

Spatial patterns of road mortality of medium–large mammals in Mato Grosso do Sul, Brazil

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Abstract

Context. Brazil has one of the richest biodiversity and one of the most extensive road networks in the world. Several negative impacts emerge from this interaction, including wildlife–vehicle collisions (WVC), which may represent a significant source of non-natural mortality in several species. The understanding of the main drivers of WVC is, therefore, crucial to improve the safe coexistence between human needs (transportation of goods and people) and animal populations.

Aims. We aimed to (1) evaluate the relative influence of land-cover patterns on the distribution of WVC, (2) assess whether WVCs are clustered forming hotspots of mortality, and, if so, (3) evaluate the benefits of mitigating only hotspot sections.

Methods. We collected WVC data involving medium–large mammals (4–260 kg) along three road transects (920 km), fortnightly over 1 year ($n = 1006$ records). We used boosted regression trees to relate the WVC locations with a set of environmental variables including a roadkill index, reflecting overall habitat suitability and landscape connectivity, while accounting for spatial autocorrelation effects. We identified hotspots of mortality using Ripley’s K statistic and testing whether data follow a random Poisson distribution correcting for Type I error.

Key results. We found a strong association between WVC probability and roadkill index for all focal species. Distance to riparian areas, tree cover, terrain ruggedness and distance to urban areas were also important predictors, although to a lesser extent. We detected 21 hotspots of mortality, yet with little spatial overlapping as only four road sections (2%) were classified as hotspot for more than one species.

Conclusions. Our results supported that WVC mainly occur in road sections traversing areas with more abundant and diverse mammal communities. Hotspots of mortality may provide important information to prioritise road sections for mitigation, but this should be used in complement with roadkill indexes accounting for overall mortality.

Implications. The results support focusing on hotspots and habitat quality and landscape connectivity for a better assessment of road mortality. At the local scale, a larger number and improved road passages with exclusionary fencing of appropriate mesh size in riparian areas may provide safe crossings for many species and constitute a promising mitigation measure.

Additional keywords: hotspots, road management, road mitigation, spatial clustering, wildlife–vehicle collisions.

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Introduction

Roads have several negative impacts on animal populations, including habitat fragmentation and reduction in habitat quality (Trombulak and Frissell 2000; Holderegger and Di Giulio 2010; van der Ree *et al.* 2015). Perhaps the most visible and problematic impact of roads is the wildlife–vehicle collisions (WVC), often representing a significant contributor to non-natural mortality in several species, including insects (Muñoz *et al.* 2015), amphibians (Gibbs and Shriver 2005), reptiles (Row *et al.* 2007; Beaudry *et al.* 2010), birds (Bordade-Água *et al.* 2014) and mammals (Ramp and Ben-Ami 2006; Haines *et al.* 2006; Diniz and Brito 2013). Furthermore, WVC may exacerbate road-barrier effects for animals by removing would be crossers, therefore limiting the gene flow among populations from each roadside (Jackson and Fahrig 2011). The combined effect of population depletion and subdivision may accelerate the loss of genetic variation due to random drift and increased inbreeding, potentially leading to local extinctions (Saccheri *et al.* 1998; Westemeier 1998; Reed *et al.* 2007).

Wildlife–vehicle collisions can be of particular concern for medium to large mammals, which generally have low reproductive rates and population sizes, and require larger areas to survive. High demand in food requirements and wide-ranging behaviour often bring larger mammals into conflict with human activities (Poessel *et al.* 2014; Ripple *et al.* 2014), namely the occurrence of WVC with often fatal consequences for human lives or goods (Romin and Bissonette 1996; Huijser *et al.* 2013). Larger territories are more likely to be intersected by roads, and, consequently, medium to large mammals face a higher roadkill risk because of higher crossing rates (Colino-Rabanal *et al.* 2011; Ascensão *et al.* 2014). This may greatly diminish their abundances (Benítez-López *et al.* 2010; Rytwinski and Fahrig 2013) and the probability of population persistence (Frair *et al.* 2008).

The understanding of the main drivers of WVC is, therefore, crucial to improve the safe coexistence between human needs (transportation of goods and people) and animal populations. A bulk of research has tried to identify the main drivers leading to the occurrence and aggregation patterns of WVC (Clevenger *et al.* 2003; Ramp *et al.* 2005; Gunson *et al.* 2011). Some generalities have emerged from the literature, including the high importance of land cover in explaining WVC patterns. In fact, WVC are more common in areas where roads bisect favourable habitat and when roads cut through drainage-movement corridors (Gunson *et al.* 2011). Hence, by focusing on land cover-related predictors, one might be able to identify areas with a higher probability of WVC occurrence.

Road sections with higher concentration of WVC are usually referred as mortality hotspots (Malo *et al.* 2004; Ramp *et al.* 2005; Santos *et al.* 2015). These sections are generally prioritised to apply mitigation measures such as faunal passages or drift fences (Clevenger *et al.* 2001; Olsson and Widen 2008; Polak *et al.* 2014), particularly when there is a high number of species of conservation concern (Soanes *et al.* 2013). In other cases, mitigation aims to reduce the probability of WVC involving species that, because of their size, pose a serious threat to human lives, such as mule deer (*Odocoileus hemionus*) or capybara (*Hydrochoerus hydrochaeris*; Bissonette *et al.* 2008; Huijser *et al.* 2013). However, cross-species benefit of mitigating

certain road segments because of the species' conservation status or because of the safety reasons, has seldom been addressed. A simple approach would be counting the number of casualties from non-target species that could have been prevented if road mitigation had been implemented.

Here, we analysed the spatial patterns of WVC of medium to large mammals in the state of Mato Grosso do Sul, central-western Brazil. We aimed to (1) evaluate the relative influence of land cover and related predictors on the spatial distribution of WVC, (2) assess whether WVCs are spatially clustered forming hotspots of mortality, and, if so, (3) evaluate the cross-species benefit of mitigating only hotspot sections from problematic species. The present study is, therefore, useful to road planners interested in mitigating the impacts of roads, as well as ecologists and conservation biologists who study the effects of roads on population processes.

Materials and methods

Study area

The present study was conducted in Mato Grosso do Sul (MS) in Brazil (Fig. 1). Road density in MS is 0.17 km km⁻², of which ~13% are two-lane paved roads (www.dnit.gov.br, accessed 20 April 2016). The land cover bordering the surveyed roads was dominated by grassland and agriculture, with scattered areas of cerrado, and crossing several riparian areas (Fig. 1). The climate throughout MS is wet from October to March and dry from April to September (Koppen's As or Aw), with mild year-round temperatures (range 21–32°C). Average annual rainfall ranges between 1000 and 1500 mm (Alvares *et al.* 2013).

Roadkill data

Surveys were conducted along three different road transects (920 km), hereafter, referred as 'T1', 'T2' and 'T3', all two-lane and paved roads radiating from the city of Campo Grande, as follows: (T1) along the BR-262 to the bridge over the Paraguay River (340 km); (T2) along the BR-262 to Três Lagoas (305 km); and (T3) along the BR-163, BR-267 and MS134 to Nova Andradina (275 km; see Fig. 1). Traffic counts for 2015 reported an average of 5082 vehicles per day for BR262 in Transect T1 and 6227 vehicles per day for BR163 (T3; DNIT 2016). No recent traffic counts were available for T2 or for BR267 (T3). Previous counts date back to Year 2001, in which, for BR262, the estimate was 2193 vehicles per day for Transect T1 and 2146 vehicles for T2. For T3 the estimates were 4783 vehicles per day for BR163 and 3797 for BR267 (DNIT 2016). Surveys were conducted year-round, between March 2013 and April 2014, on a fortnightly basis (25 surveys), totaling 23 000 km. Each survey took 3 days (1 day per road transect), driving at ~40–50 km h⁻¹ searching for road-killed mammals (>1 kg) on both lanes and shoulders. Each observation was classified to species level (when possible) and its location was recorded with hand-held GPS. The carcass was then removed from the road.

Data analyses

Modelling WVC occurrence

Environmental predictors. A set of environmental predictors was assembled aiming to detect associations with the WVC

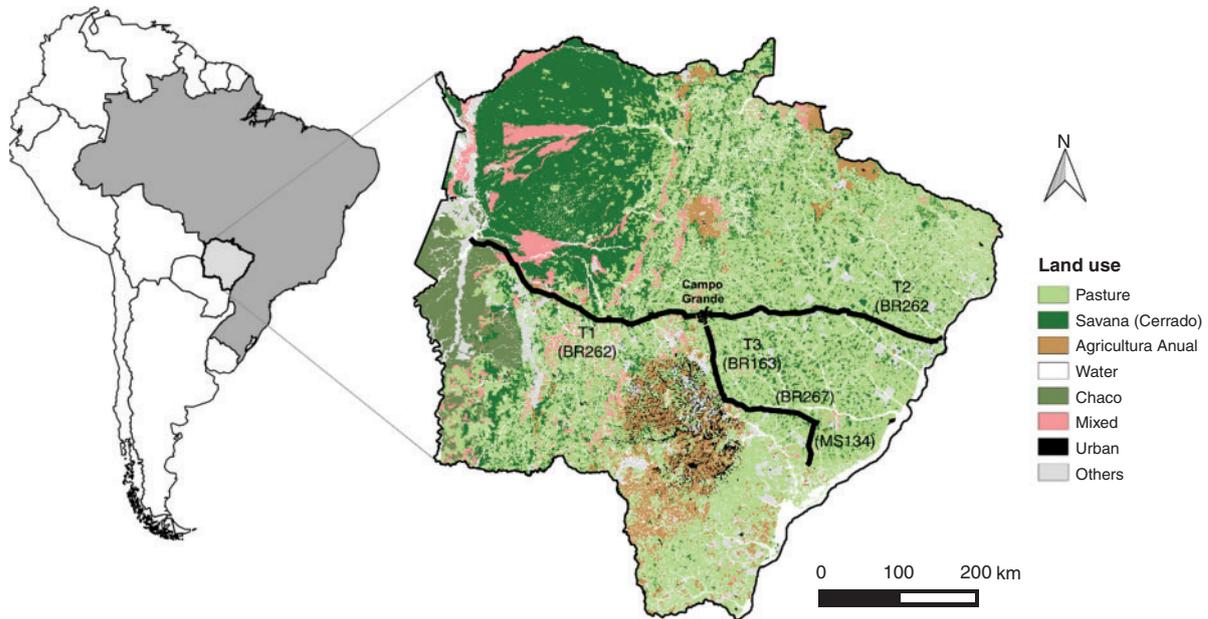


Fig. 1. Location of surveyed roads in Mato Grosso do Sul (MS; smaller figure is MS location in Brazil). Main classes of land cover and road network (from openstreetmap.org) are also presented. T1, T2 and T3 had 342 km, 308 km and 508 km, respectively.

patterns observed. Land cover was obtained from the GeoMS project (Silva *et al.* 2011), a land cover map of MS being built using CBERS 2 images from 2007 with 20-m resolution. This map has 78 different classes, grouped into 11 major classifications. We reclassified this map into eight classes (mostly based on the major classifications), namely: pasture, cerrado, agriculture, chaco, mixed, urban, riparian, water bodies and others (Fig. 1). The map was rasterised using a grid cell of 20 m in size. From this raster, we further created two other layers denoting the Euclidean distance to riparian areas and to urban areas (also with 20-m resolution). We complemented this information with data from the MODIS sensor of satellite Terra, the Vegetation Continuous Fields (MOD44B product, with ~250-m resolution at equator), which provides an estimate of percentage tree cover for each grid cell. We used the data from 2014, downloaded from <https://lpdaac.usgs.gov> (accessed 9 November 2015). We also included topographic ruggedness because of its important role in vegetation distribution (Bennie *et al.* 2008). We used the data from the Shuttle Radar Topography Mission (SRTM) digital elevation model at the spatial resolution of ~90 m (Jarvis *et al.* 2008). We quantified ruggedness as the mean of the absolute differences in slope between the value of a cell and the value of its eight surrounding cells. Summary statistics of all variables for the vicinity of surveyed roads are shown in Table S1, available as Supplementary material to this paper.

A weighted distance-based roadkill index was also included in the models, representing the intrinsic roadkill risk. We adapted the index suggested by Santos *et al.* (2013), by using the number and also the proximity of other WVC at each location (i.e. excluding the records of modelled species). For each WVC of the target species, we calculated the index as follows:

$$\sum_{i=1}^n \left(1 - \frac{d_i}{r}\right),$$

where $i \dots n$ represent all WVC with other species (not the target species) presented in a given radius r from the target individual, and d_i is the distance between i and the target individual. We used $r = 5000$ m, coincident with the value used in hotspot identification (see below). The use of a weighted distance was preferred to compensate the wide radius used in calculation and, therefore, give more importance to nearby records. The use of this index is meant to reduce confounding effects related to road characteristics, habitat suitability and landscape connectivity, and to overcome a lack of data regarding characteristics such as driver visibility, traffic volume and speed (Santos *et al.* 2013). We assumed that such locations with a high overall mortality have also a high intrinsic risk for focal species.

Modelling procedures. We selected the most represented species (number of WVC > 30) as the focal species in further analyses, to facilitate modelling procedures, while ensuring broad representativeness in terms of conservation status and body size (see Table 1). For each focal species, we generated the same number of random points (minimum distance to WVC of 1000 m). For each point, we assigned the mean value of land-cover classes, tree cover and ruggedness within a buffer of 5000-m radius, the roadkill index, the distance to riparian areas and urban distances.

We used boosted regression-tree analysis (BRT; Elith *et al.* 2008) to establish a multivariable empirical relationship between the distribution of WVC locations and the environmental predictors along the surveyed roads. Boosted regression-tree analysis is a machine-learning approach that can automatically model complex functions and the interactions between variables without making assumptions about the shape of the fitted functions or the interactions among variables de (De'ath 2007;

Table 1. Summary of roadkill data

Species are sorted by number of records. The top seven species ($N > 30$, marked with *), referred as focal species throughout the text, were retained for modelling procedures (boosted regression-tree analysis (BRT), see text for details). IUCN, International Union for Conservation of Nature (IUCN) conservation status; BM, approximate mean body mass in kilograms based on Paglia *et al.* (2012); N , total number of records

Common name	Scientific name	IUCN	BM	N
Crab-eating fox*	<i>Cerdocyon thous</i>	LC	6.5	239
Six-banded armadillo*	<i>Euphractus sexcinctus</i>	LC	5.4	224
Giant anteater*	<i>Myrmecophaga tridactyla</i>	VU	30.5	124
Southern tamandua*	<i>Tamandua tetradactyla</i>	LC	5.2	116
Capybara*	<i>Hydrochoerus hydrochaeris</i>	LC	50	106
Nine-banded armadillo*	<i>Dasyops novemcinctus</i>	LC	3.6	79
Lowland tapir*	<i>Tapirus terrestris</i>	VU	260	36
Crab-eating raccoon	<i>Procyon cancrivorus</i>	LC	5.4	27
Ring-tailed coati	<i>Nasua nasua</i>	LC	5.1	14
Collared peccary	<i>Pecari tajacu</i>	LC	17–35	12
Maned wolf	<i>Chrysocyon brachyurus</i>	NT	2.2	7
Ocelot	<i>Leopardus pardalis</i>	LC	8.0–11.0	7
White-eared opossum	<i>Didelphis albiventris</i>	LC	0.5–2.7	5
Hoary fox	<i>Lycalopex vetulus</i>	LC	4	5
Pantanal cat	<i>Leopardus braccatus</i>	NE	3	3
Black-and-gold howler monkey	<i>Alouatta caraya</i>	LC	3.8–8.2	1
Neotropical otter	<i>Lontra longicaudis</i>	DD	6	1

Elith *et al.* 2008). Boosted regression-tree analysis can accommodate different types of predictor variables and missing values, is immune to the effects of extreme outliers and to the inclusion of irrelevant predictors. Boosted regression-tree analysis, thus, provides a powerful tool for analysing complex ecological datasets, and examining the relations between environmental predictors and the spatial patterns of WVC. Boosted regression-tree analysis requires two important parameters that must be provided in advance, the learning rate (lr) and tree complexity (tc). The former determines the contribution of each tree to the growing model, whereas the latter determines the complexity of variable interactions that may be fitted; a value of one fits an additive model, a value of two fits a model with two-way interactions and so on. Elith *et al.* (2008) provided more details of these parameters and provided rules of thumb for selecting appropriate settings. Here, BRT models had a lr between 0.005 and 0.01 and tc of 3 and were optimised so that a minimum of 1000 trees was fitted for each model (Elith *et al.* 2008). In BRT, stochasticity is controlled by the parameter ‘bag fraction’ (the proportion of data to be selected at each step), which was set to 0.50 or 0.75.

Model performance was assessed using 10-fold cross-validation. This procedure compares fitted values from 10 individual models, each derived from a random subset of the full data, against the portion of the data withheld from the model (Elith *et al.* 2006). We used the cross-validated correlation, which provides a measure of correlation between the recorded observations and the model fitted values, and the area under the receiver-operator curve (AUC). Area under the receiver-operator curve ranges between 0.5 and 1, with higher values indicating a better performance of the BRT

model in discriminating between WVC locations and random locations. We also assessed the explained deviance (of the full model), which provides a measure of the goodness-of-fit between the predicted and raw values, and was calculated as $1 - (\text{residual deviance}/\text{total deviance})$.

The relative importance of each predictor was assessed on the basis of how often each predictor was selected for splitting, and the improvement to the model as the result of a variable being selected (Elith *et al.* 2008). Partial dependence plots were used to visualise the fitted functions from the BRT models. These plots showed the effect of a predictor on the response, while controlling for the average effect of all other variables in the model, therefore providing a useful basis for interpretation (Elith *et al.* 2008). Partial-dependence plots must be interpreted with caution when the variables are strongly correlated because of confounding effects among these variables. Hence, before analyses, we checked for correlations between predictors using pairwise Spearman correlations. All values were < 0.5 .

Spatial autocorrelation in model residuals may inflate model accuracy (Veloz 2009), leading to Type I errors (Dormann *et al.* 2007) and, therefore, to erroneous model inferences (Kühn 2007). Several methods have been developed to account for the effects of spatial autocorrelation (Legendre 1993; Dormann *et al.* 2007; Bardos *et al.* 2015). Here, we used an autocovariate similar to the roadkill index previously described but using only the location data of conspecific casualties. This autocovariate was meant to capture the typical aggregation pattern in roadkill data, which generally leads to higher autocorrelation values.

Identification of hotspots of mortality

A modified Ripley’s K statistic was used to determine the scales at which roadkill of focal species was significantly spatially aggregated using the SIRIEMA v1.0 software (Coelho *et al.* 2008). The process consists of calculating the average number of points within a Distance d from each point in the dataset and then dividing this amount by the overall road length to give $K(d)$. The value d is gradually increased by a given distance, until it matches the total road length. The difference between $K(d)$ and the values that would be expected if the points were randomly distributed along the road is referred to as the L statistic, where values above the confidence interval indicate clustering of WVCs at that scale, whereas values below the confidence interval imply dispersion in the data (Coelho *et al.* 2008). Because of our mammalian dataset, we set an initial search distance d of 1000 m, with increments of 1000 m for each step, and 999 simulations for each species and road to evaluate the significance of clustering.

Roads were then split into sections of equal length on the basis of aggregation patterns across focal species and roads, and records were aggregated by road section. For each species and road transect separately, hotspots were defined by comparing the observed number of collisions per section with the number of collisions expected under a random Poisson distribution (Malo *et al.* 2004). We used the false discovery-rate approach (Benjamini and Hochberg 1995) to correct for multiple significance testing Type I error, using $\alpha = 95\%$ cut-off.

Across-species benefits of road mitigation

We wanted to assess the effectiveness of targeting road management to mitigate hotspots of all focal species and for

the most problematic species. We classified as ‘problematic’ those focal species for which collisions can pose a considerable risk to human lives and/or that are of conservation concern, including lowland tapir, giant anteater and capybara. The first two species were classified as such due to their body mass and conservation status and the third mostly due to its body mass (Table 1). Effectiveness was measured as the proportion of individuals, from focal species and remaining species, that would have been ‘saved’ from collisions if proper mitigation had been applied to hotspots.

All calculations (except for SIRIEMA) and plots were produced in R environment (R Core Team 2016). BRT analyses were performed using the ‘gbm’ (Ridgeway 2015) and ‘dismo’ (Hijmans *et al.* 2015) packages, supplemented with functions from Elith *et al.* (2008). The spatial autocorrelation was assessed by Moran’s *I* as implemented in the R package ‘spdep’ (Bivand and Piras 2015).

Results

WVC composition

We recorded 1006 road-killed mammals from 18 species (Table 1) that encompass ~42% of species with bodyweight over 1 kg present in MS (Cáceres *et al.* 2008). T1 had the highest proportion of records (52%), followed by T2 (29%) and T3 (27%). These numbers represent 154 records per 100 km per year for T1, 96 for T2 and 100 for T3.

We selected the following seven focal species that we used for further analyses: lowland tapir (*Tapirus terrestris*), capybara (*Hydrochoerus hydrochaeris*), giant anteater (*Myrmecophaga tridactyla*), southern tamandua (*Tamandua tetradactyla*), crab-eating fox (*Cerdocyon thous*), six-banded armadillo (*Euphractus sexcinctus*) and nine-banded armadillo (*Dasybus novemcinctus*). These species had between 36 and 239 records, which together accounted for 92% of records (Table 1). Their body mass ranges between ~4 and 260 kg, and they are classified as ‘Least Concern’ or ‘Vulnerable’ by the IUCN (Table 1). It is noteworthy that we also recorded other species of conservation concern, including the maned wolf (*Chrysocyon brachyurus*), pantanal cat (*Leopardus braccatus*) and Neotropical otter (*Lontra longicaudis*), but these were not included in the analyses because of low sample sizes.

Spatial patterns and environmental drivers

The spatial autocorrelation was greatly reduced by using the autocovariate, which ranked first in six of the seven models,

having a relative importance between 16% for lowland tapir and 51% for six-banded armadillo (mean 34%). Moran’s *I* was always non-significant in all cases. Cross-validation results suggested that models had a reasonable adjustment to data, with correlations ranging between 0.35 ± 0.05 and 0.73 ± 0.02 (value \pm standard error), and AUC ranging between 0.70 ± 0.03 and 0.88 ± 0.01 . The deviance explained ranged between 0.14 and 0.46 (Table 2).

The roadkill index also ranked as a high-importance variable (mean 14%) determining WVC occurrence, particularly for nine-banded armadillo (importance 24%). Overall, the probability of occurring WVCs was generally higher where both measures were also higher (Fig. 2). The presence of water and distance to riparian areas were important drivers shaping the spatial patterns of WVC, particularly for capybara and lowland tapir, species associated with water environment, but also to crab-eating fox, giant anteater and southern tamandua. According to the results, the likelihood of WVC increases when a few proportion of the surrounding area is covered by water bodies or in the proximity of riparian areas (Fig. 2). The distance to urban areas had a considerable importance (mean 18%), particularly for lowland tapir and giant anteater. However, the partial plots suggested a contrasting influence of this variable for the two species; for lowland tapir (and nine-banded armadillo), the probability of WVC occurring increased with an increasing distance from urban areas, whereas, for the giant anteater, higher probabilities seemed to be related to a close proximity of urban areas (Fig. 2). In contrast, the probability of WVC for southern tamandua seemed to follow a bimodal pattern, with higher values occurring both near and far from urban areas. Regarding land-use variables, the cover of cerrado and pasturelands, and the proportion of trees had an importance below 10% across species. Higher cover of pastureland was related to a higher likelihood of roadkill of giant anteater and southern tamandua, whereas, for capybara, higher probabilities were found for areas with less than 60–70% cover of this land use. Areas dominated by cerrado (>20%) had a clear higher probability of having more roadkills of crab-eating fox and six-banded armadillo. The amount of tree cover seemed to have some influence in the collision patterns of giant anteater and southern tamandua. Finally, higher topographic ruggedness was associated with a higher likelihood of mortality of both armadillos and giant anteater, whereas smoothest areas had a higher probability of roadkill for capybara and lowland tapir.

Table 2. Summary of boosted regression-tree analysis (BRT) models

Deviance refers to deviance explained (of the full model). AUC, area under the curve; Moran’s *I* refers to the *P*-value of spatial autocorrelation measure. Correlation and AUC are the mean values from cross-validation procedures, with the standard errors in parentheses. Species are sorted by number of records

Species	Moran’s <i>I</i>	Correlation	Deviance	AUC
Crab-eating fox	0.983	0.381 (0.030)	0.226	0.720 (0.017)
Six-banded armadillo	0.371	0.526 (0.036)	0.332	0.810 (0.021)
Giant anteater	0.764	0.210 (0.060)	0.140	0.624 (0.032)
Southern tamandua	0.415	0.457 (0.076)	0.341	0.757 (0.044)
Capybara	0.130	0.624 (0.051)	0.445	0.832 (0.029)
Nine-banded armadillo	0.385	0.574 (0.033)	0.459	0.814 (0.021)
Lowland tapir	0.384	0.539 (0.075)	0.395	0.795 (0.044)

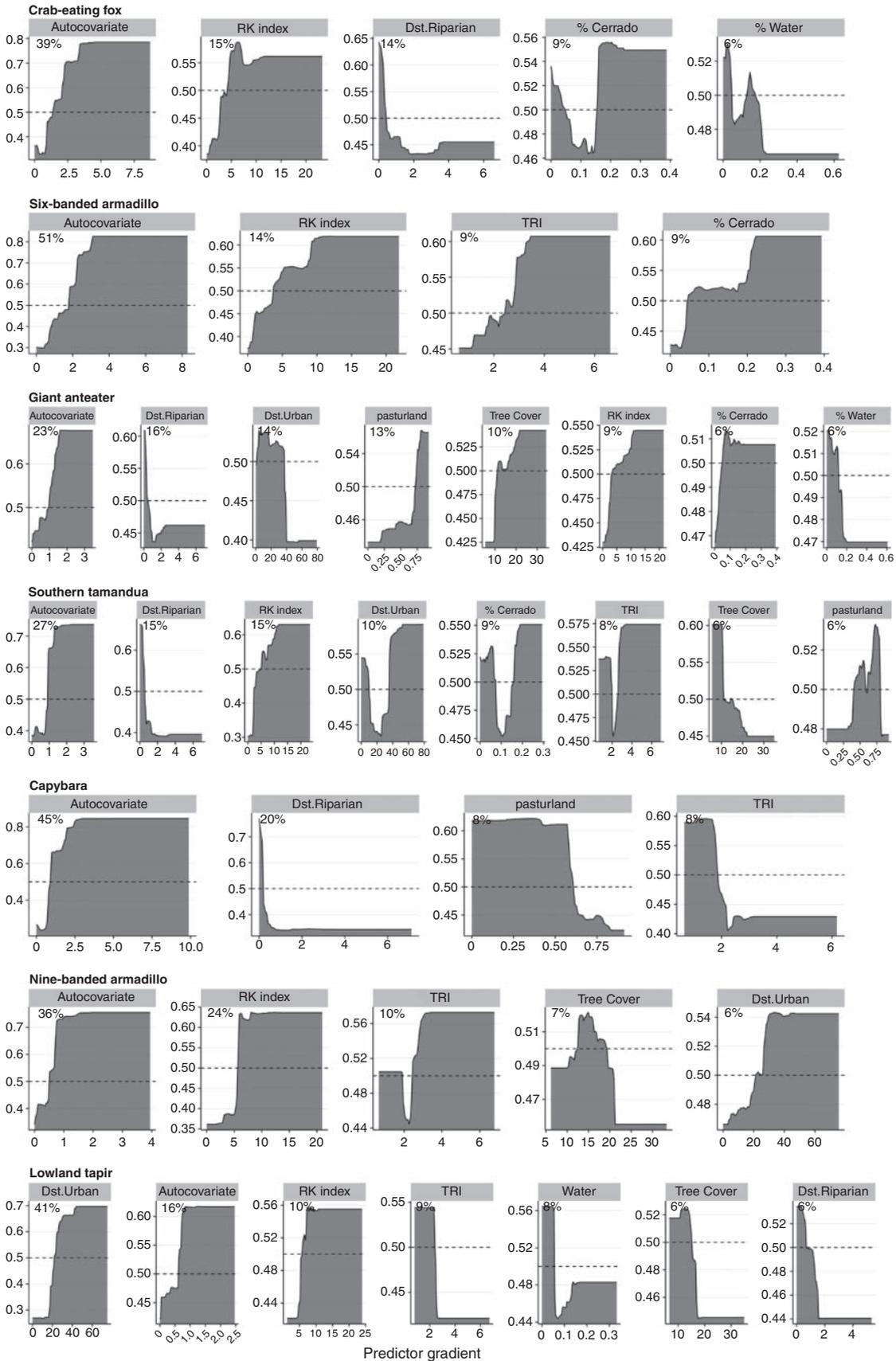


Fig. 2. (continued)

Hotspots of mortality and cross-species benefits of implementing road mitigation

We detected significant clustering over a wide range of scales for the seven focal species (Fig. S1, available as Supplementary material to this paper). We used 5000-m section lengths to detect hotspots, because all species showed significant clustering at this distance along at least one of the road transects. Also, this length allowed reasonable aggregation of casualties for less recorded species.

In total, we identified 21 sections (12% of the road transects) that were classified as hotspots for at least one focal species, eight being in T1, five in T2 and eight in T3 (Fig. 3). There was considerable variation in the location of hotspots among focal species. In fact, only four sections (~2%) were hotspots for more than one species, whereas only giant anteater had hotspots in all three roads (Fig. 3). These hotspots comprised 26% of the overall WVC records, including, 32% of six-banded armadillo, 29% of nine-banded armadillo, 21% of crab-eating fox and 23% of southern tamandua. Nearly half ($n=12$) of the hotspots were so for at least one problematic species, i.e. lowland tapir, giant anteater and capybara, and covered 42% of capybara casualties, 39% of lowland tapir and 16% of giant anteater. These 12 sections represent ~7% of the surveyed roads, which, if properly mitigated, would have prevented only 10% of the remaining WVC. Moreover, no other conservation concern species was detected in these 12 sections.

Discussion

We surveyed three main roads throughout Mato Grosso do Sul, Brazil, searching for medium to large mammal roadkill. We recorded casualties involving at least 18 species, including important species of conservation concern such as lowland tapir, giant anteater, maned wolf, Pantanal cat and Neotropical otter. These results highlighted the conservation value of this region (Costa *et al.* 2005; Silva *et al.* 2006) and showed that roadkill affects a large number of medium–large mammals present therein (Cáceres *et al.* 2008). Hence, our results reinforced the need for management actions to reduce the number of WVCs in study area (Cáceres *et al.* 2010; de Souza *et al.* 2015). Our numbers are likely to be conservative for some species, given that the periodicity of our surveys was fortnightly and small carcasses may disappear in a few days (Santos *et al.* 2011, 2016; Teixeira *et al.* 2013). Moreover, because the scavenger activity may be variable along the territory (Santos *et al.* 2016), we acknowledge that the spatial patterns of mortality may be biased. However, because we focussed on medium–large mammal species (>4 kg), the persistence of carcasses is expected to be longer, and, therefore, these biases probably had a minor impact in analyses.

The BRT models indicated that the roadkill index was one of the most important variables explaining the WVC locations, together with the autocovariate that related the roadkill

location with the number and distance to other conspecific casualties. The roadkill index can be regarded as a proxy of roadkill likelihood (Santos *et al.* 2013). The rationale is that a higher number and neighbouring casualties of other species should reflect several road and landscape characteristics that are likely to influence the overall mortality, either because of higher population abundance or roadkill probability (Santos *et al.* 2013). Likewise, although the autocovariate was used to capture the typical aggregation pattern found in roadkill data and reduce the effect of spatial autocorrelation, it came out also as an important explanatory variable. The high importance found for both measures supported the fact that WVC mainly occur in road sections traversing areas with more abundant and diverse communities (D'Amico *et al.* 2015). In fact, many species do not show road avoidance (Jaeger *et al.* 2005) and, thus, it is plausible to believe that a higher abundance will lead to a higher number of casualties of a certain species, given the expected higher number of crossings. Likewise, communities with a higher species richness will lead to a higher number of species road-killed. Hence, these indexes are likely to reflect more the effect of the landscape connectivity and resource distribution for multiple species (Santos *et al.* 2013). For example, it was demonstrated that areas of high connectivity are associated with higher WVC rates of stone marten (*Martes foina*; Grilo *et al.* 2011).

The variables used to characterise the road-surrounding environment, namely the land cover and ruggedness, generally had a lower importance in BRT models. Perhaps the variables used were not able to capture the main drivers explaining the observed patterns of mortality. For example, variation in the distribution of resources (e.g. food) within the same land-cover class, or the different collision risk related to vehicle speed and traffic volumes. However, this information was not available in our study area, preventing its use. Contrary to expectations, the land-cover predictors were less important in explaining the WVC patterns. One possibility is that the modelled species, despite being common savanna dwellers, can inhabit and move through a wide range of habitats (Herrera and Macdonald 1989). Moreover, these species were recorded throughout the surveyed roads, suggesting that their populations are spread, thus supporting the possibility that the land-cover matrix provides adequate conditions for animal persistence or, at least, movement of individuals. Nevertheless, we were able to distinguish interesting relationships between WVC probability and the explanatory variables employed. WVCs were generally related to proximity to riparian areas and water availability, particularly for capybara and southern tamandua. Well preserved riparian areas are known to provide quality habitat for these species (Bueno *et al.* 2015) and probably serve as movement corridors for many others (Lees and Peres 2008; de Freitas *et al.* 2014b). Our study corroborated others showing that WVCs of several medium–large mammals tend to occur near riverine habitats, including capybara (Cáceres *et al.* 2010; Bueno *et al.* 2015), crab-eating fox (de Freitas *et al.* 2014b),

Fig. 2. Partial dependence plots for the variables influencing wildlife–vehicle collisions (WVC) of focal species in Mato Grosso do Sul, Brazil. Plots are sorted by species' number of records (see Table 1). Y-axes express the probability of occurring WVC for a variable of interest when all other variables are held constant (partial dependence). For each species, we considered only variables with an influence above 5%. The variables are sorted according to its relative influence (%), per species (top left). Dotted line stands for 50% probability. Note that the range of the both axis varies within and among variables.

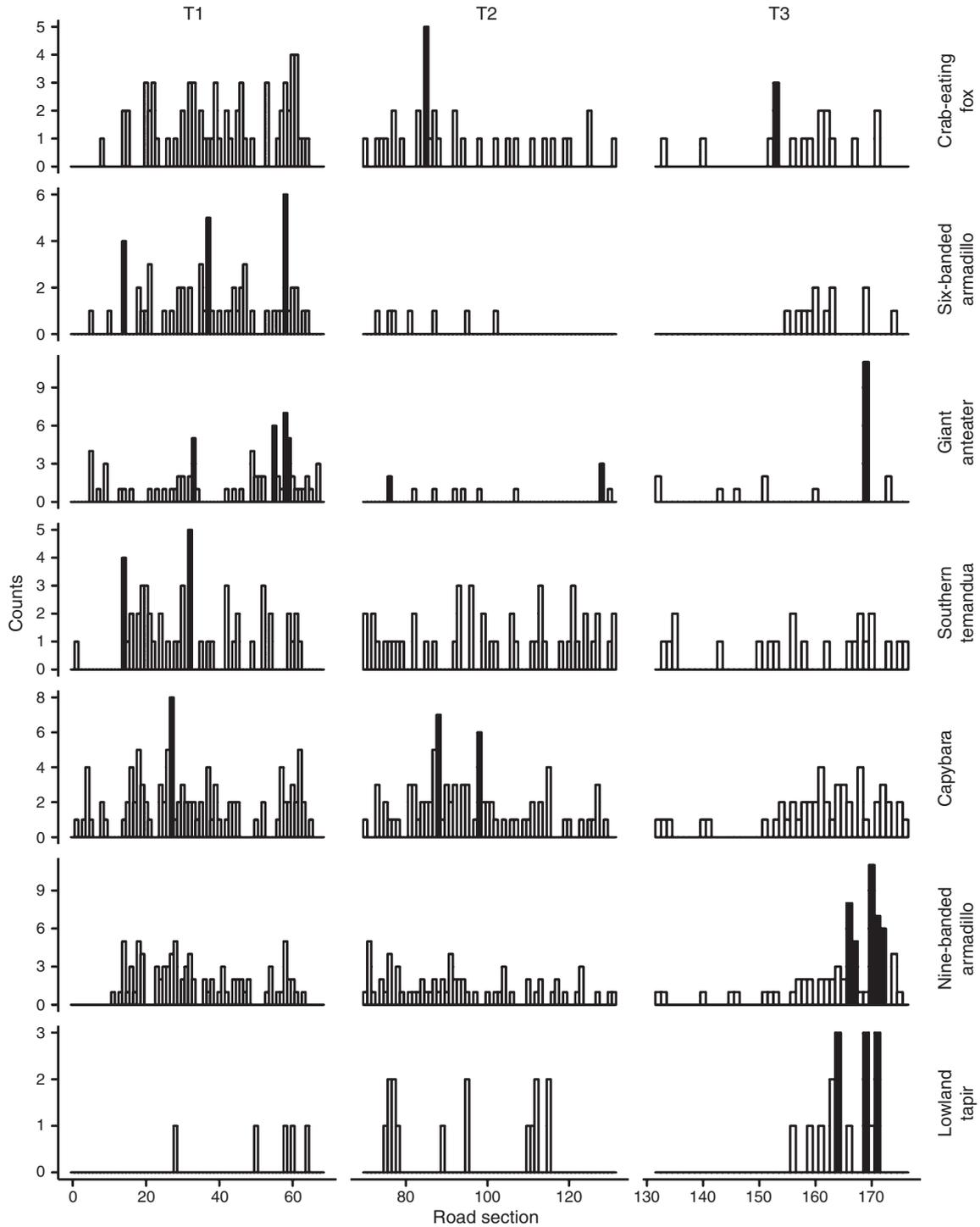


Fig. 3. Counts of wildlife–vehicle collisions (WVC) for each section of 5 km, per road transect and species. Hotspot sections are filled in black (after correcting for Type I errors). Transect section numbers start at Campo Grande city (see Fig. 1). Plots are sorted by species’ number of records (see Table 1).

European otter, *Lutra lutra* (Philcox *et al.* 1999), and white-tailed deer, *Odocoileus virginianus* (Finder *et al.* 1999).

Regarding distance to urban areas, the lowland tapir showed a clear pattern of higher WVC probability in more distanced road

stretches. Perhaps this response reflects the lower anthropogenic pressure far from urban areas, which is known to be an important factor shaping species occupancy (Cáceres *et al.* 2010; Licona *et al.* 2011). However, the opposite pattern was found for giant

anteater. Traffic volumes are generally more intense near urban areas, and, therefore, intentional vehicle strikes towards this species may occur more frequently (Bertassoni 2012). Ruggedness played an important role shaping the WVC occurrence for southern tamandua, both armadillos, capybara and lowland tapir. However, its effect was also distinct across species, with capybara and tapir casualties occurring more in plain areas, and those of the remaining species occurring in steeper areas. These species are known to prefer grasslands, generally in flat areas, where they find abundant food. However, during floods, these areas become inaccessible and individuals search for higher elevated areas, namely road corridors where they become prone to collisions (de Souza *et al.* 2015).

We detected several hotspot sections along the surveyed roads that are good candidates to apply mitigation measures. However, we advocate that the selection of sections for mitigation should not rely only on hotspot location. For example, roadkill surveys generally detect many records for few species, but few observations for several other species. Hotspots may be difficult to detect for species with low representation, such as rare and low-density species often of high conservation concern. However, even if there are many casualties, but they are evenly distributed along the road (i.e. not concentrated), hotspots may never emerge. Moreover, a large proportion of casualties of a given species can occur outside the hotspot sections. For example, if all hotspots involving lowland tapir were properly mitigated, our records indicated that its WVC would still be striking, representing a mortality rate of at least one individual per year per 100 km. This rate could represent significant costs for both humans and vehicles, as well as for tapir populations (Medici and Desbiez 2012). Likewise, the impact of WVC on giant anteater would still be considerable even if all hotspots of this species were mitigated. High mortality rates for this species have continuously been recorded in the region (Cáceres *et al.* 2010; de Freitas *et al.* 2014a; de Souza *et al.* 2015), which is probably due to a combination of factors, including high populations densities (owing to high-quality habitat), slow reaction time to traffic (Stahl *et al.* 2012) and higher activity at periods of higher traffic volume (Mourão and Medri 2007). Hence, this species is likely to be severely depleted if such high-roadkill rates persist (Diniz and Brito 2013).

Even for more common species, focusing mitigation on hotspots may fail to prevent population depletion. Crab-eating fox was the most frequently encountered roadkill. This species is abundant throughout the territory (Faria-Corrêa *et al.* 2009; Cáceres 2011), and is often recorded in roadkill studies, including in MS (Cáceres *et al.* 2010; Freitas *et al.* 2013; de Souza *et al.* 2015). However, the mortality rate we have presented is remarkably high for a carnivore. Albeit this species being likely to have a large effective population size in MS, it has only one reproductive period per year and a low density (0.24–0.78 individuals km⁻²; Faria-Corrêa *et al.* 2009; Desbiez *et al.* 2010). Also, focusing mitigation efforts on roadkill hotspots may ignore populations that have been reduced by past traffic-related mortality (Eberhardt *et al.* 2013; Teixeira *et al.* 2017). Moreover, although we have used a simple procedure to evaluate the cross-species benefit of mitigation, we have shown that hotspots may have a limited overlap across species and so mitigation focussed on the WVC of certain problematic

species may have limited benefit for other species (Clevenger and Waltho 2005). Hence, despite being important tools to prioritise road sections for mitigation, the identification of mortality hotspots might omit several other species and/or records of WVC.

Management implications

For such wide-ranging species, the question remains as to how road management may significantly decrease WVCs. Our results and other studies have suggested a relationship between the probability of WVC and habitat preferences (Grilo *et al.* 2011; D'Amico *et al.* 2015). Thus, the challenge is to understand how different species occupy the landscapes surrounding road networks, so as to identify displacement corridors for multiple species (Mimet *et al.* 2013). We suggest that roadkill research should focus more in habitat-quality and -connectivity analyses at the community level, together with hotspot identification. Such approach may provide a better assessment of potential roadkill impacts, as well a good criterion for ranking where to install mitigation measures.

At the local scale, management should focus on installing or improving crossing points in junctures between riparian strips and roads, because they are known to be preferred locations used by animals for road crossings (Lesbarrères and Fahrig 2012). This is also supported by our results, because several WVCs occurred near riparian areas. Previous research has shown that road passages connected to exclusionary fencing with proper mesh size can effectively reduce WVCs for several medium–large mammals (Clevenger *et al.* 2001; Lesbarrères and Fahrig 2012; Rytwinski *et al.* 2016). Moreover, cost–benefit analyses clearly support the implementation of these mitigation measures where human lives are endangered (Huijser *et al.* 2009, 2013). Note that fencing all road length may result in detrimental barrier effects (Jaeger and Fahrig 2004), and so drift fences should have the necessary length to channel wildlife to passages (Ascensão *et al.* 2013). Other mitigation measures should also be considered, including reduced traffic speed and effective signage (Hobday 2010; Lester 2015), as well as environmental education to improve driver attitudes (Neumann *et al.* 2012).

Our study has provided knowledge that may prompt road planners for installing mitigation measures in more sensitive areas during the planning phase. This is crucial in regions with a rich biodiversity, such as in Brazil (Myers *et al.* 2000; Brooks *et al.* 2006; Laurance *et al.* 2009; Visconti *et al.* 2011), which has also one of the most extensive road networks in the world. Inevitably, the interactions between the high biodiversity value and the vast road network result in conflict, namely in high rates of roadkill (Laurance and Balmford 2013). Moreover, the road network is expanding, further, reinforcing the negative consequences for wildlife. In the face of this growth of development, we suggest that more ambitious measures are required to ensure sustainable coexistence between human development and Brazilian wildlife (Faleiro and Loyola 2013). A reconciliatory approach between land use and conservation is necessary, highlighting the extreme benefits of preserving roadless areas in terms of their ecosystem services (Selva *et al.* 2011). Maintaining roadless areas may increase the probability of species presence throughout the territory, which, in turn, may function as a source for surrounding

areas. Areas of high conflict between road networks and wildlife should be targeted (Laurance and Balmford 2013) for broad-scale management to preserve Brazilian biodiversity.

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