region (e.g., Brito *et al.* 2004) appear on the temporal series of roadkill on this stretch of BR-101/RJ Norte road. Nevertheless, all recorded species had already been reported for those studies, which could indicate the species whose biological and behavioral characteristics make them susceptible to collide with vehicles across the road, even if it is sporadically. In terms of relative abundance, the most notable species in the inventory at the Poço das Antas Biological Reserve was *Carollia perspicillata* (Baptista & Mello 2001), however, this pattern was not reflected among the roadkill records of the road BR-101/Norte RJ, where *Artibeus lituratus* was predominant.

Although there are studies that show the reproductive, nutritional, and migratory seasonal behaviors about subtropical and tropical bat species (e.g., Fleming & Heithaus 1986, Fleming *et al.* 1993), the variation of roadkill records of this study does not corroborate the assumption of a temporal pattern. This result may be explained by the fact that most of the recorded species is not dependent on floral or fruitful specific resources, thus would not be influenced by environmental conditions according to the season. Insectivore bats compose most species roadkilled, the most numerous was *A. lituratus*, capable of feeding on extensive amount of resources such as dozens of fruits, leaves, nectar, and insects (e.g., Zortea & Mendes 1993, Sazima *et al.* 1994, Zortea & Chiarello 1994, Passos & Graciolli 2004). The combination of high environmental flexibility, large body mass, slow flight, and inaccurate echolocation contribute to the fact that

A. lituratus and other frugivore and nectarivore species are more likely to have higher roadkill rates. On the other hand, many studies have showed that insectivore bats detect the noise of motors up to ten meters away and avoid flying over highways (Zurcher *et al.* 2010).

The hotspots of bats roadkill exist due to the presence of preferential aerial routes or due to the formation of favorable habitats for bats along the road margins according to each species-specificity (e.g. Lesiński 2007, Russell *et al.* 2009, Medinas *et al.* 2013). Although each species has a different behavior towards the open area formed by the lanes and its associated disturbs, this mortality scenarios is because most bat species recorded flies slowly in proximity to the ground and have a less accurate echolocation apparatus, which favors risk of collision (Russel *et al.* 2009, Berthinussen & Altringham 2012). In this context, the sensibility of bats regards traffic is related directly to avoiding behavior that each species has against artificial light and noise, which will vary according to the number of vehicles on the highway (Siemers & Schaub 2011).

The movement of vehicles may be interpreted as a threat for some bat species, which causes defense behaviors against predators, causing them to deviate from the road (Baxter *et al.* 2006). All those factors interfere on foraging efficiency of species close to the road (Schaub *et al.* 2008). On the other hand, if species do not react on this way, a traffic increased may cause a direct increment on the roadkill risk due to the facility those individuals to come near the highway (Fensome & Mathews 2016). The most of species on this study was tolerant to the road disturbances, thus facilitating that increase of traffic resulted in a high number of roadkilled individuals. This result is in line with the pattern expected by Altringham & Kerth (2016), which suggests that despite the lack of empirical data,

increased vehicular traffic volume would tend to increase bat roadkill rate in the short-term.

We observed a negative relation between the area covered by native forest and the occurrence of roadkill, in other words, the increase of the area covered by native forest in the road margins may take to a reduction of bat roadkills. This may be explained because of the greater supply of favorable resources and habitats, which reduces the need for bats to widen their use area and to perform considerable displacement. Species specialized in cluttered habitats like the interior of forests tend to avoid open areas that expose them, which consequently causes them not to leave forest fragments to cross the road linear clearing (Fensome & Mathews 2016). This can explain why few records of these species were observed. The majority of our roadkill records is from *A. lituratus* (46%), a frugivore phyllostomid adapted to explore open areas and to move across great distances (Passos & Passamani 2003, Barros *et al.* 2006, Menezes *et al.* 2008, Reis *et al.* 2012).

The relation between area covered by pasture and the occurrence of roadkill was also negative. Areas covered by pasture scarcely offer shelter or food, which makes them commonly avoided by many bat species (Rydell *et al.* 1994, Walsh & Harris 1996, Lesiński *et al.* 2000). Various species that necessarily depend on covered areas for shelter and do not have the ability to move across long distances do not flight on pasture areas (Lesiński *et al.* 2007). Thus, as bats require a larger area than what is observed for small-sized mammals (Kelt & Van Vuren 1999), they tend to be extremely sensitive to habitat fragmentation, which force bats to fly long distances to access needed resources (Fensome & Mathews 2016). In this context, in regions fragmented by roads, while some species are affected by the barrier effect that interrupts their natural movements, some individuals from other species that attempt to cross open spaces are under the risk of collision (Altringham & Kerth 2016). However, *A. lituratus* is an example of high plasticity phenotypic species (Nogueira *et al.* 2007, Pacheco *et al.* 2010, Barquez *et al.* 2015), so being the most common species on the study does not mean that occur a deleterious effect over its original population, capable to compromise its population viability.

Finally, it should be pointed out that the roadkill rates found in the present study are probably underestimated in relation to the real magnitude of the bat mortality on the road. All bat species are smaller in comparison to other commonly recorded mammal species, which implies an accelerated removal rate of their carcasses in the lane (Santos *et al.* 2011). Small animals usually end up having a low permanence time on the road due to the action of scavengers (common in the region of the study area), natural decomposition, influence of rains and of the constant vehicular traffic (Slater 2002, Ratton *et al.* 2014). In addition, the observer detectability during monitoring can be improved to some degree, but it is also inevitably limited by the carcasses size, which leads to underestimates bats and other small animals (Teixeira *et al.* 2013b).

Based on the results, the main mitigation measure that would benefit all bat species affected by roadkill is to modulate traffic through the imposition of speed limit. This limitation could be imposed through the installation of electronic radars on points with the higher rates of species movement, indicated by the current roadkill hotspots. Other initiatives to minimize the impacts of collisions over bats on hotspots include the presence of fences, which do not prevent them to cross the roadway, but force them to fly higher than the vehicles avoiding collisions (Zurcher *et al.* 2010). In conclusion, this study presents unpublished results about the impacts of roads over bats in tropical regions and serves as a comparative parameter with other areas. We elucidated mortality patterns related to affected species, temporal dynamic, spatial distribution, and landscape features that are determinant to the occurrence of bat roadkill. In this context, we recommend that the already existing systematic efforts of data collection about fauna roadkill on highways remain continuous. It is important to consolidate extensive databases so that the decisions of the environmental administration of the highway can be grounded on scientifically analyzed data.

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REFERENCES

- Albrecht, L., Meyer, C. F., & Kalko, E. K. 2007. Differential mobility in two small phyllostomid bats, *Artibeus watsoni* and *Micronycteris microtis*, in a fragmented neotropical landscape. *Acta Theriologica*, 52(2), 141-149. DOI: 10.1007/BF03194209
- Altringham, J., & Kerth, G. 2016. Bats and roads. In: C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: conservation of bats in a changing world*. pp. 35-62. New York: Springer International Publishing.
- Autopista Fluminense. 2016. Institucional. Retrieved July 7, 2016, from <http://www.autopistafluminense.com.br/?link=institucional>
- Avila-Cabadilla, L. D., Sanchez-Azofeifa, G. A., Stoner, K. E., Alvarez-Añorve, M. Y., Quesada, M., Portillo-Quintero, C. A. 2012. Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary forests. *PLoS One*, 7(4), e35228. DOI: 10.1371/journal.pone.0035228
- Bager, A., Borghi, C. E., & Secco, H. 2015. The influence of economics, politics, and environment on road ecology in South America. In: R. van der Ree, D. Smith & C. Grilo (Eds.), *Handbook of road ecology*. pp. 407-413. Wiley-Blackwell, Oxford.
- Baptista, M., & Mello, M. A. R. 2001. Preliminary inventory of the bat species of the Poço das Antas Biological Reserve, RJ. *Chiroptera Neotropical*, 7(1-2), 133-135.
- Barquez, R., Perez, S., Miller, B., Diaz, M. 2015. *Artibeus lituratus*. The IUCN Red List of Threatened Species 2015. Retrieved July 7, 2016, from <http://www.iucnredlist.org/details/2136/0>
- Barros, R. D., Bisaggio, E. L., & Borges, R. C. 2006. Morcegos (Mammalia, Chiroptera) em fragmentos florestais urbanos no município de Juiz de Fora, Minas Gerais, Sudeste do Brasil. *Biota Neotropica*, 6(1), 1-6. DOI: 10.1590/S1676-06032006000100012
- Barthelmess, E. L., & Brooks, M. S. 2010. The influence of body-size and diet on road-kill trends in mammals. *Biodiversity and Conservation*, 19(6), 1611-1629. DOI: 10.1007/s10531-010-9791-3
- Baxter, D. J., Psyllakis, J. M., Gillingham, M. P., O'Brien, E. L. 2006. Behavioral response of bats to perceived predation risk while foraging. *Ethology*, 112(10), 977-983. DOI: 10.1111/j.1439-0310.2006.01249.x
- Bennett, V. J., Sparks, D. W., & Zollner, P. A. 2013. Modeling the indirect effects of road networks on the foraging activities of bats. *Landscape ecology*, 28(5), 979-991. DOI: 10.1007/s10980-013-9874-0
- Bernard, E., & Fenton, M. B. 2003. Bat mobility and roosts in a fragmented landscape in central Amazonia, Brazil. *Biotropica*, 35(2), 262-277. DOI: 10.1111/j.1744-7429.2003.tb00285.x
- Bernard, E., Aguiar, L. M. S., Brito, D., Cruz-Neto, O. P., Gregorin, R., Machado, R. B., Oprea, M., Paglia, A. P., Tavares, V. C. 2012. Uma análise de horizontes sobre a conservação de morcegos no Brasil. In: T. R. O. Freitas, & E. M. Vieira (Eds.), *Mamíferos do Brasil: Genética, Sistemática, Ecologia e Conservação*. Vol. II. pp. 19-35. Rio de Janeiro: Sociedade Brasileira de Mastozoologia.
- Berthinussen, A., & Altringham, J. 2012. Do bat gantries and underpasses help bats cross roads safely? *PloS one*, 7(6), e38775. DOI: 10.1371/journal.pone.0038775
- Berthinussen, A., Richardson, O. C., & Altringham, J. D. 2014. Bat conservation: global evidence for the effects of interventions. Exeten, UK: Pelagic Publishing: p. 120.
- Bianconi, G. V., Mikich, S. B., & Pedro, W. A. 2006. Movements of bats (Mammalia, Chiroptera) in Atlantic Forest remnants in southern Brazil. *Revista Brasileira de Zoologia*, 23(4), 1199-1206. DOI: 10.1590/S0101-81752006000400030
- Blake, D., Hutson, A. M., Racey, P. A., Rydell, J., Speakman, J. R. 1994. Use of lamplit roads by foraging bats in southern England. *Journal of Zoology*, 234(3), 453-462. DOI: 10.1111/j.1469-7998.1994.tb04859.x
- Bolívar-Cimé, B., Laborde, J., MacSwiney, G., Cristina, M., Muñoz-Robles, C., Tun-Garrido, J. 2013. Response of phytophagous bats to patch quality and landscape attributes in fragmented tropical semi-deciduous forest. *Acta Chiropterologica*, 15(2), 399-409. DOI: 10.3161/150811013X679026
- Bolívar-Cimé, B., Bolívar-Cimé, A., Cabrera-Cruz, S. A., Muñoz-Jiménez, Ó., Villegas-Patraca, R. 2016. Bats in a tropical wind farm: species composition and importance of the spatial attributes of vegetation cover on bat fatalities. *Journal of Mammalogy*, 97(4), 1197-1208. DOI: 10.1093/jmammal/gyw069
- Bredt, A., & Uieda, W. 1996. Bats from urban and rural environments of the Distrito Federal, mid-western Brazil. *Chiroptera Neotropical*, 2(2), 54-57.
- Brito, D., Oliveira, L. C., & Mello, M. A. R. 2004. An overview of mammalian conservation at Poço das Antas Biological Reserve, southeastern Brazil. *Journal for Nature Conservation*, 12(4), 219-228. DOI: 10.1016/j.jnc.2004.09.001
- Burnham, K. P., & Anderson, D. R. 2002. *Model selection and inference: a practical information-theoretic approach*. 2nd ed. New York, NY: Springer-Verlag: p. 488.
- Cáceres, N. C. 2011. Biological characteristics influence mammal road kill in an Atlantic Forest–Cerrado interface in southwestern Brazil. *Italian Journal of Zoology*, 78(3), 379-389. DOI: 10.1080/11250003.2011.566226
- Coelho, I. P., Kindel, A., & Coelho, A. V. P. 2008. Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. *European Journal of Wildlife Research*, 54(4), 689.
- Coelho, A. V. P., Coelho, I. P., Kindel, A., Teixeira, F. Z. 2011. *SIRIEMA: Manual do Usuário v1.1*. Porto Alegre, RS: Universidade Federal do Porto Alegre: p. 23.
- Coelho, I. P., Teixeira, F. Z., Colombo, P., Coelho, A. V. P., Kindel, A. 2012. Anuran road-kills neighboring a peri-urban reserve in the Atlantic Forest, Brazil. *Journal of Environmental Management*, 112, 17-26.
- Coffin, A. W. 2007. From roadkill to road ecology: a review of the ecological effects of roads. *Journal of transport Geography*, 15(5), 396-406.

- Colwell, R. K. 2004. EstimateS: statistical estimation of species richness and shared species from samples. Version 7. User's guide and application. Retrieved from <http://viceroy.eeb.uconn.edu/estimates>
- Cserkés, T., Ottlecz, B., Cserkés-Nagy, Á, Farkas, J. 2013. Interchange as the main factor determining wildlife-vehicle collision hotspots on the fenced highways: spatial analysis and applications. *European Journal of Wildlife Research*, 59(4), 587-597. DOI: 10.1007/s10344-013-0710-2
- D'Amico, M., Román, J., Reyes, L. de los, Revilla, E. 2015. Vertebrate road-kill patterns in Mediterranean habitats: Who, when and where. *Biological Conservation*, 191, 234-242. DOI: 10.1016/j.biocon.2015.06.010
- Dinerstein, E. 1986. Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. *Biotropica*, 18(4), 307-318. DOI: 10.2307/2388574
- DNIT. 2014. Sistema Viário Nacional, Departamento Nacional de Infraestrutura de Transportes. Retrieved from <http://www.transportes.gov.br/transporte-rodoviario.html>
- Dussault, C., Poulin, M., Courtois, R., Ouellet, J. P. 2006. Temporal and spatial distribution of moose-vehicle accidents in the Laurentides Wildlife Reserve, Quebec, Canada. *Wildlife Biology*, 12(4), 415-425. DOI: 10.2981/0909-6396(2006)12[415:TASDOM]2.0.CO;2
- ESRI. 2012. ArcGIS, E. S. R. I. "10.3.". Redlands, CA: Environmental Systems Research Institute.
- Everette, A. L., O'Shea, T. J., Ellison, L. E., Stone, L. A., McCance, J. L. 2001. Bat use of a high-plains urban wildlife refuge. *Wildlife Society Bulletin*, 29(3), 967-973.
- Fahrig, L., & Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and society*, 14(1), 21.
- Fensome, A. G., & Mathews, F. 2016. Roads and bats: a meta analysis and review of the evidence on vehicle collisions and barrier effects. *Mammal Review*, 46(4), 311-323. DOI: 10.1111/mam.12072
- Fielding, A. H., & Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation*, 24(1), 38-49.
- Fleming, T. H., & Heithaus, E. R. 1986. Seasonal foraging behavior of the frugivorous bat *Carollia perspicillata*. *Journal of Mammalogy*, 67(4), 660-671. DOI: 10.2307/1381127
- Fleming, T. H., Nuñez, R. A., & Sternberg, L. D. S. L. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. *Oecologia*, 94(1), 72-75. DOI: 10.1007/BF00317304
- Forman, R. T. T., & Alexander, L. E. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29, 207-231. DOI: 10.1146/annurev.ecolsys.29.1.207
- Forman, R. T. T. 2003. Road ecology: science and solutions. Washington, DC: Island Press: p. 504.
- Frank, K. D. 1988. Impact of outdoor lighting on moths: an assessment. *Journal of the Lepidopterists' Society*, 42(2), 63-93.
- Freitas, S. R., Oliveira, A. N., Ciocheti, G., Vieira, M. V., Matos, D. M. S. 2015. How landscape features influence road-kill of three species of mammals in the Brazilian Savanna? *Oecologia Australis*, 18, 35-45.
- Gaisler, J., Øehák, Z., & Bartonička, T. 2009. Bat casualties by road traffic (Brno-Vienna). *Acta Theriologica*, 54(2), 147-155. DOI: 10.1007/BF03193170
- Gibbs, J. P., & Shriver, W. G. 2005. Can road mortality limit populations of pool-breeding amphibians? *Wetlands Ecology and Management*, 13(3), 281-289. DOI: 10.1007/s11273-004-7522-9
- Goosem, M. 2007. Fragmentation impacts caused by roads through rainforests. *Current Science*, 93(11), 1587-1595.
- Gregorin, R., & Taddei, V. A. 2002. Chave artificial para a identificação de molossídeos brasileiros (Mammalia, Chiroptera). *Mastozoología Neotropical*, 9(1), 13-32.
- Grilo, C., Bissonette, J. A., & Santos-Reis, M. 2009. Spatial-temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. *Biological conservation*, 142(2), 301-313. DOI: 10.1016/j.biocon.2008.10.026
- Hammer, Ø, Harper, D. A. T., & Ryan, P. D. 2001. PAST-Palaeontological STatistics, ver. 1.89. *Palaeontologia electronica*, 4(1), 1-9.
- Heithaus, E. R., Fleming, T. H., & Opler, P. A. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology*, 56(4), 841-854. DOI: 10.2307/1936295
- Huijser, M. P., Abra, F. D., & Duffield, J. W. 2013. Mammal road mortality and cost-benefit analyses of mitigation measures aimed at reducing collisions with capybara (*Hydrochoerus hydrochaeris*) in São Paulo State, Brazil. *Oecologia Australis*, 17(1), 129-146.
- Jackson, N. D., & Fahrig, L. 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biological Conservation*, 144(12), 3143-3148. DOI: 10.1016/j.biocon.2011.09.010
- Jacobson, S. L., Bliss Ketchum, L. L., Rivera, C. E., Smith, W. P. 2016. A behavior based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere*, 7(4), DOI: 10.1002/ecs2.1345
- Jaeger, J. A., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., Toschanowitz, K. T. von 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling*, 185(2), 329-348. DOI: 10.1016/j.ecolmodel.2004.12.015
- Jones, G., & Rydell, J. 2003. Attack and defense: interactions between echolocating bats and their insect prey. In: T. H. Kunz & M. B. Fenton (Eds.), *Bat ecology*. pp. 301-345. Chicago, IL: University of Chicago Press:.
- Kelt, D. A., & Vuren, D. van 1999. Energetic constraints and the relationship between body size and home range area in mammals. *Ecology*, 80(1), 337-340. DOI: 10.2307/177002
- Kiefer, A., Merz, H., Rackow, W., Roer, H., Schlegel, D. 1995. Bats as traffic casualties in Germany. *Myotis*, 32(33), 215-220.
- Kitzes, J., & Merenlender, A. 2014. Large roads reduce bat activity across multiple species. *PLoS one*, 9(5), e96341. DOI: 10.1371/journal.pone.0096341
- Köppen W. 1948. *Climatologia*. Translated by Pedro R.H. Perez. Buenos Aires: Gráfica Panamericana: p. 478.

- Kunz, T. H. 1982. Roosting ecology of bats. In: T. H. Kunz (Ed.), Ecology of bats. pp. 1-55. Springer US.
- Kunz, T. H., & Pierson, E. D. 1994. Bats of the world: an introduction. In: R. M. Nowak (Ed.), Walker's Bats of the World. pp. 1-46. Baltimore and London: The Johns Hopkins University Press.
- Lacoeuilhe, A., Machon, N., Julien, J. F., Le Bocq, A., Kerbiriou, C. 2014. The influence of low intensities of light pollution on bat communities in a semi-natural context. PLoS one, 9(10), e103042. DOI: 10.1371/journal.pone.0103042
- Laurance, W. F., Goosem, M., & Laurance, S. G. 2009. Impacts of roads and linear clearings on tropical forests. Trends in Ecology & Evolution, 24(12), 659-669. DOI: 10.1016/j.tree.2009.06.009
- Lesiński, G., Fuszara, E., & Kowalski, M. 2000. Foraging areas and relative density of bats (Chiroptera) in differently human transformed landscapes. Zeitschrift für Saugetierkunde, 65(3), 129-137.
- Lesiński, G. 2007. Bat road casualties and factors determining their number. Mammalia, 71(3), 138-142. DOI: 10.1515/MAMM.2007.020
- Lesiński, G. 2008. Linear landscape elements and bat casualties on roads-an example. Annales Zoologici Fennici, 45(4), 277-280. DOI: 10.5735/086.045.0406
- Lesiński, G., Sikora, A., & Olszewski, A. 2011. Bat casualties on a road crossing a mosaic landscape. European Journal of Wildlife Research, 57(2), 217-223. DOI: 10.1007/s10344-010-0414-9
- Levine, N. 2000. CrimeStat, Version 1.1. Annandale, VA: Ned Levine and Associates.
- McCullagh, P., & Nelder, J. A. 1989. Generalized Linear Models. 2nd ed. London, UK: Chapman, & Hall: p. 532.
- Medinas, D., Marques, J. T., & Mira, A. 2013. Assessing road effects on bats: the role of landscape, road features, and bat activity on road-kills. Ecological Research, 28(2), 227-237. DOI: 10.1007/s11284-012-1009-6
- Menezes, J. L., Duarte, A. C., Novaes, R. L. M., Façanha, A. C., Peracchi, A. L., Costa, L. M., Dias e Fernandes, A. F. P., Esbérard, C. E. L. 2008. Deslocamento de *Artibeus lituratus* (Olfers, 1818) (Mammalia, Chiroptera) entre ilha e continente no Estado do Rio de Janeiro, Brasil. Biota Neotropica, 8(2), 243-245.
- Nogueira, M. R., Peracchi, A. L., & Moratelli, R. 2007. Subfamília Phyllostominae. In: N. R. Reis, A. L. Peracchi, W. A. Pedro & I. P. Lima (Eds.), Morcegos do Brasil. pp. 61-97. Londrina, PR: Universidade Estadual de Londrina.
- Nogueira, M. R., de Lima, I. P., Moratelli, R., da Cunha Tavares, V., Gregorin, R., Peracchi, A. L. 2014. Checklist of Brazilian bats, with comments on original records. Check List, 10(4), 808-821. DOI: 10.15560/10.4.808
- Nowak, R. M. 1994. Walker's bats of the world. Baltimore and London: The Johns Hopkins University Press: p. 287.
- Orłowski, G., & Nowak, L. 2006. Factors influencing mammal roadkills in the agricultural landscape of south-western Poland. Polish Journal of Ecology, 54(2), 283-294.
- Pacheco, S. M., Sodré, M., Gama, A. R., Bredt, A., Cavallini, E. M., Marques, R. V., Guimarães, M. M., Bianconi, G. 2010. Morcegos urbanos: status do conhecimento e plano de ação para a conservação no Brasil. Chiroptera Neotropical, 16(1), 630-647.
- Passos, F. C., & Gracioli, G. 2004. Observações da dieta de ações da dieta de *Artibeus lituratus* (Olfers) (Chiroptera, Phyllostomidae) em duas áreas do sul do Brasil. Revista Brasileira de Zoologia, 21(3), 487-489.
- Passos, J. G., & Passamani, M. 2003. *Artibeus lituratus* (Chiroptera, Phyllostomidae): biologia e dispersão de sementes no Parque do Museu de Biologia Prof. Mello Leitão, Santa Teresa (ES). Natureza on line, 1(1), 1-6.
- Peracchi, A. L., Lima, I. P., Reis, N. R., Nogueira, M. R., & Ortêncio-Filho, H. 2006. Ordem Chiroptera. In: N. R. Reis, A. L. Peracchi, W. A. Pedro, & I. P. Lima (Eds.), Mamíferos do Brasil. pp. 153-230. Londrina, PR: Universidade Estadual de Londrina.
- Primo, P. B., & Völker, C. M. 2003. Bacias hidrográficas dos rios São João e das Ostras: águas, terras e conservação ambiental. Rio de Janeiro, RJ: CILSJ: p. 179.
- R Development Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing: p. 3501.
- Ratton, P., Secco, H., & Rosa, C. A. 2014. Carcass permanency time and its implications to the roadkill data. European Journal of Wildlife Research, 60(3), 543-546.
- Reis, N. R., Peracchi, A. L., Pedro, W. A., & de Lima, I. P. (Eds.). 2007. Morcegos do Brasil. Londrina, PR: Universidade Estadual de Londrina: p. 254.
- Reis, N. R., Fregonezi, M. N., Peracchi, A. L., Rossaneis, B. K. 2012. Metapopulation in bats of Southern Brazil. Brazilian Journal of Biology, 72(3), 605-609. DOI: 10.1590/S1519-69842012000300025
- Reis, N. R., Fregonezi, M. N., Peracchi, A. L., Shibatta, O. A. (Eds.). 2013. Morcegos do Brasil: guia de campo. Rio de Janeiro, RJ: Technical Books: p. 252.
- Rosa, C. A., & Bager, A. 2012. Seasonality and habitat types affect roadkill of Neotropical birds. Journal of Environmental Management, 97, 1-5. DOI: 10.1016/j.jenvman.2011.11.004
- Russell, A. L., Butchkoski, C. M., Saidak, L., McCracken, G. F. 2009. Road-killed bats, highway design, and the commuting ecology of bats. Endangered Species Research, 8, 49-60.
- Rydell, J., Bushby, A., Cosgrove, C. C., Racey, P. A. 1994. Habitat use by bats along rivers in northeast Scotland. Folia Zoologica-Praha, 43(4), 798-804.
- Rydell, J. 2006. Bats and their insect prey at streetlights. In: C. Rich & T. Longcore (Eds.) Ecological consequences of artificial night lighting. pp. 43-60. Washington, DC: Island Press.
- Santos, S. M., Carvalho, F., & Mira, A. 2011. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. PLoS One, 6(9), e25383.
- Sazima, I., Fischer, W. A., Sazima, M., Fischer, E. A. 1994. The fruit bat *Artibeus lituratus* as a forest and city dweller. Ciencia e Cultura, 46(3), 164-168.
- Schaub, A., Ostwald, J., & Siemers, B. M. 2008. Foraging bats avoid noise. Journal of Experimental Biology, 211(19), 3174-3180.
- Siemers, B. M., & Schaub, A. 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic

- predators. *Proceedings of the Royal Society of London B: Biological Sciences*, 278(1712), 1646-1652. DOI: 10.1098/rspb.2010.2262
- Slater, F. M. 2002. An assessment of wildlife road casualties—the potential discrepancy between numbers counted and numbers killed. *Web Ecology*, 3(1), 33-42.
- Simmons, N. B. 2005. Chiroptera. In: D. E. Wilson & D. M. Reeder (Eds.), *Mammal Species of the World – a taxonomic and geographic reference*. Third Edition. pp. 312-529. Baltimore, MD: Hopkins University Press.
- Stone, E. L. 2013. *Bats and lighting: Overview of current evidence and mitigation*. Bristol, UK: University of Bristol: p. 78.
- Svensson, A. M., & Rydell, J. 1998. Mercury vapour lamps interfere with the bat defence of tympanate moths (*Operophtera* spp., Geometridae). *Animal Behaviour*, 55(1), 223-226. DOI: 10.1006/anbe.1997.0590
- Tavares, V. C., Gregorin, R., & Peracchi, A. L. 2008. A diversidade de morcegos no Brasil: lista atualizada com comentários sobre distribuição e taxonomia. In: S. M. Pacheco, R. V. Marques, & C. E. L. Esbérard (Orgs.), *Morcegos no Brasil: biologia, sistemática, ecologia e conservação*. pp. 25-58. Porto Alegre, RS: Armazém Digital.
- Teixeira, F. Z., Coelho, I. P., Esperandio, I. B., Oliveira, N. R., Peter, F. P., Dornelles, S. S., Delazeris, N. R., Tavares, M., Martins, M.B., Kindel, A. 2013a. Are road-kill hotspots coincident among different vertebrate groups? *Oecologia Australis*, 17(1), 36-47.
- Teixeira, F. Z., Coelho, A. V. P., Esperandio, I. B., Kindel, A. 2013b. Vertebrate road mortality estimates: effects of sampling methods and carcass removal. *Biological Conservation*, 157, 317-323.
- Trombulak, S. C., & Frissell, C. A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, 14(1), 18-30.
- Van der Ree, R., Smith, D. J., & Grilo, C. 2015. The ecological effects of linear infrastructure and traffic: challenges and opportunities of rapid global growth. In: R. Van der Ree, D. J. Smith & C. Grilo (Eds.), *Handbook of road ecology*. Oxford, UK: John Wiley, & Sons.
- Verboom, B., Boonman, A. M., Limpens, H. J. 1999. Acoustic perception of landscape elements by the pond bat (*Myotis dasycneme*). *Journal of Zoology*, 248(1), 59-66. DOI: 10.1111/j.1469-7998.1999.tb01022.x
- Walsh, A. L., & Harris, S. 1996. Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology*, 33(3), 508-518.
- Wilkinson, G. S., & South, J. M. 2002. Life history, ecology and longevity in bats. *Aging cell*, 1(2), 124-131.
- Wray, S., Reason, P., Wells, D., Cresswell, W., & Walker, H. 2005. Design, installation and monitoring of safe crossing points for bats on a new highway scheme in Wales. In: C. L. Irwin, P. Garrett, & K. P. McDermott (Eds.), *Proceedings of the International Conference of Ecology and Transport*. pp. 369-379. Raleigh, NC.
- Zortéa, M., & Mendes, S. L. 1993. Folivory in the big fruit-eating bat, *Artibeus lituratus* (Chiroptera: Phyllostomidae) in eastern Brazil. *Journal of Tropical Ecology*, 9(1), 117-120. DOI: 10.1017/S0266467400007057
- Zortéa, M., & Chiarello, A. G. 1994. Observations on the big fruit-eating bat, *Artibeus lituratus*, in an urban reserve of south-east Brazil. *Mammalia*, 58(4), 665-670.
- Zurcher, A. A., Sparks, D. W., & Bennett, V. J. 2010. Why the bat did not cross the road? *Acta Chiropterologica*, 12(2), 337-340. DOI: 10.3161/150811010X537918
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media: p. 574.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3-14. DOI: 10.1111/j.2041-210X.2009.00001.x

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