An Acad Bras Cienc (2022) 94(Suppl. 3): e20220041 DOI 10.1590/0001-3765202220220041
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ECOSYSTEMS

Differences in Wildlife Roadkill Related to Landscape Fragmentation in Central Brazil

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Abstract: The interaction between animal movement and roads is pervasive, but little is known of the effects of the land-use patterns in roadside landscapes on roadkill events. Here, we compared wildlife roadkill along two road stretches that cross landscapes with different land-use patterns, including the presence of protected areas in Central Brazil. Sampling was conducted in 2017 and 2018 in two seasons (dry and rainy). We expected roadkill events to be more frequent bordering the protected area. Roadkill occurred more frequently in the rainy season in the unprotected landscape. Birds were most frequently recorded in the unprotected (44%, n = 76) than in the protected landscape (37%, n = 48). The least recorded group in the unprotected landscape was Squamata (11%, n = 18), while mammals were less detected in the protected landscape (14%, n = 18). Classes 'agriculture' and 'savanna' were related to amphibian roadkill numbers. For Squamata, we observed the effect of the presence of forests in the protected landscape. Bird roadkill was affected by protection level, while the presence of pasture and the level of protection explained mammal roadkill. Differences in roadkill patterns reinforce the need for long-term management of this source of mortality for the Cerrado fauna.

Key words: Cerrado, protected areas, seasonality, vehicle collision, vertebrates.

INTRODUCTION

Road infrastructure is a ubiquitous and transforming element in a landscape, causing considerable impacts on the environment and wildlife (Neumann et al. 2012, Rosa et al. 2018). Besides causing roadkill directly, roads and highways are an anthropogenic source of spatial heterogeneity (Laurance et al. 2009, Munro et al. 2018), causing habitat loss, fragmentation, changes in ecosystem water flux (Jaarsma & Willems 2002, Coffin 2007, Strevens et al. 2008, Ascensão et al. 2013, Walker et al. 2013), and altering the relief configuration of the landscapes (Trombulak & Frissell 2000). Therefore, the main objective of Road Ecology is to understand the environmental impacts related to road infrastructure, while seeking to mitigate these effects (Forman & Alexander 1998, Coffin 2007). The extent and frequency of these impacts are often related to landscape patterns, as well as species traits (Laurance et al. 2009, Simmons et al. 2010, Ascensão et al. 2013, Galetti et al. 2013).

The resulting degraded environments along roads can attract species with higher environmental plasticity while undermining landscape use by more sensitive and habitat specialist species (Beisiegel et al. 2013, Rosa et al. 2018). Generalist species are attracted to roads and highways due to their serving as high mobility connectors (paths without obstacles), as a refuge (drains, bridges, tunnels, etc), as a source of dietary resources (such as seeds, grasses, and carcasses) (Harris & Scheck 1991, Forman & Alexander 1998, Le Viol et al. 2012), and for thermoregulation (Colino-Rabanal & Lizana 2012, Camacho 2013, Hill et al. 2021).

These attractive elements, located on or by the side of roads, can function as ecological traps due to the risk of vehicle collision (Harris & Scheck 1991, Coffin 2007). Therefore, roads may have deep impacts on wildlife mortality, and serve as population sinks in the landscape (Clevenger et al. 2001, Gunson et al. 2012, Abra et al. 2021). These impacts can make roads a severe threat to wildlife worldwide, with the potential to modify the structure and composition of biological communities (Gaddy & Kohlsaat 1987, Forman & Alexander 1998, Munro et al. 2018).

The permanence of dead animals on the roads or road shoulders after a vehicle-animal collision allows the direct observation and measurement of roadkill events, and subsequently the analysis of roadkill patterns and their underlying mechanisms (Clevenger et al. 2001, Ascensão et al. 2013, Galetti et al. 2013). Roadkill patterns and their impacts on animal populations are likely affected by land cover in the surrounding landscapes (Forman & Alexander 1998, Coffin 2007, Benítez-López et al. 2010). Protected areas and their surroundings, for example, are critical environments which need conservation actions related to roadkill, and several studies in Road Ecology take place along roads crossing or bordering protected areas (Garriga et al. 2012, D'Amico et al. 2015, Braz & França 2016). Animal abundance and richness are expected to be higher within protected areas in comparison to human-altered landscapes so that protected areas should act as a source of animals dispersing through the landscape (Carranza et al. 2014, Gray et al. 2016). Some studies have shown that higher frequencies of roadkill events are observed around nature reserves with higher levels of protection (Garriga et al. 2012, Kioko et al. 2015).

Protected areas, however, are just one element in complex human-dominated landscapes, which present other land-use classes, circumstantially crossed by roads and highways. In fragmented landscapes, the effects of roads can act synergistically with other anthropogenic impacts, such as habitat loss. Therefore, the interaction between animal movements and roadkill events in fragmented landscapes is largely pervasive for animal populations (Van der Ree et al. 2011, Magioli et al. 2016, Rosa et al. 2018), but little is known of the effects of protected areas and unprotected landscapes on roadkill patterns.

The Brazilian savanna (Cerrado biome), located in Central Brazil, is the largest open vegetation domain in South America (ca. 2 million Km²), and the second-largest biome in Brazil (covering approximately 24% of the country), after the Amazon forest (Klink & Machado 2005, Werneck 2011). The biome is a world biodiversity hotspot, having a high biological diversity which is severely threatened by natural habitat loss, driven by agricultural activities, in addition to the introduction of exotic species (Myers et al. 2000, Klink & Machado 2005, Moro et al. 2012). Currently, the Cerrado is experiencing an unprecedented expansion in its road infrastructure (Klink & Machado 2005, Carvalho et al. 2009, Miranda et al. 2017), specially designed to allow the outflow of agricultural production (especially soybean) for exportation (Klink & Machado 2005, da Cunha et al. 2010, Souza et al. 2015). The corollary is that more frequent vehicle-animal collisions on roads in these human-dominated landscapes are becoming increasingly common (Carvalho et al. 2009, Souza et al. 2015, de Freitas et al. 2015, Braz & França 2016, Miranda et al. 2020).

Herein, we compared the rates of wildlife roadkill events along roads crossing landscapes with different land cover patterns in Central Brazil. We compared roadkill patterns in terms of the absolute number of events, the number of species affected, and the taxonomic group involved (amphibians, reptiles, birds, or mammals). We predicted that roadkill events were more frequent and affected more species of different taxonomic groups in the road stretch bordering a protected area in an iconic Cerrado region (Chapada dos Veadeiros), where higher amounts of natural vegetation (forest and savanna) were to be found along the roads. We also investigated the effect of seasonality on roadkill events for different species and taxonomic groups.

MATERIALS AND METHODS

Study area

We conducted the study in the Northeastern State of Goiás (GO), Central Brazil. The Cerrado biome is formed by a mosaic of vegetation formations, from natural grassland, woodland savannas, and dense forests (Ribeiro & Walter 1998). The climate in the region is Köppen's *Aw* (rainy tropical), with a marked seasonality between the dry and rainy seasons (Alvares et al. 2013, Cardoso et al. 2015). The annual average precipitation is 1500–1750 mm, with mean temperatures varying between 20°C and 26°C (Nimer 1989). The rainy season is typically concentrated between October and March, while the dry season spreads from April to September (Ribeiro & Walter 1998), with small variations according to region and year. In the present study, we restricted the rainy season from November to April, and the dry season from May to October, following the cumulative daily rainfall obtained from the Alto Paraíso de Goiás municipality weather station (INMET 2018).

We monitored two road stretches located in the Pouso Alto Environmental Protection Area (Pouso Alto APA) (Figure 1). Despite the name, APAs (a protected area category from the Brazilian legislation similar to IUCN protected areas category VI) are not strictly directed to environmental conservation since it allows several types of land use, and are not effective to avoid deforestation (Françoso et al. 2015). The Pouso Alto APA encompasses a wide area (8.720 Km²), which comprises highly fragmented and deforested land cover classes, and the Chapada dos Veadeiros National Park (PNCV), the latter being the only area intended for strict environmental protection in the studied landscape.

The first stretch was placed along 33.6 Km of the highway BR-010, from the town of Alto Paraíso de Goiás (14°08.533'S and 47°31.300'W) to the APA southern border (14°25.742'S and 47°30.444'W). We refer to this road stretch as the 'unprotected landscape' (Figure 2), where the the predominant surrounding classes include extensive areas converted to human economic activities (pasture, agriculture, and forestry). In this area, there is currently a considerable ongoing expansion of cropland by mechanized industrial agriculture as well as urban encroachment in the town of Alto Paraíso de Goiás. Moreover, in the last years the highway system has been expanded seeking to facilitate the outflow of crop products and the promotion of mass tourism.

The second stretch comprehended two roads bordering – and at some points crossing – the PNCV. It runs 31 km along the BR-010 road from Alto Paraíso de Goiás (14°10.725'S and 47°48.517'W) toward the municipality of Teresina de Goiás (13°54.229'S and 47°22.704'W), and 39 km along the GO-239 road, from Alto Paraíso de Goiás (14°08.550'S and 47°31.323'W) toward the municipality of Colinas do Sul (14°10.771'S and 47°48.971'W). This stretch was termed 'protected landscape' in our study, due to being adjacent to the PNCV, where the predominant landscape classes surrounding these roads are native vegetation (forests, savannas, and grasslands), with few and sparse areas of pasture farms (Figure 2).

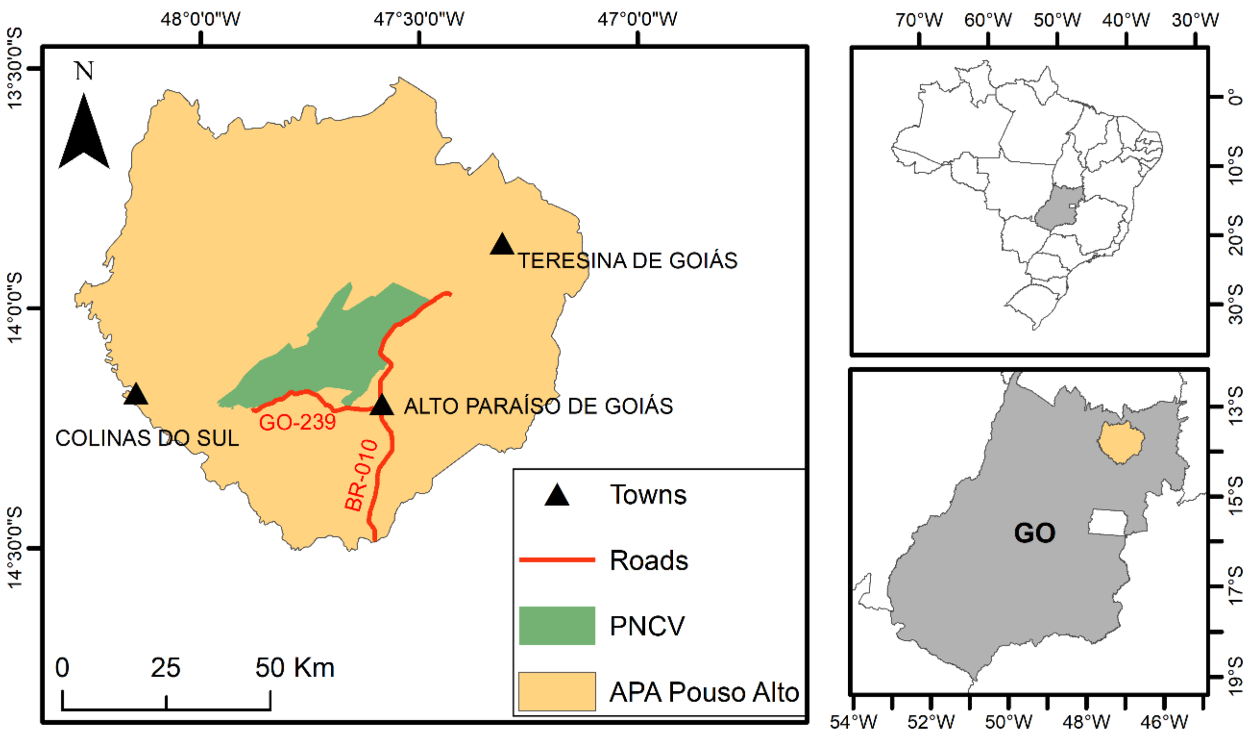

Figure 1. Monitored road stretches: BR-010 (South of Alto Paraíso de Goiás), and BR-010 (North of Alto Paraíso de Goiás)/GO-239 within the Pouso Alto APA limits in the Northeastern state of Goiás, Brazil. Towns are indicated by triangles. The Chapada dos Veadeiros National Park (PNCV) limits were updated in June 5, 2017.

Roadkill sampling

Sampling was conducted over twelve months between 2017 and 2018, covering both seasons in the Cerrado. The road stretch in the unprotected landscape (BR-010) was monitored four times each month, which resulted in 48 independent samples (sampling campaigns). The protected landscape road stretch (BR-010 and GO-239) was monitored twice a month, resulting in 24 sampling campaigns.

Both the BR-010 and the GO-239 highways are single-lane roads, 7 m wide, with a single asphalt surface shared between both ways. At the time of sampling, only a portion of the GO-239 stretch (in the protected landscape) presented speed reducers for the sake of protecting human lives and wildlife. The BR-010 (with stretches in both protected and unprotected landscapes) presented a few traffic signs indicating animal crossings. These roads are busier during school vacations and long holidays.

Monitoring was performed by car, by two observers, at a speed between 40 to 50 Km/h (according to the minimum speed limits imposed by Brazilian legislation on highways). In the unprotected landscape, monitoring took place between 06:00 and 08:00 hs. from the South northwards, and between 16:00 and 18:00 hs in the opposite direction. In the protected landscape, since the monitored stretch was longer, sampling hours were randomly assigned, between 06:00 and 18:00 hs, both from the South northwards (along BR-010) and from the East westward (along GO-239).

For every roadkill event, we recorded the place and date where it was found (on the road or at its shoulders), photographed, identified, and took local coordinates. Subsequently, every carcass was removed from the road to avoid

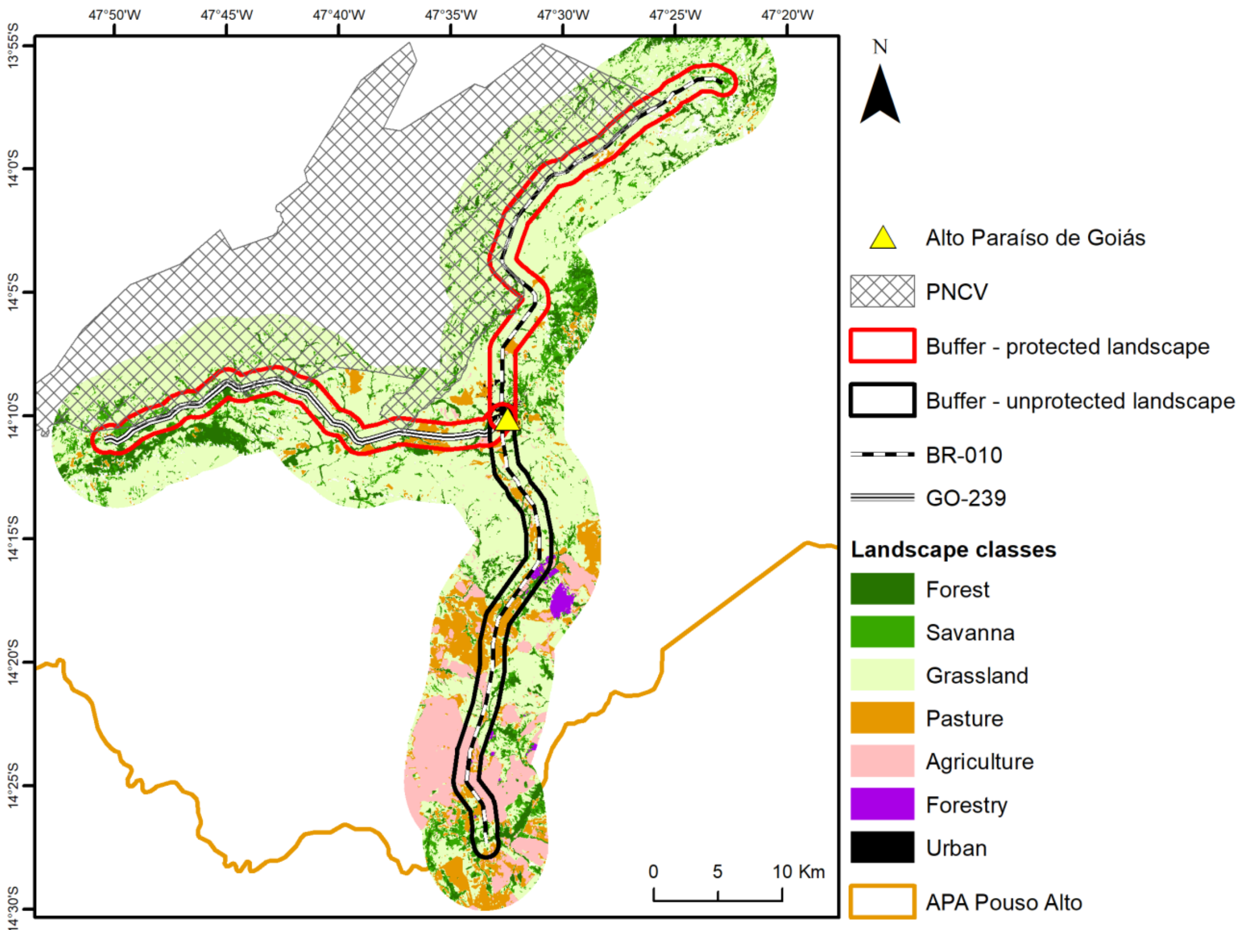

Figure 2. Land use classes around each monitored road stretches in the Pouso Alto APA, which were subsequently related to roadkill patterns. The 'unprotected landscape' stretch (BR-010) was the road within the black buffer, where most anthropogenic land uses are found, and the 'protected landscape' stretch (BR-010 and GO-239) was the one within the red buffer, bordering the limits of the Chapada dos Veadeiros National Park (PNCV). The PNCV limits were updated in June 5, 2017.

re-counting. Identification of the animals was done to the smallest taxonomic level possible, within four groups (Amphibia, Aves, Squamata, and Mammalia). Our response variable is therefore the number of roadkill events recorded in each of the taxonomic groups.

Landscape map

The classified land use and land cover in a buffer along the monitored roads were obtained from the Mapbiomas platform version 2.1 (www.mapbiomas.org). Mapbiomas is a national-scale classification using historical and current Landsat images, with 30-m resolution. We used a land-use classification from 2016, the latest available date. We observed a few discrepancies in the classification concerning gallery forests (included in the 'forest' landscape class). For that reason, we corrected the map by manually drawing the forest polygons on Google Earth based on high-resolution images (1-m Ikonos images available on Google Earth), and then updating the original Mapbiomas map using the new forest polygons. These forests, sometimes narrower than the spatial resolution of Landsat pixels, are important landscape elements, potentially functioning as landscape connectors (Johnson et al. 1999). Because of this, the manual correction was vital for a realistic representation of the landscape elements available. Therefore, our landscape classification presents a 30-m resolution, except for gallery forests, which present a resolution of 1 m. Other small discrepancies were observed in the map, such as the classification of native grasslands as pasture, which is a common problem in remote sensing the Cerrado biome (Ferreira et al. 2013). These issues were manually corrected based on our experience of the landscape.

We evaluated land use in a 5-Km buffer around the road stretches, to provide a general context of the landscape and allowing the identification of classes for manual correction when necessary (Figure 2). However, landscape predictors used in our analysis (see below) were quantified within a 1 Km buffer along each monitored road stretch. This distance was selected to match the cluster analysis done with the roadkill records (see below), which divided each road stretch into 1 Km segments. This buffer width too seems to be efficient for encompassing short-term movements for all studied taxonomic groups in our study (Tozetti & Toledo 2005, Tozetti et al. 2009, Brandão et al. 2018, Henrique & Grant 2019). Generated landscape predictors included, for each segment, (1) proportion of savanna; (2) proportion of forest; (3) proportion of native grassland; (4) proportion of cropland (including areas of agriculture and forestry); (5) proportion of pastures; (6) distance of the segment's center to the nearest gallery forest. These predictors presented no multicollinearity.

All landscape analyses were done in ArcGIS 10.4 (ESRI 2016), except for the gallery forest delineation, which was done manually in Google Earth. Multicollinearity was tested using the 'stats' package in R 3.4.3 (R Core Team 2017).

Analyses

We used rarefaction curves, based on record abundance for each taxonomic group (Gotelli & Cowell 2001), for describing the sufficiency sampling.

Roadkill rates in each monitored stretch were compared between landscapes (protected and unprotected), for each taxonomic group, and for the most recorded species. The rate was defined as the total number of individuals divided by the total extent of the road stretch sampled per day. Daily rates are thus presented as the number of individuals/Km/day. To evaluate the seasonal variation in daily roadkill rates, we compared seasons (rainy and dry) and study areas using an Analysis of Coraviance for each of the four taxonomic groups and for the three most recorded species.

Roadkill records were analyzed in a cluster analysis, aiming to evaluate the more suitable scale to relate roadkill patterns of each taxonomic group to the landscape around road stretches. Cluster analysis was conducted using Ripley's K tool. In this procedure, a density function (L(d)) is tested over varying grouping radiuses, to verify whether records are grouped ($L_{observed} > L_{expected}$), dispersed ($L_{observed} < L_{expected}$), or randomly distributed ($L_{observed} = L_{expected}$). Based on this result, we obtained an ideal grouping distance of 1 Km, which defined the length of the segments into which the road stretches were divided. Therefore, we quantified landscape predictors (land cover) for each of these 1-Km segments.

We used a model ranking approach to compare generalized linear models (GLM) (McCullagh & Nelder 1989) and evaluate the effect of landscape predictors in the number of roadkill events. Modeling was fitted using Poisson family error terms. The complete model (GLM, family = Poisson) considered the following variables to be independent: level of protection (binary), landscape classes related to human activities (proportion of pastures and croplands), and to natural vegetation (proportion of forest, savanna, and grassland). For the model ranking procedure, we followed Zuur et al. (2009). In this procedure, a stepwise removal of independent predictors was performed, based on the results of a likelihood ratio test. At each step, the predictor with the highest value of p was removed, until the removal of any other variable significantly affected the model. The final model was visually assessed based on the normality and homoscedasticity of residuals.

We performed the cluster analysis in ArcGIS 10.4 (ESRI 2016), and richness rarefaction, seasonality analysis, and statistical modeling were done in R 3.4.3 (R Core Team 2017), using the 'MuMIn' (Barton 2018), 'BiodiversityR' (Kindt & Coe 2005), and 'vegan' (Oksanen et al. 2016) packages.

RESULTS

We recorded 301 roadkill events of 75 taxa of wild vertebrates (Table I). In the unprotected landscape, we sampled 1,615 Km and recorded 172 roadkill individuals, of which 124 were identified to the species level (54 species, distributed in 50 genera, 33 families, and 21 orders). Due to carcass condition, 49 individuals could not be identified to the species level. In the protected landscape we sampled 1,680 Km and recorded 129 roadkill events, of which 105 were identified to the species level (41 species belonging to 40 genera, 23 families, and 14 orders).

In the unprotected landscape, birds (Aves) were the most frequently recorded group, corresponding to 44% (n = 76) of the roadkill records, followed by Amphibia (23%, n = 40), Mammalia (22%, n = 38), and Squamata (11%, n = 18). In this landscape, the most frequently recorded species were *Cerdocyon thous* (n = 17), *Volatinia jacarina* (n = 13), and *Rhinella diptycha* (n = 11).

Bird roadkill also dominated the roadkill records in the protected landscape (37%, n = 48), followed by amphibians (28%, n = 36), Squamata (21%, n = 27), and mammals (14%, n = 18). In this landscape, the most affected species were *Rhinella diptycha* (n = 35), followed by *Crotalus durissus* (n = 6), *Cerdocyon thous* (n = 5), and *Sicalis flaveola* (n = 5).

Rarefaction curves did not reach an asymptote for any of the taxonomic groups, either in the unprotected or in the protected landscape (Figure 3). This indicated that the number of species affected by roads is likely to be much higher. The patterns observed in the rarefaction analysis did not indicate a significant difference in the number of roadkill events between landscapes for all taxa, except for amphibians, which were more abundant in the unprotected landscape. On the other hand, the rarefaction curve for this group was far from presenting any asymptotic pattern, rendering the comparison inconclusive.

Roadkill rates differed between landscape categories and among groups (Table II). Roadkill occurred more frequently in the rainy season (224 records: 130 in the unprotected landscape, and 94 in the protected landscape).

The number of roadkill events in the rainy season was higher for all taxonomic groups (Figure 4). However, seasonal differences in the unprotected landscape were significant only for Amphibia ($F = 12.910$, $p < 0.001$), and Aves ($W = 6.632$, $p = 0.018$); and did not differ for Squamata ($F = 3.808$, $p = 0.065$), and for Mammalia ($F = 0.099$, $p = 0.756$). Between the studied landscapes, difference in the number of roadkill events was significant for Mammalia only ($F = 9.430$, $p = 0.006$), and did not differ for Amphibia ($F = 1.235$, $p = 0.279$), Squamata ($F = 0.588$, $p = 0.452$), and Aves ($F = 2.246$, $p = 0.149$). Two of the three

Table I. **Number of wildlife roadkill records obtained in the unprotected and protected landscapes. Taxonomic group/species = lowest taxonomic level associated with roadkill (genera/species); Dry/Rainy = number of records per season.**

TAXA	Common name	Protected landscape (BR-010 + GO-239)		Unprotected landscape (BR-010)	
		DRY	RAINY	DRY	RAINY
Amphibia					
Anura NI	---	0	0	0	7
Boana albopunctata (Spix, 1824)	Yellow-spotted Treefrog	0	0	0	2
Leptodactylus labyrinthicus (Spix, 1824)	Labyrinth Frog	0	0	0	1
Leptodactylus sertanejo Giaretta and Costa, 2007	Creek Frog	0	1	0	0
Odontophrynus salvatori Caramaschi, 1996	Savannah Frog	0	0	0	1
Physalaemus nattereri (Steindachner, 1863)	Cuyaba Dwarf Frog	0	0	0	4
Physalaemus sp.	Barking Frog	0	0	0	1
Pithecopus sp.	Monkey Treefrog	0	0	0	1
Rhinella diptycha (Cope, 1862)	Cururu Toad	3	32	0	11
Rhinella rubescens (Lutz, 1925)	Toad	0	0	0	4
Rhinella sp.	Toad	0	0	2	1
Scinax sp.	Common Frog	0	0	0	1
Siphonops paulensis Boettger, 1892	Boettger's Caecilian	0	0	0	4
Squamata					
Ameiva ameiva (Linnaeus, 1758)	Giant Ameiva	1	0	0	3
Amphisbaena alba Linnaeus, 1758	White Worm-lizard	0	0	0	2
Bothrops marmoratus Da Silva & Rodrigues, 2008	Marbled lancehead	0	1	0	0
Crotalus durissus Linnaeus, 1758	South American Rattlesnake	1	5	1	1
Epicrates crassus (Linnaeus, 1758)	Rainbow Boa	0	0	0	1
Erythrolamprus poecilogyrus (Wied-Neuwied, 1825)	Trash Snake	0	1	0	0
Erythrolamprus macrosoma (Linnaeus, 1758)	Royal Ground Snake	0	0	0	1
Palusophis bifossatus (Raddi, 1820)	Rio Tropical Racer	0	1	0	0
Oxyrhopus guibei Hoge & Romano, 1977	False Coral Snake	0	2	0	0
Oxyrhopus sp.	False Coral Snake	0	3	0	4
Philodryas aestiva (Duméril, Bibron & Duméril, 1854)	Brazilian Green Tree Snake	1	0	0	0
Philodryas agassizii (Jan, 1863)	Burrowing Night Snake	0	1	0	0
Pseudablabes patagoniensis (Girard, 1858)	Patagonian Savanna Racer	1	3	0	0
Polychrus acutirostris Spix, 1825	Brazilian Bush Anole	1	0	0	1

Table I. Continuation.

Salvator merianae (Duméril & Bibron, 1839)	Black Tegu	1	0	1	0
Squamata NI	---	1	0	0	1
Taeniophallus occipitalis (Jan, 1863)	Striped Snake	1	0	0	0
Tropidurus oreadicus Rodrigues, 1987	Lava Lizard	1	0	0	0
Xenodon merremii (Wagler, 1824)	Merrem's False Pit Viper	0	1	1	0
Aves					
Ammodramus humeralis (Bosc, 1792)	Grassland Sparrow	1	1	0	0
Aves NI	---	4	11	2	9
Baryphthengus ruficapillus (Vieillot, 1818)	Rufous-capped Motmot	0	0	1	0
Brotogeris sp.	Parakeet	0	0	0	1
Caracara plancus (Miller, 1777)	Southern Caracara	0	0	0	2
Cariama cristata (Linnaeus, 1766)	Red-legged Seriema	0	0	0	3
Coereba flaveola (Linnaeus, 1758)	Bananaquit	1	0	0	0
Colaptes campestris (Vieillot, 1818)	Campo Flicker	1	0	0	2
Colibri serrirostris (Vieillot, 1816)	White-vented Violet-ear	0	0	1	0
Columbina talpacoti (Temminck, 1810)	Ruddy Ground-Dove	0	0	2	0
Coragyps atratus (Bechstein, 1793)	Black Vulture	0	0	0	1
Crotophaga ani Linnaeus, 1758	Smooth-billed Ani	0	0	1	1
Crypturellus parvirostris (Wagler, 1827)	Small-billed Tinamou	0	2	2	1
Emberizoides herbicola (Vieillot, 1817)	Wedge-tailed Grass-Finch	1	1	1	1
Eupetomena macroura (Gmelin, 1788)	Swallow-tailed Hummingbird	0	0	1	1
Guira guira (Gmelin, 1788)	Guira Cuckoo	0	0	1	2
Heliactin bilophus (Temminck, 1820)	Horned Sungem	1	0	0	1
Mimus saturninus (Lichtenstein, 1823)	Chalk-browed Mockingbird	1	1	0	0
Nothura maculosa (Temminck, 1815)	Spotted Nothura	1	2	0	0
Nystalus chacuru (Vieillot, 1816)	White-eared Puffbird	0	1	0	0
Phacellodomus ruber (Vieillot, 1817)	Greater Thornbird	0	0	1	0
Rhynchotus rufescens (Temminck, 1815)	Red-winged Tinamou	1	1	1	3
Sicalis citrina Pelzeln, 1870	Stripe-tailed Yellow-Finch	0	0	0	1
Sicalis flaveola (Linnaeus, 1766)	Saffron Finch	1	4	0	3
Sicalis sp.	Finch	0	0	0	2
Sporophila nigricollis (Vieillot, 1823)	Yellow-bellied Seedeater	0	3	0	0
Sporophila sp.	Seedeater	0	1	1	8
Synallaxis sp.	Spinetail	0	0	1	0
Stilpnia cayana (Linnaeus, 1766)	Burnished-buff Tanager	1	0	0	1

Table I. Continuation.

Thraupis sayaca (Linnaeus, 1766)	Sayaca Tanager	0	0	0	1
Thamnophilus doliatus (Linnaeus, 1764)	Barred Antshrike	1	0	0	0
Troglodytes musculus Naumann, 1823	Southern House Wren	0	0	0	1
Turdus amaurochalinus Cabanis, 1850	Creamy-bellied Thrush	0	0	1	0
Turdus rufiventris Vieillot, 1818	Rufous-bellied Thrush	0	0	1	0
Volatinia jacarina (Linnaeus, 1766)	Blue-black Grassquit	0	4	1	13
Zonotrichia capensis (Statius Muller, 1776)	Rufous-collared Sparrow	1	0	0	0
Mammalia					
Caviidae NI	---	0	1	0	0
Cerdocyon thous (Linnaeus, 1766)	Crab-eating Fox	3	2	9	8
Chiroptera NI	---	1	1	0	1
Chrysocyon brachyurus (Illiger, 1815)	Maned-wolf	2	0	0	1
Conepatus semistriatus (Boddaert, 1785)	Striped Hog-nosed Skunk	0	0	2	3
Dasypodidae NI	---	0	0	1	0
Dasypus septemcinctus Linnaeus, 1758	Seven-banded Armadillo	0	1	0	3
Dasypus sp.	Armadillo	0	1	0	0
Didelphis albiventris Lund, 1840	White-eared Opossum	0	0	1	1
Galea spixii (Wagler, 1831)	Spix's Yellow-toothed Cavy	1	0	0	0
Lycalopex vetulus (Lund, 1842)	Hoary Fox	1	0	2	0
Muridae NI	---	0	0	1	2
Molossus sp.	Bat	0	1	0	0
Nasua nasua (Linnaeus, 1766)	South American Coati	0	0	0	1
Oecomys sp.	Rodent	0	0	1	0
Ozotoceros bezoarticus (Linnaeus, 1758)	Pampas Deer	0	1	0	0
Pteronotus parnellii (Gray, 1843)	Parnell's Mustached Bat	0	1	0	0
Sylvilagus brasiliensis (Linnaeus, 1758)	Common Tapeti	0	1	0	0
Tamandua tetradactyla (Linnaeus, 1758)	Southern Tamandua	0	0	1	0
Total		**36**	**93**	**42**	**130**

most frequently recorded species were affected by seasonality (*Rhinella diptycha*, F = 12.93, p = 0.001; *Volatinia jacarina*, F = 13.84, p = 0.001).

As a function of landscape structure, the proportion of the classes 'agriculture' and 'savanna' was related to the number of amphibian roadkill events (Table III). The number of Squamata was assessed only for the protected landscape, where we observed a significant influence of the proportion of forests (Figure 5 and Table IV). Bird roadkill events were affected by the level of protection only (Figure 5 and Table V), while for mammals, the class 'grassland' and level of protection explained roadkill events (Figure 5 and Table VI).

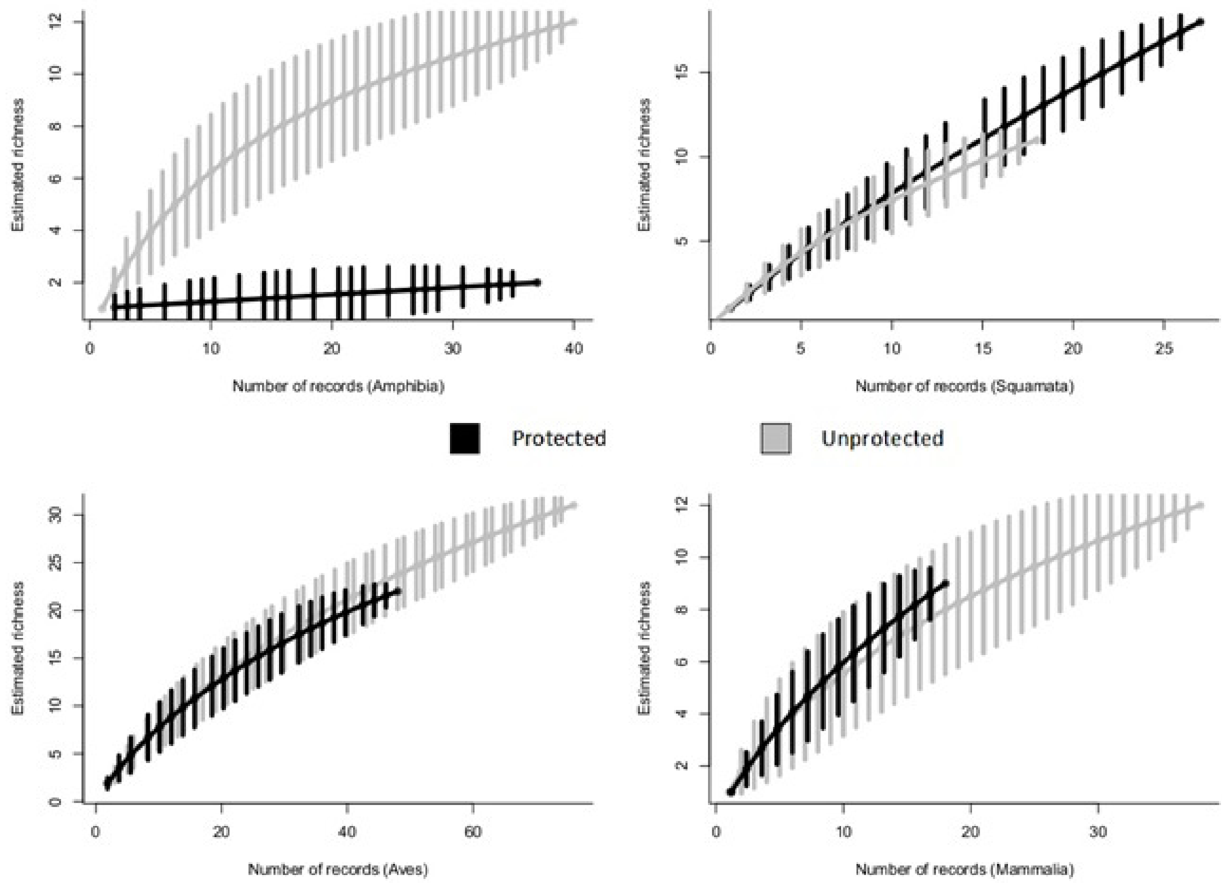

Figure 3. Rarefaction curves based on record abundance by taxonomic group (Amphibia, Squamata, Aves, and Mammalia) in each of the sampled landscapes (unprotected landscape: gray curve; and protected landscape: black curve). A 95% confidence interval for the sake of statistical comparison between curves is also shown as vertical lines.

Table II. Roadkill rates (individuals/Km/day) per taxonomic group, between seasons (rainy and dry), and landscapes (protected and unprotected).

	Dry		Rainy	
	Protected	Unprotected	Protected	Unprotected
Amphibia	0.04	0.06	0.49	1.13
Squamata	0.11	0.09	0.27	0.45
Aves	0.23	0.56	0.46	1.69
Mammalia	0.11	0.54	0.14	0.59

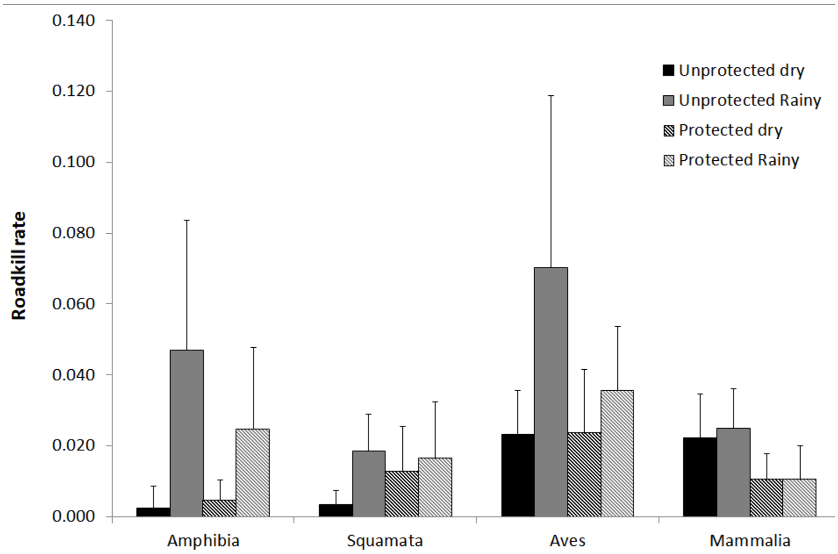

Figure 4. Seasonal variation in roadkill rates for each wild vertebrate group both in the unprotected and the protected landscapes. Errors at a 5% significance level are presented above bars.

Table III. Statistical results (coefficient estimates, standard error [SE], t value, and p-value) for the best model selected to explain the number of roadkill events of Amphibia in areas with different levels of protection in Alto Paraíso de Goiás, Goiás state, Brazil. Significant values at α<0.05 are in bold.

	Coefficient	SE	t	p
Intercept	-0.357	0.180	-1.979	0.051
Agriculture	-0.439	0.219	-2.006	**0.048**
Savanna	-0.600	0.164	-3.666	**>0.001**

DISCUSSION

We had expected higher roadkill rates in the protected landscape, but only Squamata corroborated our initial expectations. Overall, roadkill rates were higher in the unprotected landscape for all taxa, and richness and abundance patterns corroborated those results. However, Squamata presented higher roadkill rates in the protected landscape only during the dry season, probably reflecting their environmental requirements and natural history aspects (Garriga et al. 2012). The richness of Cerrado Squamata is higher in open habitats, including dry grasslands and savanna than in forested habitats (França & Braz 2013). Corroborating this pattern, we reported lower rates of Squamata roadkill in areas with a larger proportion of forest cover, where snakes corresponded to 85% of total roadkill events. All recorded snakes belonged to generalist species, strongly associated to open habitats (Sazima & Haddad 1992, França & Braz 2013, Mesquita et al. 2013), including the three more frequently recorded species (*Crotalus durissus*, *Philodryas nattereri*, and *Pseudablabes patagoniensis*) (Sazima & Haddad 1992, França & Braz 2013, Mesquita et al. 2013).

In general, vertebrates that were most frequently found as roadkill, both in the unprotected and protected landscapes, were generalist species, presenting high plasticity in habitat use. The observed patterns can thus be related to a higher dispersal of generalist species through degraded areas, and the more flexible habitat use by these species (Bernardino & Dalrymple 1992, Forman et al. 2003, Barrientos & Bolonio 2009), which can also use areas

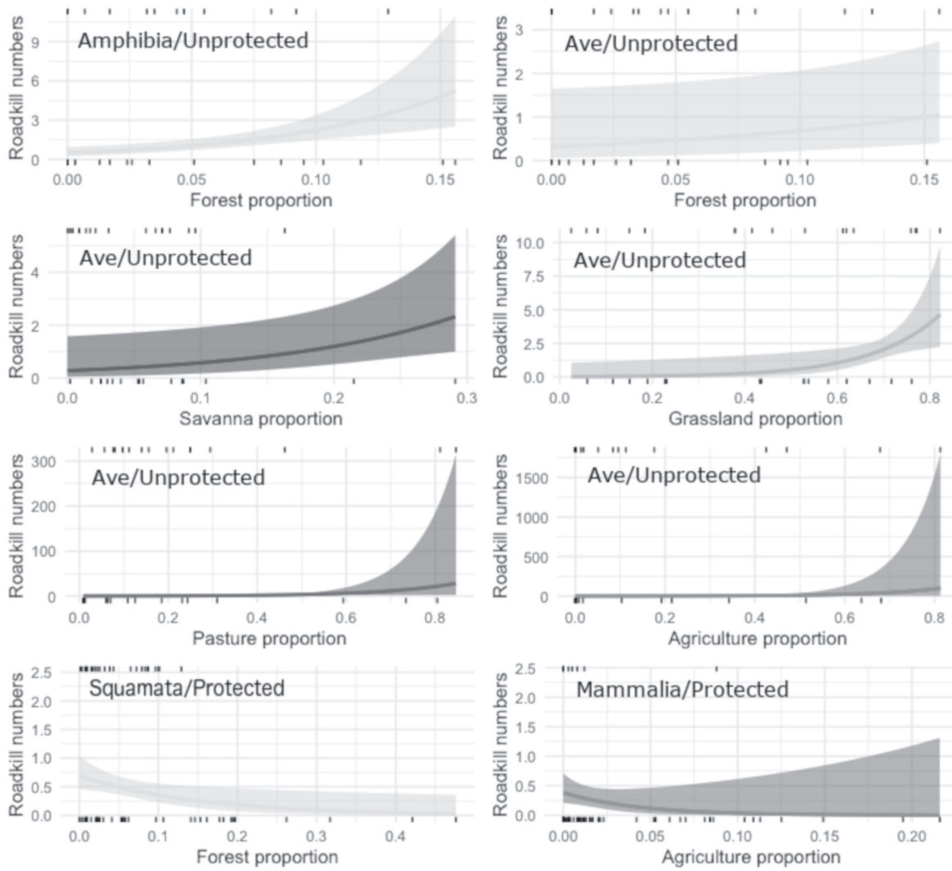

Figure 5. **Significant effects found of different landscape attributes on roadkill patterns of each taxonomic group (Amphibia, Squamata, Aves, and Mammalia) for different levels of protection (protected and unprotected).**

surrounding the road even in the less altered landscape. The landscape changes in the Pouso Alto APA region (except inside the PNCV) may be favoring opportunistic species, with higher plasticity in habitat use, and eventually causing regional biotic homogenization (Beisiegel et al. 2013, Gámez-Virués et al. 2015).

In the Cerrado, human-modified and degraded areas, adjacent to roads, present a higher incidence of exotic grasses, which is one of the main drivers of environmental change in the biome (Hoffmann et al. 2004, Klink & Machado 2005, Moro et al. 2012). Vehicle traffic also contributes to the dispersal of exotic species, mainly by grain spilling along the roads (Forman 2000, Hansen & Clevenger 2005). Granivore birds (such as *Volatinia jacarina* and *Sicalis flaveola*) are attracted by exotic grass seeds (Forman & Alexander 1998, Hansen & Clevenger 2005, Carvalho et al. 2007). Scavengers (such as *Cerdocyon thous*) are also attracted to the roads by the availability of carcasses (Forman & Alexander 1998, Alves et al. 2018). The availability of these resources can explain the higher frequency of roadkill of these opportunistic species in our findings.

In our study, birds were the most affected taxa in both landscapes. Among the birds, passerines were the most frequently observed in

Table IV. **Statistical results (coefficient estimates, standard error [SE], t value, and p-value) for the best model selected to explain roadkill events of Squamata in the protected landscape in Alto Paraíso de Goiás, Goiás state, Brazil. Significant values at α<0.05 are in bold.**

z	Coefficient	SE	t	p
Intercept	-0.898	0.188	-4.782	**<0.001**
Forest	-0.643	0.283	-2.268	**0.027**

the unprotected (*Volatinia jacarina*) and in the protected landscape (*Sicalis flaveola*). Santos et al. (2018) also recorded a large number of roadkill of *Volatinia jacarina* in roads that border protected areas in the Cerrado. In the protected landscape adjacent to the GO-239 highway, Braz & França (2016) recorded *Ammodramus humeralis* Bosc, 1792 (passerine) as the most abundant roadkill bird. *Volatinia jacarina* and *Ammodramus humeralis* are passerines highly associated with grass incidence at the margins of roads (Carvalho et al. 2007, Dias et al. 2009). Moreover, these species present short and low flights, which favor their being hit by vehicles when they are foraging close to the roads (Gwynne et al. 2010).

Amphibia was the second taxon most affected by vehicle collision in our study, both in the protected and in the unprotected landscapes. However, almost all events corresponded to the bufonid *Rhinella diptycha*. Bufonids are common victims of roadkill, as has been observed in African savannas (Kioko et al. 2015), in the Iberic Peninsula (Garriga et al. 2012), in Australia (Beckmann & Shine 2012), and in the Brazilian Cerrado (Melo & Santos-Filho 2007, Braz & França 2016, Miranda et al. 2017). The killing of toads due to road collisions can be related to their seasonal migration habits (Lemckert 2004, Vimercati et al. 2017), to the slow pace at which they disperse (Cunnington et al. 2014), or even to the use of roads as dispersal corridors (Brown et al. 2006). On the other hand, toad carcasses, due to the presence of toxic substances on their skin glands, are likely to be avoided by scavengers, lasting more time on roads when compared to other similar-sized frogs.

Small-sized vertebrates can be more easily underestimated in studies that use cars for roadkill counting (Antworth et al. 2005, Langen et al. 2007, Santos et al. 2016). Rains, scavenger activity, or even other vehicles can easily remove small and light-weight carcasses from the roads (Teixeira et al. 2013, Ratton et al. 2014, Santos et al. 2016), affecting their detectability. The very small richness of amphibians observed in our study, when compared to the local species pool (e.g. Santoro & Brandão 2014), can be an indication of this effect.

In the rainy season, we recorded higher roadkill rates for amphibians, Squamata, and birds, during which amphibians and birds were more often killed in the protected landscape. Higher roadkill rates during the rainy season in the Cerrado were also reported in previous studies (Coelho et al. 2008, Braz & França 2016, Miranda et al. 2017), as well as in other countries (e.g. Forman & Alexander 1998, Smith & Dodd 2003, Pinowski 2005, Garriga et al. 2017). This finding probably relates to higher species activity due to higher dietary resource availability during the rainy season (Dalponte & Lima 1999, Batalha & Martins 2004, Machado & Silveira 2010). Moreover, the rainy season is the breeding season for several taxa in the Cerrado, and it is expected that animals present higher activity in the search for resources and mates

Table V. Statistical results (coefficient estimates, standard error [SE], t value, and p-value) for the best model selected to explain roadkill events of birds in the unprotected landscape in Alto Paraíso de Goiás, Goiás state, Brazil. Significant values at α<0.05 are in bold.

	Coefficient	SE	t	p
INTERCEPT	0.834	0.126	6.598	**<0.001**
Level of protection (binary)	-0.901	0.192	-4.688	**<0.001**

(Gascon 1991, Oliveira & Gibbs 2002, Oliveira & Marquis 2002, Oda et al. 2009).

The temporal and spatial occurrence of water in the landscape constrain amphibian activity, causing it to be more active and conspicuous during the rainy season (Goosem 2004, Kioko et al. 2015), especially for seasonal biomes, as the Brazilian Cerrado (Santoro & Brandão 2014). Seasonal differences on herpetofauna roadkill were also recorded in other regions of the Cerrado biome (Melo & Santos-Filho 2007, Miranda et al. 2017). Amphibians were more abundant in the unprotected landscape, which might suggest that they tend to cross the road more often in landscapes with less available reproductive habitats (Lemckert 2004, Brown et al. 2006).

In the unprotected landscape, the proportion of forest explained the observed roadkill rates for amphibians. Most of the forest cover in this landscape corresponds to gallery forests (Ribeiro & Walter 1998), narrow strips of riparian forest that run along rivers and streams in the Cerrado. It is interesting to note that wet grasslands, the habitats more often used by Cerrado amphibians (Santoro & Brandão 2014), are commonly located adjacent to gallery forests. Although these riparian forests are protected by the Brazilian environmental legislation, the associated grasslands are not, and are often removed for the establishment of pastures and agricultural fields (Becker et al. 2010, Toledo et al. 2010). Gallery forests are mesic habitats during the dry season and are ombrophilous habitats effectively used by several animals as dispersal corridors and as a refuge (Johnson et al. 1999).

The wild canids were the most affected mammals in both landscapes. The crab-eating fox (*Cerdocyon thous*) is one of the mammals most affected by vehicle collision in the Cerrado (Vieira 1996, Melo & Santos-Filho 2007, da Cunha et al. 2010, de Freitas et al. 2015). *Cerdocyon thous* is a very common and opportunistic species, presenting large home ranges, over which they intensively forage both in preserved as well as in altered habitats, such as road margins (Clarke et al. 1998, Juarez & Marinho-Filho 2002, Beisiegel et al. 2013). In addition, the maned-wolf (*Chrysocyon brachuyrus*) is a near-threatened canid according to the IUCN red list (Paula & DeMatteo 2015), and the hoary-fox (*Lycalopex vetulus*) is considered a vulnerable species (Beisiegel et al. 2013, Lemos et al. 2013). Both were found as roadkill in the unprotected and the protected landscapes. Overall, all Cerrado wild canids are severely threatened by roads and are experiencing fast declines in the biome due to a myriad of factors (Beisiegel et al. 2013, Paula et al. 2013, de Freitas et al. 2015, Abra et al. 2021).

Although we did not find any relationship between land use and mammal roadkill rate in the unprotected landscape, 77% of *Cerdocyon thous* carcasses were found in this landscape, showing that rural landscapes are frequently

Table VI. Statistical results (coefficient estimates, standard error [SE], t value, and p-value) for the best model selected to explain roadkill events of Mammalia in the protected landscape in Alto Paraíso de Goiás, Goiás state, Brazil. Significant values at α<0.05 are in bold.

	Coefficient	SE	t	p
Intercept	0.459	0.223	2.064	**0.042**
Level of protection (binary)	-20.326	0.415	-4.894	**<0.001**
Grassland	-0.389	0.185	-2.108	**0.038**

used by the species (Juarez & Marinho-Filho 2002, de Barros et al. 2010, de Freitas et al. 2015). Occupancy-based modeling suggested that wildlife-vehicle collisions in the Cerrado tend to happen more often in areas covered by open natural habitats or agriculture (Santos et al. 2018). This result may be explained by the high roadkill rate of *Cerdocyon thous*, as well as of other species that also explore altered landscapes in similar ways (e.g. Bernardino & Dalrymple 1992, Forman et al. 2003).

Interestingly, mammal roadkill events in the protected landscape were negatively related to the proportion of farming activities. Although medium-sized and large mammals (about 50% of our records for that taxa) can disperse through different landscape classes, including crops, pastures, and forestry areas (Oliveira et al. 2009, Bocchiglieri et al. 2010, Martin et al. 2012, de Freitas et al. 2015, Magioli et al. 2016), highest mammal richness and abundance are found in natural remnants (Trolle et al. 2007, Bocchiglieri et al. 2010, Martin et al. 2012, Magioli et al. 2016). Similarly, other studies showed that mammal roadkill patterns are, indeed, related to the presence of natural remnants (e.g. Freitas et al. 2013, Braz & França 2016, Brum et al. 2016).

The resource distribution in the environment is one of the main factors that regulate habitat use by animals (Law & Dickman 1998), and the presence and proportion of different land use classes affect the distribution of resources. It is also noteworthy that protected areas are a source of individuals for other natural remnants (Naranjo & Bodmer 2007), thus preventing the collapse of animal populations in more fragmented areas, even for opportunistic species (Beisiegel et al. 2013, Paula et al. 2013, de Freitas et al. 2015). It is expected that in deeply altered habitats, such as soybean croplands in the Cerrado, mammal roadkill rates tend to decrease over time both in terms of richness and abundance. This can be mainly explained by local extinctions (but see Colino-Rabanal et al. 2012 for the case of invasive mammals) and is an interesting question for future studies.

Along with other factors (such as seasonality, traffic flux, and spatial location), landscape structure effectively affects animal roadkill patterns (Seo et al. 2015), and the management of the impacts of roads on animal populations should include larger and smaller-scale landscape analyses as well as long-term monitoring (Andrews 1990, Van der Ree et al. 2011). Special attention should be given to particular landscape features, such as the presence of humid or mesic habitats (Seo et al. 2015), fragmentation degree, and ecological requirements of the studied groups (Forman 2000, Laurance et al. 2009, Galetti et al. 2013). Seasonal differences in roadkill rates related to landscapes and taxa reinforce the need for long-term management of this relevant source of mortality for the Cerrado fauna in protected and unprotected landscapes.

Acknowledgments

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES for providing scholarship and finantial support to SM, and the Centro de Estudos do Cerrado da Chapada dos Veadeiros for support to CRR, SM and LPF. RAB thanks to Conselho Nacional de Desenvolvimneto Científico e Tecnológico - CNPq for Research Productivity Grant (Process #306644/2020-7 - PQ). The research was developed by license number 58742 provided by the Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio.

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How to cite

FRAGA LP, MACIEL S, ZIMBRES BQC, DE CARVALHO PJ, BRANDÃO RA & ROCHA CR. 2022. Differences in Wildlife Roadkill Related to Landscape Fragmentation in Central Brazil. An Acad Bras Cienc 94: e20220041. DOI 10.1590/0001-3765202220220041.

Manuscript received on January 16, 2022;
accepted for publication on March 19, 2022

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