



Wild fauna as roadkill on a highway in the semiarid region of northeastern Brazil

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ABSTRACT

The death of wild vertebrates run over by motor vehicles on highways is one of the main causes of the loss of wildlife diversity. The aim of the present study was to investigate the diversity of wild fauna in roadkill incidents on a stretch of highway in the semiarid region of Brazil. The survey was conducted between March 2020 and May 2021 through active searches using a motorcycle. Killed vertebrates were analyzed and photographed *in situ*. Wild fauna was studied based on ecological descriptors, speed of movement and average rate of roadkill incidents. We compared total observed richness to that expected using nonparametric estimators. A total of 464 road-killed vertebrates were represented by two species of amphibians, 17 reptiles, 17 birds and 10 mammals. Amphibians were the most affected, totaling 245 individuals. Colubridae was the family with the largest number of species affected. *Boiruna sertaneja* and *Boa constrictor* were the only medium-size to large snakes killed. *Herpailurus yagouaroundi* and *Leopardus tigrinus* are respectively categorized as “least concern” and “vulnerable” according to the IUCN. The species accumulation curves continued to rise, showing no sign of approaching to an asymptote. Chao 2 and Jack 2 were the main estimators for road-killed wild vertebrates considering total richness. The diversity reported here is considered to be underestimated and greater monthly sampling efforts are required. Conservation strategies are urgently needed for the protection of wild vertebrate fauna to mitigate the staggering loss of biodiversity caused by the construction and operation of roads and highways in Brazil.


Keywords: Caatinga, highway impacts, landscape ecology, wild fauna, vertebrate mortality.

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SIGNIFICANCE STATEMENT

Wild vertebrates are particularly vulnerable to roadkill events on roads and highways due to their active habits. Official records of wildlife killed due to collisions with motor vehicles are likely underestimated and scientific knowledge on this issue remains insufficient. This article presents a comprehensive survey of wild vertebrates run over by motor vehicles on a stretch of highway in the semiarid region of Brazil and reveals a diversity of fauna (464 road-killed vertebrates) represented by amphibians, birds, mammals and reptiles. Fauna was studied based on quantitative data, categorized into functional groups and classified according to vulnerability and conservation status. Future conservation strategies urgently need to be implemented for all groups of animals to mitigate the staggering loss of biodiversity caused by the construction and operation of roads and highways in Brazil.

INTRODUCTION

Our planet is currently undergoing unprecedented anthropogenic changes, which result in the rapid, continuous loss of biological diversity. Deforestation and urbanization are considered to be central drivers of extinction rates in the Holocene epoch, which extends to the present day in the so-called Anthropocene (Steffen *et al.* 2007; Ceballos *et al.* 2015, 2017). Recent studies further confirm that current extinction rates due to anthropogenic factors are up to 1000 times higher in comparison to previous mass extinctions indicated in the fossil record (Barnosky *et al.* 2011; Youngsteadt *et al.* 2019).

Terrestrial vertebrates are among the most affected by habitat fragmentation and the alarming population declines recorded in recent years point to a sixth major mass extinction event (Steffen *et al.* 2007; Ceballos *et al.* 2015, 2017). Deforestation, pollution, fire, energy production and road building, which are consequences of unbridled urban growth, are among the most significant threats to this group (IUCN 2023a,b,c,d).

The constant need for road expansion and the corresponding increase in traffic exert negative effects that threaten natural wild populations. Habitat fragmentation due to road expansion produces the “barrier effect”, which prevents animal movements, negatively affecting bioecological aspects of wild fauna (Seiler 2001; Keller *et al.* 2005), such as reproduction [including loss of genetic variability (Goosem 1997; Trombulak and Frissel 2000; Dirzo and Raven 2003; Santana 2012)], foraging and the avoidance of predators (Ferreira *et al.* 2017). Environmental degradation also produces physical and chemical disturbances, causing direct harm to wildlife (Seiler 2001; Orlandin *et al.* 2015).

Brazil has the fourth largest road network in the world and this network is growing (Rosa and Mauhs 2004; Milli and Passamani 2006; Santos *et al.* 2016; ACNTT 2019; Teodoro *et al.* 2019). The high demand for roads is one of the central causes of habitat fragmentation in the country and has produced significant changes to the phytophysiology of

ecosystems (Mader 1984). Road building is one of the main threats to terrestrial biodiversity due to the negative impacts on wildlife (Santana 2012; Ramos-Abrantes *et al.* 2018). Without a doubt, roadkill incidents involving wild vertebrates constitute a major contributor to the loss of biodiversity in Brazil (Oliveira and Silva 2012; Sássi *et al.* 2013; Orlandin *et al.* 2015). Although dead animals are common on Brazilian highways, official records of wildlife killed due to collisions with motor vehicles are likely underestimated and scientific knowledge on this issue remains insufficient (Tumeleiro *et al.* 2006; Sássi *et al.* 2013).

Wild vertebrates are particularly vulnerable to roadkill events due to their active habits (Orlandin *et al.* 2015). Estimates suggest that approximately 473,000,000 vertebrates are killed each year by motor vehicles on Brazilian highways. Small vertebrates (e.g., frogs, birds, snakes, etc.) are, by far, the most affected, accounting for about 90% of roadkill, followed by medium-sized vertebrates (e.g., opossums, hares and primates), which account for about 9%, and large vertebrates (e.g., jaguars, foxes, maned wolves, tapirs and capybaras), accounting for about 1%. Roadkill incidents are more frequent in the southeastern region of the country, followed in descending order of frequency by the southern, northeastern, central western and northern regions (CBEE 2020).

The major vertebrate groups affected by urbanization worldwide include around 2040 endangered species of amphibians, 910 species of reptiles, 554 species of birds and 825 species of mammals (IUCN 2023a,b,c,d). These groups are also the most common victims of roadkill in Brazil (Milli and Passamani 2006; Coelho *et al.* 2008; Hegel *et al.* 2012; Junior *et al.* 2012; Oliveira and Silva 2012; Santana 2012; Sássi *et al.* 2013; Neto *et al.* 2015; Orlandin *et al.* 2015; Ramos-Abrantes *et al.* 2018). Recent estimates show that the vertebrate fauna of Brazil is composed of about 1188 species of amphibians (Segalla *et al.* 2021), 795 species of reptiles (Costa and Bérnils 2018), 3000 species of birds (CTFB 2021) and 722 species of mammals (Percequillo and Gregorin 2021). The *Caatinga* (semiarid) biome has about 1400 vertebrate species, 23% of which are endemic to the bi-

ome, with 98 amphibian, 224 reptile (Garda *et al.* 2018; Silva *et al.* 2018), 548 bird (Araujo and Silva 2017) and 183 mammal species (Carmignotto and Ástua 2017). Representatives of 28 species among a total of 131 endangered species in this biome often die from collisions with motor vehicles on roads and highways (ICMBio 2018).

Annually, thousands of wild vertebrates are run over by motor vehicles on highways and roads in Brazil (Weiss and Vianna 2012; Pinheiro and Turci 2013; Silva *et al.* 2013; Carvalho *et al.* 2014; Braz *et al.* 2016; Corrêa *et al.* 2017; Ramos-Abrantes *et al.* 2018). Along with fear/disgust of animals (some of which are intentionally run over by drivers) (DNIT 2012; Oliveira *et al.* 2023), the lack of wildlife warning signs, insufficient speed control mechanisms and inadequate traffic education are central drivers of wild vertebrate roadkill (DNIT 2012).

Studies inventorying fauna killed by vehicles have been conducted in 13 states covering a vast area in Brazil (e.g., Amazonas, Acre, Pará, Maranhão, Paraíba, Pernambuco, Goiás, Minas Gerais, São Paulo, Mato Grosso do Sul, Paraná, Santa Catarina and Rio Grande do Sul) revealing that prevalence of wild fauna roadkill is underestimated (Rosa and Mauhs 2004; Hengemühle and Cademartori 2008; Dupont and Lobo 2012; Oliveira and Silva 2012; Omena Junior *et al.* 2012; Weiss and Viana 2012; Pinheiro and Turci 2013; Silva *et al.* 2013; Carvalho *et al.* 2014, 2015; Orlandin *et al.* 2015; Almeida *et al.* 2016; Braz and França 2016; Corrêa *et al.* 2017; Ramos-Abrantes *et al.* 2018; Dornas *et al.* 2019; Magioli *et al.* 2019; Miranda *et al.* 2020). Most data on roadkilled vertebrates in the country are related to highways in the states of Paraná (Weiss and Viana 2012; Carvalho *et al.* 2015), Santa Catarina (Orlandin *et al.* 2015) and Rio Grande do Sul – southern Brazil (Rosa and Mauhs 2004; Hengemühle and Cademartori 2008; Dupont and Lobo 2012; Oliveira and Silva 2012; Silva *et al.* 2013; Corrêa *et al.* 2017). Such regional studies sought mainly to assess the effect of vehicular traffic on the mortality of wild animal populations (Rosa and Mauhs 2004; Weiss and Viana 2012; Corrêa *et al.* 2017), survey the fauna of wild vertebrates killed, determine seasonal variations in the number of accidents, identify stretches with a higher incidence of collisions with animals (Hengemühle and Cademartori 2008), monitor roadkills of wild fauna to measure the impact on the fauna (Dupont and Lobo 2012), identify wild fauna roadkill, analyze monthly variations in roadkill rates correlating with the monthly rainfall volume (Oliveira and Silva 2012), determine wild vertebrate roadkill aggregations and to propose mitigation measures for local fauna (Carvalho *et al.* 2015), describe the diversity of roadkill vertebrates and correlate the incidence with the surrounding vegetation

(Orlandin *et al.* 2015) and describe the composition of vertebrates and contribute information on wild fauna (Silva *et al.* 2013).

Roadkill surveys in northern and northeastern Brazil are scarce. Among the few studies carried out in this region, Sousa and Miranda (2010) recorded five families and five species of mammals run over on the BR-230 highway, which extends from the city of Campina Grande to the city of João Pessoa in the state of Paraíba. Most of the dead animals recorded in the study were canids. Almeida *et al.* (2016) recorded two amphibian and 22 reptile species run over along a stretch of the BR-232 highway in the state of Pernambuco. The toad *Rhinella jimi* and the snakes *Boiruna sertaneja* and *Boa constrictor* were the most affected vertebrates in the area. Monitoring roadkill along a stretch of the BR-230 highway between the cities of Campina Grande and Patos in the state of Paraíba, Ramos-Abrantes *et al.* (2018) found that mammals were the most commonly killed animals and that the crab-eating fox, *Cerdocyon thous*, was the most affected species. Cezar *et al.* (2021) recorded 10 families and 12 species of mammals run over along a 134-km stretch in the state of Paraíba and also cited *C. thous* as the most affected species.

The aim of the present study was to investigate the diversity of wild vertebrates in roadkill incidents along a stretch of the PB-400 highway connecting the municipalities of Cajazeiras and Monte Horebe in the state of Paraíba (northeastern Brazil) to provide data that could assist in the implementation of management and conservation strategies by local authorities.

MATERIAL AND METHODS

Study area

Brazilian federal highway PB-400 is 102 km in length and connects the municipalities of Cajazeiras, São José de Piranhas, Monte Horebe, Bonito de Santa Fé and Conceição in the semiarid region of the state of Paraíba in northeastern Brazil. The present study was conducted along the 47 km stretch of the PB-400 highway between the municipalities of Cajazeiras (06°53'24"S, 38°33'43"W) and Monte Horebe (07°12'54"S, 38°35'09"W) (Figure 1). The study area is an asphalted highway seven meters in width with vegetation within 1.80 m of the road and constant daily traffic of small (motorcycles), medium-sized (cars, vans and pickup trucks) and large (trucks, buses and trailers) vehicles. Highway signage is either inadequate or completely absent. The average daily vehicle flow on weekdays is approximately 100 and 50 vehicles per hour in the morning and afternoon, respectively (personal observation during two monitoring days per month over a three-month period).

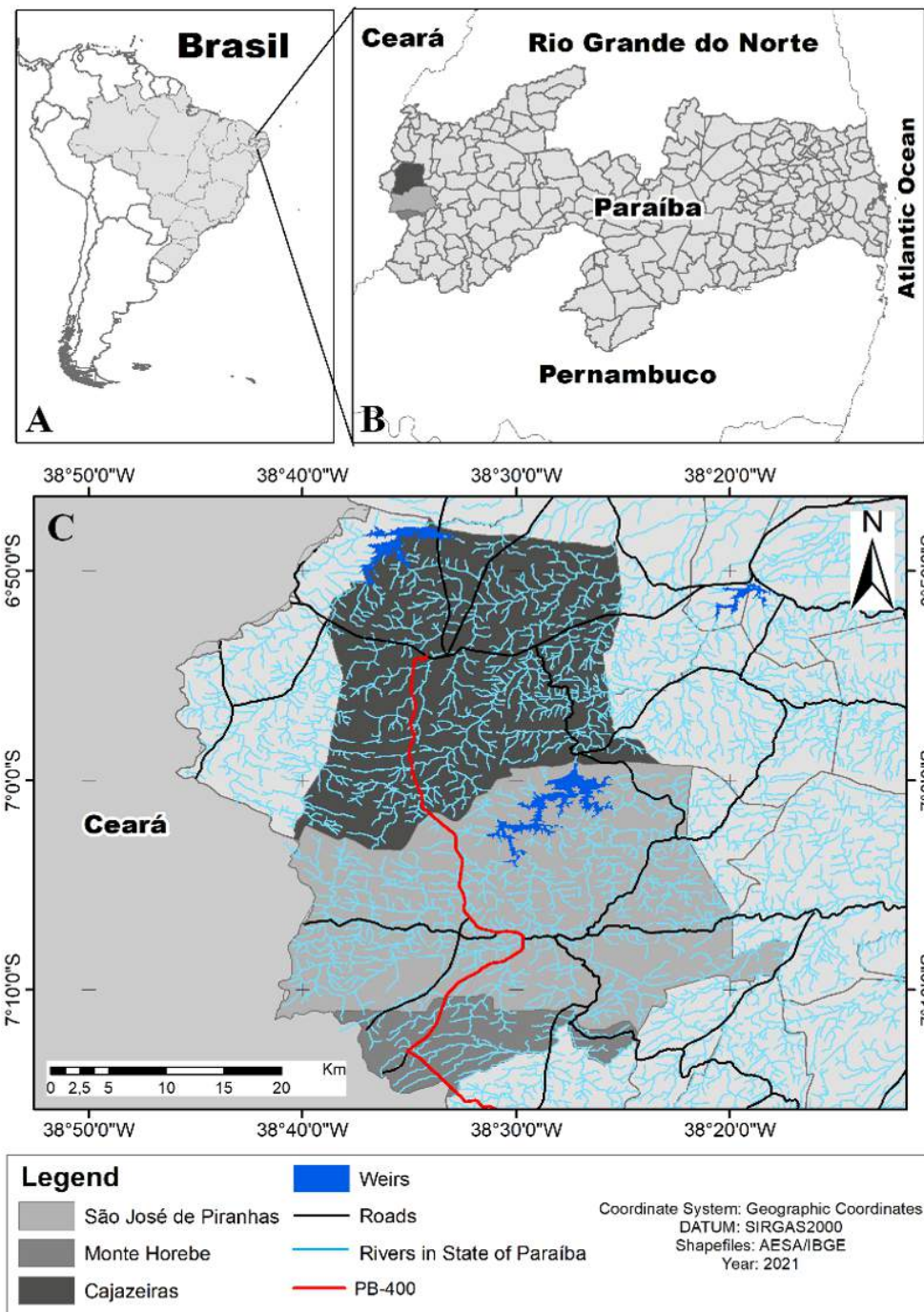


Figure 1. Map of the study area showing (A) South America highlighting Brazil; (B) the state of Paraíba highlighting the municipalities of Cajazeiras, São José de Piranhas and Monte Horebe; (C) the municipalities of Cajazeiras, São José de Piranhas and Monte Horebe highlighting the stretch of the PB-400 highway surveyed (red line).

The highway is located in the semiarid region, which has a predominantly warm, dry, tropical climate, with temperatures ranging from 12° to 30°C and annual rainfall ranging from 201.3 and 1561.3 mm. The dry season typically spans from December

to June, whereas the rainy season spans from July to November (Araújo *et al.* 2005; Francisco and Santos 2017).

The soil is composed of crystalline rocks, with a predominance of the podzolic latosol (luvisols) inters-

persed with a mix of sand and clay of yellowish, reddish and grayish colors. The relief around the highway is an extensive pediplan with elongated residual elevations, which is consistent with the typical geological features of the region (Beltrão *et al.* 2005a, b, c; Guerra and Junior 2011).

The vegetation is typical of the *Caatinga* biome – xerophilic and deciduous with herbaceous, shrubby and arboreal strata as well as cacti, bromeliads and *Mimosa* spp. (Beltrão *et al.* 2005a, b, c; Leal *et al.* 2005; Gariglio *et al.* 2010; Brito 2012). The area surrounding the highway is highly anthropized with homes as well as extensive agricultural and livestock activities.

Sampling and identification

The survey was conducted between March 2020 and May 2021, totaling 15 months of systematic monitoring. Three samples were conducted per month, with a monthly effort of 282 km and a total effort of 4230 km.

Road-killed wild vertebrates were located through active searches. The route was traveled in the morning period on weekdays using a motorcycle at an average speed of 60 km/h. Individuals were photographed *in situ* and subsequently identified based on specific literature for each vertebrate group. Carcasses were removed from the highway to avoid recounts as well as potential accidents with animals attracted by the decomposition.

Taxonomic identification was partially based on Segalla *et al.* (2021) for amphibians; Marques *et al.* (2017), Pereira-Filho *et al.* (2017) and ReptileDB (2021) for reptiles; WikiAves (2021) for birds; and Paglia *et al.* (2012), Carmignotto and Astúa (2017) and Percequillo and Gregorin (2021) for mammals. We also identified wild vertebrate species based on the *Catálogo Taxonômico da Fauna do Brasil* (CTFB 2021) [Taxonomic Catalog of the Fauna of Brazil].

The conservation status of each species was determined using data from the Chico Mendes Institute for Conservation and Biodiversity (ICMBio 2022) of the Ministry of the Environment (MMA) and the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN 2023).

Data analysis

Fauna was characterized based on quantitative data to determine species abundance (N) and richness (S). The relative abundance (RA) of each species was calculated to investigate which vertebrates had the highest incidence of being roadkill. The RA was estimated by calculating the number of records of each species in relation to the total number of road-

killed individuals recorded and expressed as percentage. Frequency of occurrence (FOC) was determined based on the number of months that each species was recorded divided by the total number of samples, multiplied by 100 and expressed as percentage. The FOC (%) was used to categorize the species as “constant” (CT [FOC > 50%]), “accessory” (AC [FOC ≥ 25 ≤ 50%]) or “accidental” (AD [FOC < 25%]) based on Dajoz (1983).

Road-killed individuals were categorized into the following functional groups based on movement speed: (1) slow – slow-moving species; (2) intermediate – intermediate-moving species; (3) fast – fast-moving species. The species were also classified according to vulnerability and conservation status (“least concern”, “vulnerable” and “endangered”) according to the Chico Mendes Institute for Biodiversity Conservation (ICMBio 2022) and the IUCN (2023).

The average rate of road-killed vertebrates was calculated as the ratio between the number of recorded individuals and the total number of kilometers of the study area (Rosa and Mauhs 2004; Odat *et al.* 2009). The data were analyzed to estimate the number of road-killed individuals per day/month/year. For such, four categories were determined: (1) animals/km/day – daily average of road-killed animals divided by 47 km (total kilometers of the stretch); (2) animals/km/month – daily average of road-killed animals multiplied by 30 (days of the month) and divided by 47 km; (3) animals/km/year – daily average of road-killed animals multiplied by 365 (days of the year) and divided by 47 km; and (4) roadkill rate – rate used to assess monthly variation, which was calculated based on the number of individuals run over per kilometer in the month.

Finally, we investigated whether the sample size was sufficient to ascertain the maximum number of species in the region based on species richness and individual abundance data to produce collector curves (1000 randomizations) for each taxonomic group using the EstimateS 9.1.0 software. Observed richness was compared to estimated richness determined using the nonparametric ACE, ICE, Chao 1 and 2, Jack 1 and 2 and Bootstrap estimators considering each group as well as curves considering all species (Colwell and Coddington 1994; Colwell *et al.* 2004; Magurran 2004; Colwell 2013).

RESULTS

A total of 464 road-killed vertebrates (131 and 333 in the dry and rainy seasons, respectively) were found during 45 field trips. Representatives of the class Amphibia were the most affected, with a total of 245 road-killed vertebrates corresponding to about 53% of all individuals, followed by reptiles (86 individuals;

18%), mammals (73 individuals; 16%) and birds (60 individuals; 13%) in the stretch studied (Figure 2A). The individuals belonged to two families, two genera and two species of amphibians (4% of total richness); nine families, 16 genera and 17 species of reptiles (37% of total richness); 12 families, 16 genera and 17 species of birds (37% of total richness); and nine families, 10 genera and 10 species of mammals (22% of total richness) (Figure 2B; Table 1). Most vertebrates corresponded to adult individuals (Figures 3, 4 and 5), except members of the families Iguanidae (Figure 3D) and Teiidae (Figure 3E), which included at least one juvenile.

Colubridae ($S = 8$), Thraupidae ($S = 4$), Boidae ($S = 2$), Cuculidae ($S = 2$), Columbidae ($S = 2$) and Felidae ($S = 2$) were the families with the largest number of species killed by collisions with motor vehicles (Table 1; Figures 3 and 4). These groups corresponded to about 16.8% of the vertebrate fauna studied (Table 1). The snake *Philodryas nattereri* was found in considerable abundance (Figure 4A). *Boiruna sertaneja* and *Boa constrictor* were respectively the only medium-sized and large snakes killed by motor vehicles. Venomous species were the colubrid *Oxybelis aeneus*, dipsadid *Boiruna sertaneja* and viperid *Crotalus durissus*.

The families Chelidae, Iguanidae, Teiidae, Troglodidae, Amphisbaenidae, Dipsadidae, Passeridae, Mimidae, Falconidae, Cathartidae, Mephitidae, Caviidae and Echimyidae each had one species affected (Table 1; Figures 3, 4 and 5), but each species had between two and 12 individuals killed by motor vehicles in the stretch of the PB-400 highway studied (Table 1). The families Boidae, Cuculidae, Colubridae, Felidae and Thraupidae had two to eight species affected (Table 1; Figures 3 and 4), but with a low number of individuals in each species killed, except for *Philodryas nattereri*. Leptodactylidae, Viperidae, Furnariidae, Thamnophilidae, Tyrannidae, Rallidae, Strigidae, Myrmecophagidae, Chlamyphoridae and Calitrichidae were the least affected families, each also with only one species and one individual recorded in this study (Table 1; Figures 3, 4 and 5). These groups constituted approximately 2.1% of the wild vertebrate fauna studied (Table 1).

Eight species of wild vertebrates accounted for about 80% of roadkill occurrences. Bufonidae was the most abundant family, but was represented only by *Rhinella* sp. (Figure 3A), with 244 road-killed individuals (Table 1: RA = 52.5; FOC = 33.3). Colubridae was the most biodiverse vertebrate group and also the second most abundant family ($N = 33$) in the study (Table 1). *Philodryas nattereri* was the colubrid with the highest number of individuals and was the fifth most recorded species (Table 1: $N = 20$; RA = 4.3; FOC = 17.7). Canidae was the third most abundant

group in this study (Table 1). The canid *Cerdocyon thous* (Figure 4Q) was the only species recorded and the second most affected, with a total of 28 dead individuals (Table 1: RA = 6.03; FOC = 24.4). Birds were the most representative in terms of richness, with a total of 17 species (Table 1). Passeriformes of the family Columbidae composed the fourth most abundant group of road-killed vertebrates in the study area. *Columbina picui* was the most representative columbid in number of dead individuals and was the third most affected species (Table 1: $N = 22$; RA = 4.7; FOC = 24.4). Didelphidae was the fifth most abundant group and the didelphid *Didelphis albiventris* (Figure 4N) was the fourth most affected species in the study area, with a total of 22 road-killed individuals (Table 1: RA = 4.7; FOC = 31.1). These families comprised 76.07% of the total abundance of individuals found killed by motor vehicles (Table 1).

Lizards corresponded to one of the most representative groups in terms of richness and occurrence in roadkill incidents (Table 1). The teiid *Salvator merianae* (Figure 3E) occupied in sixth place among vertebrates affected, with 12 individuals killed (Table 1: RA = 2.5; FOC = 20). Other lizard species included *Amphisbaena alba* (Figure 3G; Table 1: $N = 3$; RA = 0.6; FOC = 4.4), *Tropidurus hispidus* (Figure 3F; Table 1: $N = 3$; RA = 0.6; FOC = 4.4) and *Iguana iguana* (Figure 3D; Table 1: $N = 9$; RA = 1.9; FOC = 13.3), the first two of which had a small number of individuals killed (Table 1).

Mammals were the third most affected group in terms of species richness (Table 1). In contrast, taxa such as *Callithrix jacchus* (Figure 5E; Table 1: $N = 1$; RA = 0.2; FOC = 2.2), *Euphractus sexcinctus* (Figure 5B; Table 1: $N = 1$; RA = 0.2; FOC = 2.2), *Tamandua tetradactyla* (Figure 5A; Table 1: $N = 1$; RA = 0.2; FOC = 2.2), *Wiedomys pyrrhorhinos* (Figure 5D; Table 1: $N = 2$; RA = 0.4; FOC = 4.4) and *Conepatus semistriatus* (Figure 4R; Table 1: $N = 4$; RA = 0.8; FOC = 8.8) were among the wild vertebrates with the lowest numbers of roadkill/frequency of occurrence (Table 1).

A number of carcasses of medium-sized to large individuals were found on the highway struck by multiple vehicles and/or having been eaten by scavengers. In such cases, the hide or feathers helped in the identification. Snakes and amphisbaenians (49 individuals – 10.56% of the sample) were among the slow-moving vertebrates; amphibians and turtles (257 individuals – 55.38% of the sample) belonged to the functional group of intermediate-moving vertebrates; and lizards, mammals and birds (133 individuals – 34.38% of the sample) were among the taxa with fast-moving behavior.

Regarding conservation status, at least two species in this study were categorized on some concerning le-

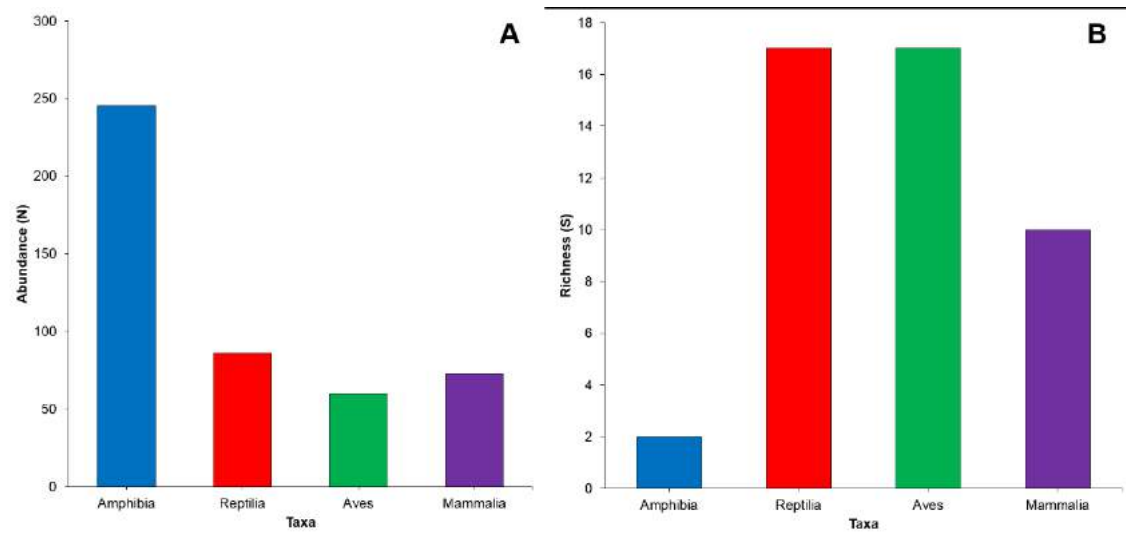


Figure 2. Road-killed vertebrates found between March 2020 and May 2021 along a stretch of the PB-400 (red line) in the municipalities of Cajazeiras and Monte Horebe, state of Paraíba, northeastern Brazil: **A.** Total number of individuals; **B.** Species richness.

vel of threat to their populations (Figure 6). The first, *Herpailurus yagouaroundi* (Figure 4O), with two roadkill records (Table 1: RA = 0.4; FOC = 4.4), is considered to be “least concern” by the IUCN, but “vulnerable” in Brazil (Table 1). The second, *Leopardus tigrinus* (Figure 4P), with one roadkill occurrence (Table 1: RA = 0.2; FOC = 2.2), is “vulnerable” and “endangered” on the international and national levels (Table 1), respectively. All amphibians, birds and reptiles found in this study belong to the “not rated” or “least concern” categories (Table 1; Figure 6). *Cercodyon thous* (Table 1: N = 28; RA = 6.03; FOC = 24.4), *Didelphis albiventris* (Table 1: N = 22; RA = 4.7; FOC = 31.1), *Cavia aperea* (Figure 5C; Table 1: N = 11; RA = 2.3; FOC = 15.5), *Conepatus semistriatus*, *Wiedomys pyrrhorhinos*, *Tamandua tetradactyla*, *Euphractus sexcinctus* (Table 1: N = 1; RA = 0.2; FOC = 2.2) and *Callithrix jacchus* are also listed as “not rated” or “least concern” in terms of international and national conservation status (Table 1). No species found in this study were considered “constant” (FOC > 50%); *Rhinella* sp. and *Didelphis albiventris* were categorized as “accessory” (25% < FOC < 50%) and most (44 species) were categorized as “accidental” throughout the sampling period (FOC < 25%) (Table 1).

The systematic monitoring of the highway revealed daily rate of 1.017, monthly rate of 30.93 and annual rate of 371 road-killed wild vertebrates. The 47-km stretch of the PB-400 highway sampled had

a mortality rate of 0.021 animals/km/day, 0.649 animals/km/month and 7.89 animals/km/year. The average rate of wild vertebrate roadkill per kilometer was 0.109 individuals.

The species accumulation curves in the present study continued to rise, showing no sign of approaching to an asymptote, clearly evidencing the need for greater sampling efforts to find more species run over on the 47 km stretch of the PB-400 highway studied (Figure 7). Table 3 and Figure 7 show that all richness estimators had higher values compared to observed richness. The species accumulation curves tended to rise approximately parallel with the observed richness curve considering the Jack 1, Jack 2 and Bootstrap estimators. The graphic analysis of the curves shows that Chao 2 and Jack 2 were the main estimators for road-killed wild vertebrate fauna considering total richness (Figure 7A; Table 3: 87.13 and 82.94, respectively) and the richness of reptiles (Figure 7C; Table 3: 27.28 and 29.62, respectively). Chao 1 and Chao 2 stood out as the estimators with the most expressive values for birds (Figure 7C; Table 3: 34.7 and 34.63, respectively). ICE estimated the most species richness for mammals and was one of the estimators that differed least from observed richness for all groups studied (Figure 7E; Table 3: 17.75). Among the estimators, ACE, ICE, Chao 1 and Chao 2 corroborated observed richness for Amphibia and Jack 1 and Bootstrap had values very close to observed richness for this group (Figure 7; Table 3).

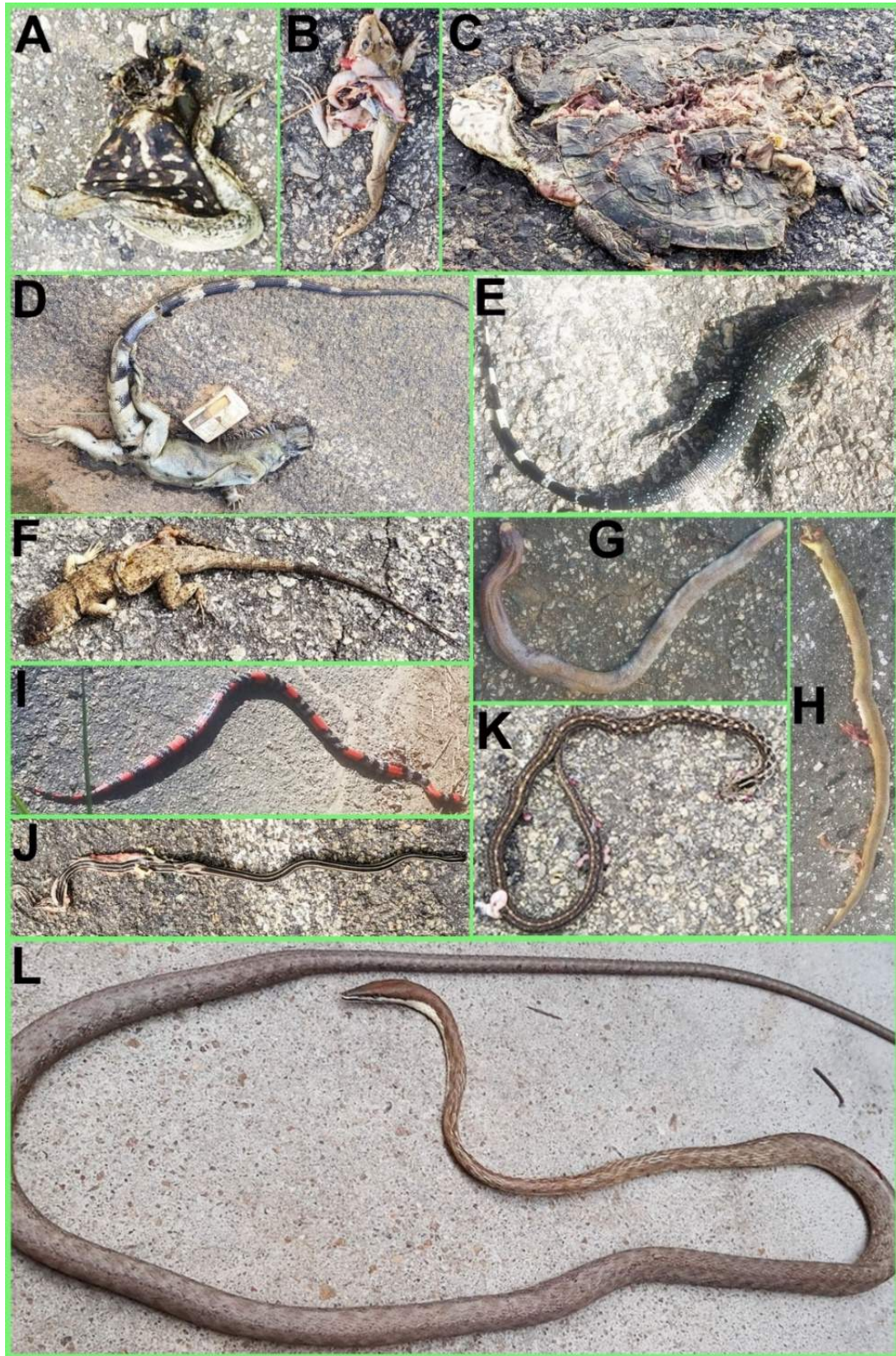


Figure 3. Amphibians and reptiles run over on the PB-400 highway in the state of Paraíba, northeastern Brazil: **A.** *Rhinella* sp.; **B.** *Leptodactylus macrosternum*; **C.** *Phrynops geoffroanus*; **D.** *Iguana iguana*; **E.** *Salvator merianae*; **F.** *Tropidurus hispidus*; **G.** *Amphisbaena alba*; **H.** *Erythrolamprus poecilogyrus*; **I.** *Oxyrhopus trigeminus*; **J.** *Lygophis dilepis*; **K.** *Thamnodynastes* sp.; **L.** *Oxybelis aeneus*.



Figure 4. Reptiles, birds and mammals run over on the PB-400 highway in the state of Paraíba, northeastern Brazil: **A.** *Philodryas nattereri*; **B.** *Boa constrictor*; **C.** *Epicrates assisi*; **D.** *Volatinia jacarina*; **E.** *Paroaria dominicana*; **F.** *C. talpacoti*; **G.** *Pseudoseisura cristata*; **H.** *Empidonomus varius*; **I.** *Mimus saturninus*; **J.** *Caracara plancus*; **K.** *Gallinula galeata*; **L.** *Crotophaga ani*; **M.** *Athene cunicularia*; **N.** *Didelphis albiventris*; **O.** *Herpailurus yagouaroundi*; **P.** *Leopardus tigrinus*; **Q.** *Cercocyon thous*; **R.** *Conepatus semistriatus*.

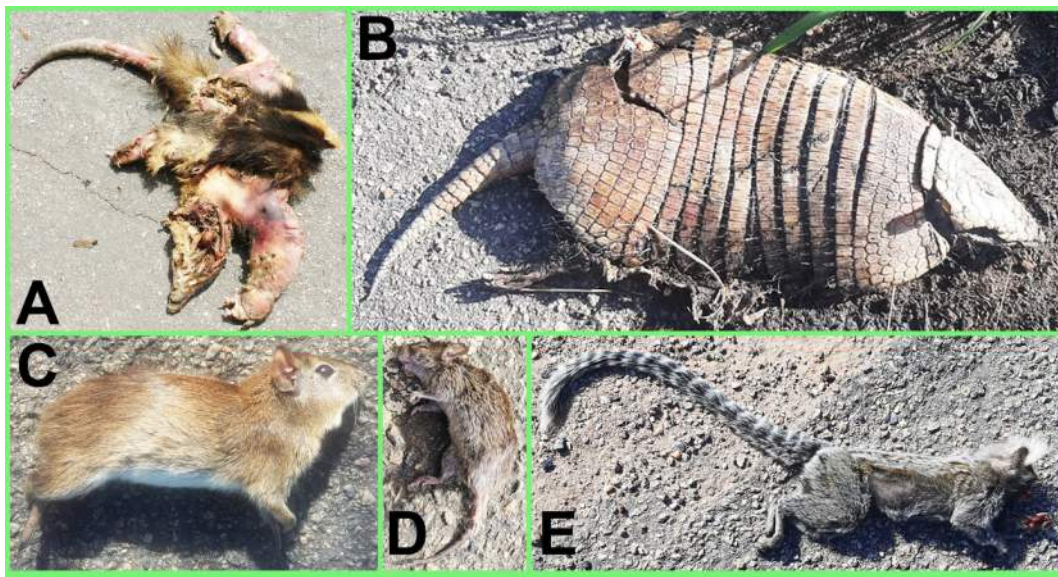


Figure 5. Mammals run over on the PB-400 highway in the state of Paraíba, northeastern Brazil: **A.** *Tamandua tetradactyla*; **B.** *Euphractus sexcinctus*; **C.** *Cavia aperea*; **D.** *Wiedomys pyrrhorhinos*; **E.** *Callithrix jacchus*.

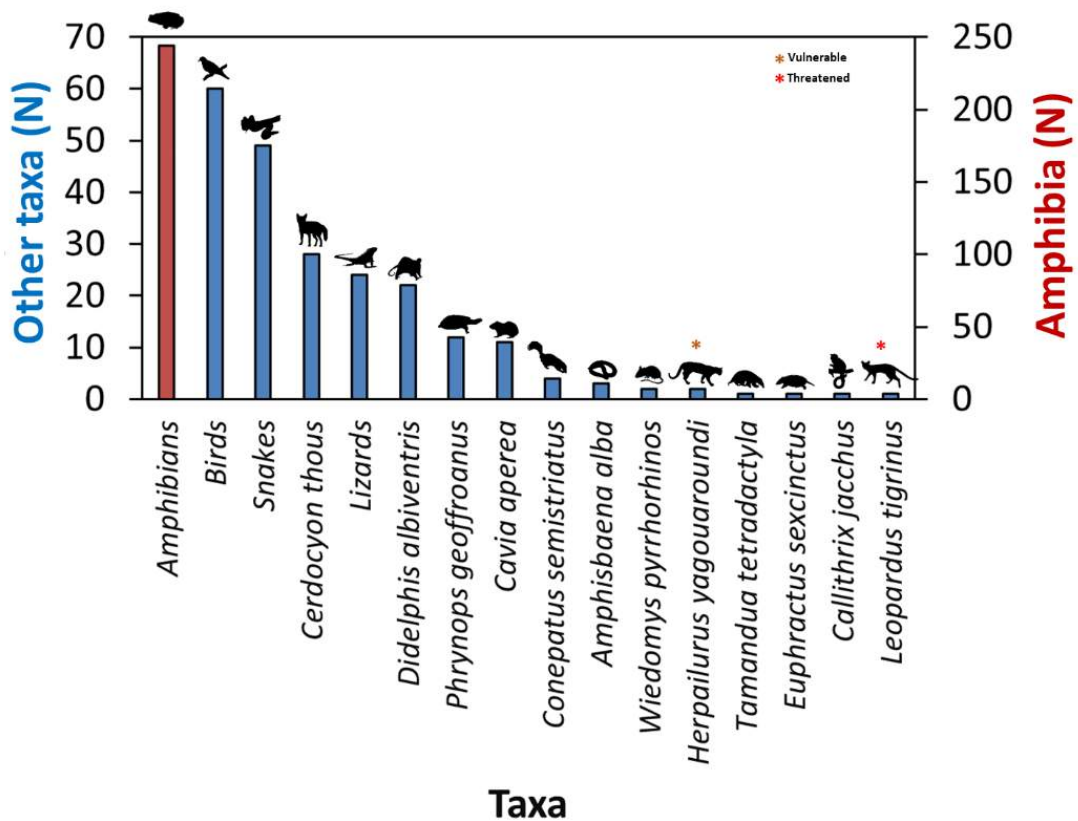


Figure 6. Abundance and conservation status of some roadkill wild vertebrates found between the municipalities of Cajazeiras and Monte Horebe, state of Paraíba, northeastern Brazil. Silhouettes: Arthur Albuquerque Pereira.

Table 1. Richness and abundance of wild vertebrate roadkill on a stretch of the PB-400 highway between the municipalities of Cajazeiras and Monte Horebe, state of Paraíba, northeastern Brazil. Abbreviations: N = number of individuals; RA = relative abundance; FOC = frequency of occurrence; ID = insufficient data; LC = least concern; VU = vulnerable; EN = endangered.

Taxa	Common names	N	RA (%)	FOC (%)	IUCN/ICMBio
Amphibia					
Anura					
Bufonidae					
<i>Rhinella sp.</i>	South American toads	244	52.5	33.3	LC/LC
Leptodactylidae					
<i>Leptodactylus macrosternum</i> Miranda-Ribeiro, 1926	Ditch frogs or white-lipped frogs	1	0.2	2.2	LC/ID
Reptilia					
Testudines					
Chelidae					
<i>Phrynops geoffroanus</i> (Schweigger, 1812)	Geoffroy's side-necked turtle or Geoffroy's toadhead turtle	12	2.5	20	LC/LC
Squamata					
Sauria					
Iguanidae					
<i>Iguana iguana</i> (Linnaeus, 1758)	American iguana or the common green iguana	9	1.9	13.3	LC/LC
Teiidae					
<i>Salvator merianae</i> AM.C. Duméril & Bibron, 1839	Argentine giant tegu or the black and white tegu	12	2.5	20	LC/LC
Tropiduridae					
<i>Tropidurus hispidus</i> (Spix, 1825)	Calango or Peter's lava lizard	3	0.6	4.4	LC/LC
Amphisbaenidae					

<i>Amphisbaena alba</i> Linnaeus, 1758	Red worm lizard	3	0.6	4.4	LC/LC
Snakes					
Colubridae					
<i>Erythrolamprus viridis</i> (Günther, 1862)	Crown ground snake	1	0.2	2.2	LC/LC
<i>E. poecilogyrus</i> (Wied-Neuwied, 1825)	Donkey's hoof	2	0.4	2.2	LC/LC
<i>Oxyrhopus trigeminus</i> Duméril, Bibron & Duméril, 1854	Brazilian false coral snake	5	1.07	11.1	LC/LC
<i>Lygophis dilepis</i> Cope, 1862	Shoelace snake	2	0.4	4.4	LC/LC
<i>Thamnodynastes</i> sp.	Jararaquinha	1	0.2	2.2	LC/LC
<i>Oxybelis aeneus</i> Wagler, 1824	Brown vinesnake	1	0.2	2.2	LC/LC
<i>Spilotes pullatus</i> (Linnaeus, 1758)	Chicken snake	1	0.2	2.2	LC/LC
<i>Philodryas nattereri</i> (Steindachner, 1870)	Run-of-fieldsnake	20	4.3	17.7	LC/LC
Dipsadidae					
<i>Boiruna sertaneja</i> Zaher, 1996	Black snake	9	1.9	13.3	LC/LC
Viperidae					
<i>Crotalus durissus</i> Linnaeus, 1758	Cascabel rattlesnake	1	0.2	2.2	LC/LC
Boidae					
<i>Boa constrictor</i> Linnaeus, 1758	Red-tailed boa	5	1.07	11.1	LC/LC
<i>Epicrates assisi</i> Machado, 1945	Rainbow boa	1	0.2	2.2	LC/LC
Aves					
Passeriformes					
Thraupidae					
<i>Volatinia jacarina</i> (Linnaeus, 1766)	Blue-black grassquit	4	0.8	6.6	LC/LC
<i>Paroaria dominicana</i> (Linnaeus, 1758)	Red-cowled cardinal	1	0.2	2.2	LC/LC
<i>Coereba flaveola</i> (Linnaeus, 1758)	Bananaquit	1	0.2	2.2	LC/LC
<i>Coryphospingus pileatus</i> (Wied, 1821)	Pileated finch	1	0.2	2.2	LC/LC
Columbidae					
<i>Columbina picui</i> (Temminck, 1813)	Picui dove	22	4.7	24.4	LC/LC

<i>C. talpacoti</i> (Temminck, 1810)	Ruddy ground-dove	4	0.8	6.6	LC/LC
Passeridae					
<i>Passer domesticus</i> (Linnaeus, 1758)	House sparrow	4	0.8	8.8	LC/LC
Furnariidae					
<i>Pseudoseisura cristata</i> (Spix, 1824)	Caatinga cachalote	1	0.2	2.2	LC/LC
Thamnophilidae					
<i>Taraba major</i> (Vieillot, 1816)	Great antshrike	1	0.2	2.2	LC/LC
Tyrannidae					
<i>Empidonomus varius</i> (Vieillot, 1818)	Variegated flycatcher	1	0.2	2.2	LC/LC
Mimidae					
<i>Mimus saturninus</i> (Lichtenstein, 1823)	Chalk-browed mockingbird	3	0.6	6.6	LC/LC
Falconiformes					
Falconidae					
<i>Caracara plancus</i> (Miller, 1777)	Southern caracara	5	1.07	11.1	LC/LC
Gruiformes					
Rallidae					
<i>Gallinula galeata</i> (Lichtenstein, 1818)	Common gallinule	1	0.2	2.2	LC/LC
Cathartiformes					
Cathartidae					
<i>Coragyps atratus</i> (Bechstein, 1793)	American black vulture	7	1.5	8.8	LC/LC
Cuculiformes					
Cuculidae					
<i>Guira guira</i> (Gmelin, 1788)	Guira cuckoo	1	0.2	2.2	LC/LC
<i>Crotophaga ani</i> Linnaeus, 1758	Smooth-billed ani	2	0.4	4.4	LC/LC
Strigiformes					
Strigidae					
<i>Athene cunicularia</i> (Molina, 1782)	Burrowing owl	1	0.2	2.2	LC/LC

Mammalia

Didelphimorphia

Didelphidae

Didelphis albiventris Lund, 1840 White-eared opossum 22 4.7 31.1 LC/LC

Carnivora

Felidae

Herpailurus yagouaroundi (É. Geoffroy Saint-Hilaire, 1803) Jaguarundi 2 0.4 4.4 LC/VU

Leopardus tigrinus Schreber, 1775 Northern Tiger Cat 1 0.2 2.2 VU/EN

Canidae

Cerdocyon thous Linnaeus, 1766 Crab-eating fox 28 6.03 24.4 LC/LC

Mephitidae

Conepatus semistriatus Boddaert, 1785 Striped hog-nosed skunk 4 0.8 8.8 LC/LC

Pilosa

Myrmecophagidae

Tamandua tetradactyla (Linnaeus, 1758) Southern tamandua 1 0.2 2.2 LC/LC

Cingulata

Chlamyphoridae

Euphractus sexcinctus (Linnaeus, 1758) Yellow armadillo 1 0.2 2.2 LC/LC

Rodentia

Caviidae

Cavia aperea Erxleben, 1777 Brazilian guinea pig 11 2.3 15.5 LC/LC

Echimyidae

Wiedomys pyrrhorhinos (Wied-Neuwied, 1821) Red-nosed mouse 2 0.4 4.4 LC/LC

Primates

Callitrichidae

Callithrix jacchus (Linnaeus, 1758) Common marmoset 1 0.2 2.2 LC/LC

DISCUSSION

The present study is a comprehensive survey of wild vertebrates run over on highways in the semiarid region of Brazil and reveals a diversity of fauna represented mainly by mammals, reptiles and birds, including species considered vulnerable and endangered according to the IUCN (2023) and ICMBio (2022). The intense traffic of medium-sized and large vehicles is the main cause wild roadkill on highways throughout the country (Rosa and Mauhs 2004; Andrade and Moura 2011; Silva *et al.* 2011; Oliveira and Silva 2012; Weiss and Viana 2012; Pinheiro and Turci 2013; Neto *et al.* 2015; Orlandin *et al.* 2015; Gordilho *et al.* 2017; Gomes *et al.* 2019), including those located in the semiarid region (Ramos-Abrantes *et al.* 2018; Cabral *et al.* 2019). The present study was conducted in the westernmost portion of the state of Paraíba, which has intense traffic between the municipalities of Cajazeiras, São José de Piranhas and Monte Horebe, especially towards Cajazeiras (municipality with greater economic activity and availability of services). Therefore, this stretch of the study area can be recognized *a priori* as one of the main stretches in the high semiarid region of the state of Paraíba with deaths.

Brazilian highways are surrounded by a mixture of areas modified by human activities and few preserved areas. Wild vertebrates are attracted to the road by vehicle sounds and lights (Omena Junior *et al.* 2012; Almeida *et al.* 2016), dropped/discarded food (Hengemühle 2008; Dupont and Lobo 2012; Almeida *et al.* 2016), the asphalt for purposes of thermoregulation (Almeida *et al.* 2016; Carmo *et al.* 2018) and putrefying carcasses (Omena Junior *et al.* 2012; Carvalho *et al.* 2015; Orlandin *et al.* 2015; Corrêa *et al.* 2017). Many wild vertebrates also move to the edge of the forest and are run over when crossing roads in search of food in agricultural areas (Orlandin *et al.* 2015) and sources of water (Omena Junior *et al.* 2012; Almeida *et al.* 2016). During fieldwork, the first author of this article viewed some of the aspects mentioned above, such as the American black vulture (*Coragyps atratus*), southern caracara (*Caracara plancus*) and white-eared opossum (*D. albiventris*) feeding on carrion; crab-eating fox (*C. thous*) and *D. albiventris* looking to feed on the highway during the day and attracted by vehicle sounds and lights at night; and snakes and lizards performing thermoregulation.

Species richness and the number of individuals of wild fauna killed by motor vehicles vary in accordance with the size of the area covered, monitoring time and environmental characteristics of the study area in different regions of the country. The diversity of vertebrates run over in the present study was much greater than that fauna reported in surveys conducted

on other highways in northeastern Brazil. In a six-month survey of wild fauna run over on two highways (BR-343 and 402) in the state of Piauí, Veras *et al.* (2016) found individuals from all vertebrate groups, the most affected of which were amphibians (75 individuals), followed by birds (22 individuals), reptiles (7 individuals) and mammals (5 individuals). Almeida *et al.* (2016) monitored amphibians and reptiles run over on a stretch of the BR-232 highway in the state of Pernambuco from 2009 to 2011, sampling a total of 89 individuals represented by two amphibian species ($n = 14$) and 22 reptile species ($n = 75$). In a 12 month survey, Ramos-Abrantes *et al.* (2018) monitored wild roadkill on a stretch of the BR-230 highway between the municipalities of Campina Grande and Patos in the state of Paraíba, finding 188 vertebrates, the most affected of which were mammals (108 individuals), followed by reptiles ($n = 37$), birds ($n = 27$) and amphibians ($n = 16$). The richness and abundance data from the present study approaches or surpasses figures reported in other road kill surveys conducted on highways in South America (see Pinowski 2005; Filius *et al.* 2020; Rivera *et al.* 2022).

Eight species stood out due to the high number of individuals sampled accounting for about 80% of roadkill incidents. The amphibian *Rhinella* sp. was among the most affected vertebrates in the present study. Pinheiro and Turci (2013), Almeida *et al.* (2016) and Ramos-Abrantes *et al.* (2018) also recognized amphibians of the genus *Rhinella* among the individuals with the highest number of roadkills in surveys carried out on highways in the states of Acre, Pernambuco and Paraíba, respectively. Intrinsic factors to the bioecology of the group, such as the small size, slow locomotion and dispersal tendencies related to reproduction and the spatial distribution of resources, strongly influence the high mortality rates due to motor vehicles on highways and roads (Trombulak and Frissel 2000; Coffin 2007; Andrews *et al.* 2008).

Some studies report that mammals are the vertebrates most run over on highways (Rosa and Mauhs 2004; Cunha *et al.* 2010; Saranholi *et al.* 2016; Ramos-Abrantes *et al.* 2018). The crab-eating fox, *Cerdocoyon thous*, was another species that stood out due to the number of road-killed individuals. This mammal is often reported in monitoring studies of wild fauna run over on roads and highways in the *Cerrado* (savanna) and *Caatinga* (semiarid) biomes of Brazil (Cunha *et al.* 2010; Oliveira *et al.* 2015; Barros *et al.* 2016; Ramos-Abrantes *et al.* 2018). The typically nocturnal foraging habit and glare of vehicle headlights are predominant factors in the occurrence of road-killed individuals of this species (Wozencraft 2005; Barthelmess and Brooks 2010). Dr. Silvio F. B. Lima (personal observations, 2021) observed three individuals of *C. thous* on different occasions running

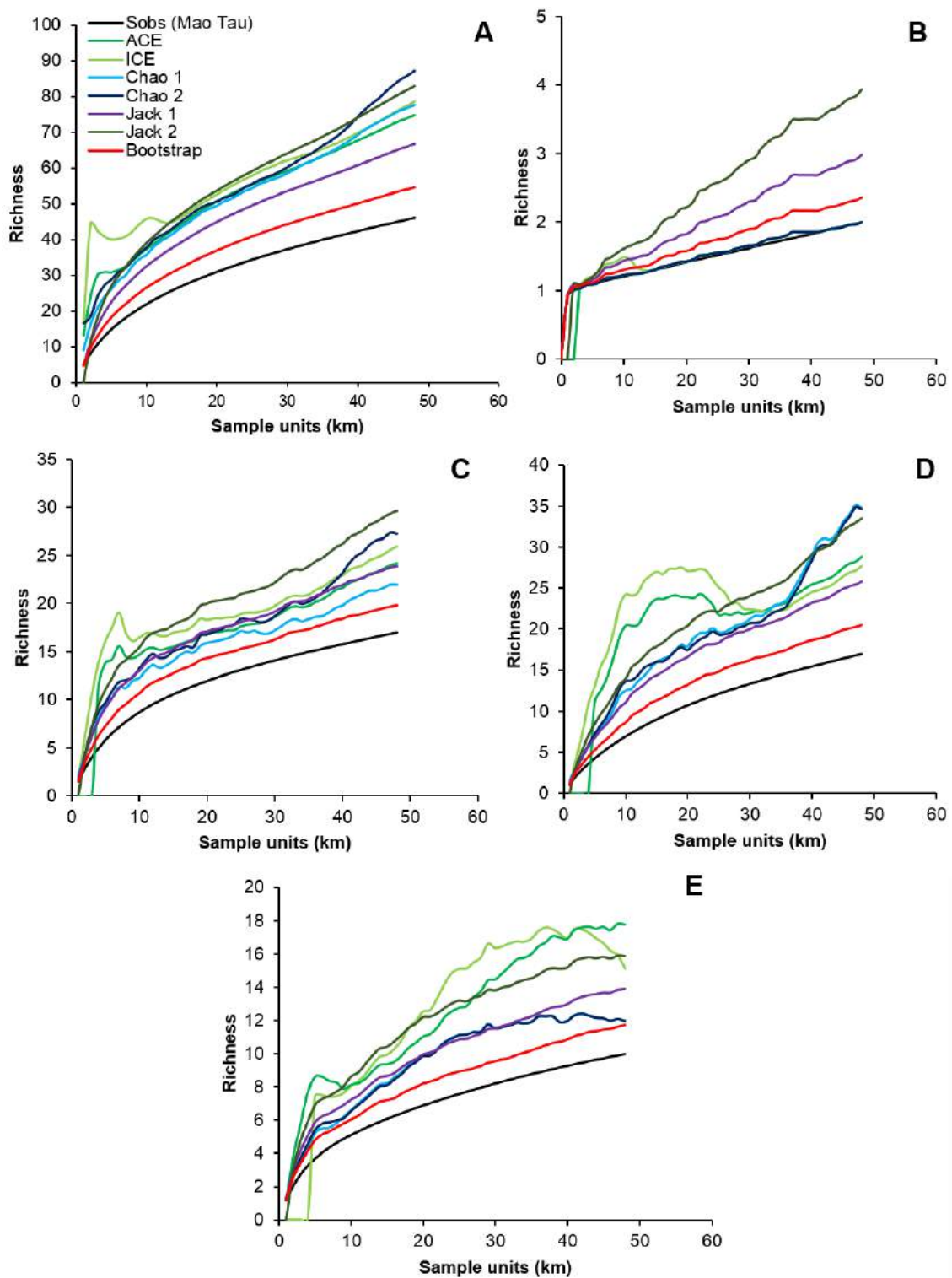


Figure 7. Species accumulation curves based on seven nonparametric richness estimators for wild vertebrate fauna run over along a 47-km stretch of the PB-400 highway between the municipalities of Cajazeiras and Monte Horebe (state of Paraíba, northeastern Brazil) between March 2020 and May 2021. Observed richness (Sobs (Mao Tau) and estimated richness for: A. All taxa, B. Amphibia, C. Reptilia, D. Aves and E. Mammalia.

alongside the PB-230 highway (Paraíba, northeastern Brazil) at night. The day after one sighting, an in-

Table 3. Values of richness estimators for wild vertebrate fauna run over along a 47-km stretch of the PB-400 highway between the municipalities of Cajazeiras and Monte Horebe, state of the Paraíba, northeastern Brazil.

Estimators	Total	Amphibia	Reptilia	Aves	Mammalia
Sobs (Mao Tao)	46.00	2.00	17.00	17.00	10.00
ACE	74.77	2.00	24.17	28.81	15.14
ICE	78.64	2.00	25.89	27.71	17.75
Chao 1	77.67	2.00	21.94	34.70	11.97
Chao 2	87.13	2.00	27.28	34.63	11.96
Jack 1	66.56	2.98	23.85	25.81	13.92
Jack 2	82.94	3.94	29.62	33.50	15.87
Bootstrap	54.43	2.36	19.80	20.54	11.73

dividual was found run over on the same stretch of highway.

Columbina picui was the most affected bird species, with 22 individuals killed on the stretch of highway surveyed. This and other small birds, such as those found in the present study, are generally run over due to their small size, which does not favor visualization by drivers, as well as the habit of foraging in adjacent crops and the occurrence of forest fragments, favoring the occurrence of individuals on roads and highways (Ramos *et al.* 2011; Husby 2016). In contrast, *Coragyps atratus* and *Caracaca plancus* are large birds, but are also highly susceptible to roadkill due to their carrion-eating habits. These species feed on putrefying vertebrates that had been victimized in motor vehicle accidents, which increases the likelihood of also being run over on roads and highways (Taylor and Goldingay 2004; Lambertucci *et al.* 2009; Kociolek *et al.* 2015).

Didelphis albiventris is a mammal of considerable ecological plasticity (Cerqueira and Tribe 2008; Almeida *et al.* 2008; Nascimento *et al.* 2019; Dias *et al.* 2020). Individuals of this species are among the most common mammals in roadkill surveys due to the fact that they can easily inhabit different phytogeographic domains, such as preserved areas, highly impacted areas, forest fragments as well as highly anthropized rural and urban zones around roads and highways (Passamani 2000; Rosa and Mauhs 2004; Rossi *et al.* 2006; Corrêa *et al.* 2017).

Individuals of the species *Cavia aperea* also were among the mammals studied. This species has been reported with considerable abundance in other roadkill surveys (Corrêa *et al.* 2013; Corrêa *et al.* 2017). The foraging behavior of these animals, especially in vegetation adjacent to the road, increases the susceptibility to accidents and deaths by motor vehicles

(Silva 1994; Deffaci *et al.* 2016).

Some studies report that reptiles constitute the predominant group killed on highways (Almeida *et al.* 2016; Braz and França 2016; Filius *et al.* 2020). Snakes were relatively abundant in the present survey, especially members of the family Colubridae, which pose no risk to humans. Some species in this and other surveys, such as *Amphisbaena alba*, *E. poecilogyrus*, *O. trigeminus*, *L. dilepis*, *Thamnodynastes* sp., *O. aeneus*, *P. nattereri*, *B. constrictor* and *E. assisi* are highly susceptible to roadkill due to their size, immobility during thermoregulation and/or slow mode of locomotion when capturing prey on roads and highways, which facilitates the occurrence of accidents with motor vehicles. Moreover, some drivers may intentionally run over animals considered dangerous and/or abhorrent, especially snakes (Rudolph *et al.* 1999; Haxton 2000; Rodrigues 2002; Turci and Bernarde 2009; Selvan *et al.* 2012; Vale 2017). The death of lizards, such as *Salvator merianae*, *Iguana iguana* and *Tropidurus hispidus* and the amphisbaena *Amphisbaena alba*, can be explained by biological factors involving thermoregulation and the generalist feeding of individuals on the road (Haxton 2000; Selvan *et al.* 2012; Almeida *et al.* 2016). According to Braz and França (2016), snakes of the genus *Crotalus* and *Oxyrhopus*, which employ a sit-and-wait foraging strategy, and slow-moving lizards, such as *Amphisbaena*, are often struck by vehicles. Furthermore, members of these genera are nocturnal terrestrial snakes (Pereira Filho *et al.* 2021) susceptible to being run over, mainly when crossing roads and highways in search of prey. *Phrynosoma geoffroanus* was the seventh most affected taxon in the present study. This species is found in limnetic ecosystems alongside the highway, such as rivers, streams and lakes, including variably polluted environments in rural and urban areas, ma-

king death by roadkill a common occurrence for this species (Martins *et al.* 2010; Santana *et al.* 2020).

Herpailurus yagouaroundi and *Leopardus tigrinus* were the only species found in this study that have a concerning level of threat to their populations. These mammals are commonly reported in road accidents (Cherem *et al.* 2007; Weiss and Vianna 2012; Preuss 2015). The IUCN categorizes the jaguarundi, *H. yagouaroundi* as “least concern” on the international level (Caso *et al.* 2015), but this species is considered “vulnerable” in Brazil (ICMBio 2022). The oncilla, *L. tigrinus*, is categorized as “vulnerable” on the international level (Payan and Oliveira 2016) and is considered “endangered” in Brazil (ICMBio 2022). The low population density of these species makes accidents with motor vehicles a determining factor of the decline in the number of individuals in certain regions of the country. Indeed, roadkill constitutes an important contributing factor to the extinction of rare species, those at risk of extinction and those with K-strategist population dynamics (Almeida *et al.* 2013; Barros *et al.* 2016).

The mortality rate in this study was estimated at 0.021 animals/km/day, which was lower than the rates reported in the surveys by Bager and Fontoura (2013) along the 15.7 km of the Taim Ecological Station in the state of Rio Grande do Sul (Brazil) from 1995 to 2002 (0.153); Filius *et al.* (2020) along 1590 km in Tena Canton, capital of the Amazonian province of Napo, Ecuador, from September to December 2017 (0.75); and Carvalho-Roel *et al.* (2021) along 47 km of the GO-341 highway tangent to Emas National Park in the state of Goiás (Brazil) from December 2017 to January 2018 (0.03). The mortality rate of 0.649 animals/km/month of the present study was also lower than the rate reported by Carvalho-Roel *et al.* (2019) on the stretch of the highway BR-050 in the state of Minas Gerais (Brazil) from April 2012 to March 2013 (0.98). The mortality rate of 7.89 animals/km/year in the present study was higher than that reported in a survey conducted by Cunha *et al.* (2010) on a stretch of 216 km between the cities of Goiânia and Iporá in the state of Goiás (Brazil) from 2004 to 2005 (0.014); and by Saranholi *et al.* (2016) on a stretch of 12 km around a protected area of the *Cerrado* biome in the state of São Paulo (Brazil) from 2012 to 2013 (1.46). In contrast, the annual mortality rate per km in the present study was lower than that reported by Carvalho-Roel *et al.* (2019) (11.90). The average wild vertebrate roadkill rate per kilometer between the municipalities studied (0.109 individuals) was much higher than the rate reported in surveys conducted on highways in the state of Paraíba (see Sousa and Miranda 2010; Junior *et al.* 2012; Ramos-Abrantes *et al.* 2018; Cezar *et al.* 2021).

Cavia aperea, *C. talpacoti*, *D. albiventris*, *E. sex-*

cinctus, *S. merianae* and *G. galeata* are among the species identified in the present study with nutritional importance for human populations in the Brazilian semiarid region (Bezerra *et al.* 2012, 2013; Ferreira *et al.* 2014; Alves *et al.* 2016; Alves & Policarpo 2017). However, there are no observations or reports of people collecting individuals of such roadkilled species in the study area for consumption. Among the taxa studied, only *E. sexcinctus* appeared in a study on human consumption of meat from roadkilled animals in the southwestern Amazon (Oliveira *et al.* 2023).

Despite the substantial species richness and number of individuals found in this study, we recognize that the diversity is somewhat underestimated and that a greater monthly sampling effort is required to find more road-killed animals on the highway before they are removed freshly dead or putrefying by other vertebrates. Indeed, increasing the sampling effort is the only viable option for encountering more taxa before individuals are removed from roads and highways (Antworth *et al.* 2005; Elzanowski *et al.* 2009).

CONCLUSION

The present study recorded a substantial number of species and individuals of amphibians, reptiles, mammals and birds as roadkill on a stretch of the PB-400 highway located in the semiarid region of Brazil. The loss of individuals by roadkill has negatively impacted the structure of the terrestrial vertebrate community in the phytogeographic domain of the *Caatinga* biome for many years causing a severe loss of wildlife biodiversity. Future conservation strategies, such as the construction of ecological corridors, underground tunnels, signs for drivers, etc., urgently need to be implemented for all groups of animals, including those vertebrates supposedly least affected to mitigate the staggering loss of biodiversity caused by the construction and operation of roads and highways around the world.

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DATA AVAILABILITY

The authors confirm that the data supporting the findings of this study are available within the article.

CONFLICT OF INTEREST

The authors declare that they have no competing interest.

CONTRIBUTION STATEMENT

ELF and SFBL conceived the research ideas and designed the study.

ELF, SFBL, JWSS and PRM performed data analysis.

All authors wrote and approved the final manuscript.

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