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# Roads as ecological traps for giant anteaters

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## Abstract

Wildlife-vehicle collisions (WVCs) represent a serious source of mortality for many species, threatening local populations' persistence while also carrying high economic and human safety costs. Animals may adapt their behaviour to road-associated threats, but roadside resources can also attract individuals to dangerous roadside habitats, ultimately acting as an ecological trap. Yet, the extent to which individuals modify their behaviour and space use to roads is largely unknown for most taxonomic groups. Using fine-scale movement data from 38 giant anteaters *Myrmecophaga tridactyla* tracked in the Brazilian Cerrado, we aimed to identify facets of movement behaviour that might exhibit plasticity to roads and traffic volume. Specifically, the analysis of daily and instantaneous movement speeds, home-range characteristics and crossing rates/times allowed us to test for an effect of road proximity, traffic volume and natural linear features on movement behaviour. We found no effect of road proximity or traffic volume on space use or movement behaviour. While individuals tended to reduce their movement speed when approaching roads and crossed roads ~3 times less than would have been expected by random chance, none of the three highways we monitored were impervious. The majority of tracked anteaters living near roads (<2 km) crossed them, with higher crossing rates for males than females. Habitat near roads may function as an ecological trap where healthy individuals occupy the territories nearby or bisected by roads but eventually are road-killed given their regular crossings, leaving the territory vacant for subsequent occupation. Crucially, we found no evidence that anteaters actively searched for passage structures to cross the roads. This suggests that crossing structures alone are unlikely to mitigate WVC-induced mortality in giant anteaters. Our research reinforces the need to implement fencing, leading to existing passages, and minimizing the amount of night-time driving to reduce the number of WVCs.

## Introduction

Human development reduces the amount of habitat available to wildlife (Venter *et al*., 2016). Animals moving through altered landscapes are coming into conflict with humans at rapidly increasing rates (Fahrig, 2007; Macdonald, 2016; Buchholtz *et al*., 2020). Of special concern are the impacts of roads on biodiversity (Forman *et al*., 2003; Van der Ree, Smith & Grilo, 2015). In particular, wildlife-vehicle collisions (WVCs) that occur while animals try to move across roads represent a serious source of mortality for many species (D'Amico *et al*., 2015; González-Suárez, Zanchetta Ferreira & Grilo, 2018; Ascensão, D'Amico & Barrientos, 2019). WVCs not only threaten the local population persistence (Desbiez, Bertassoni & Traylor-Holzer, 2020) but also carry high economic and human safety costs (Abra *et al*., 2020; Ascensão *et al*., 2021). Beyond the direct impact of WVCs, roads can also hinder species' capacities to disperse and redistribute (Clark *et al*., 2010; Long *et al*., 2010), potentially reducing gene flow and population viability (Riley *et al*., 2006; Ceia-Hasse *et al*., 2018).

While roads are important for socio-economic growth, the detrimental impacts of roads (Fahrig & Rytwinski, 2009) are expected to drive individuals living in road-bisected habitats to respond by adapting their behaviour to the requirements of roadside environments (Ascensão *et al*., 2017). Roadside foraging opportunities can act as attractants for many species (Barrientos & Bolonio, 2009; Ascensão *et al*., 2012), however, providing misleading information about habitat quality. When species perceive these attractants but fail to learn to avoid oncoming vehicles (see Jacobson *et al*., 2016) and/or fail to search for existing road passages, such as culverts (see Clevenger, Chruszcz & Gunson, 2001) for safe crossings, this can act as an ecological trap (Schlaepfer, Runge & Sherman, 2002) that may carry severe consequences. Behavioural plasticity towards roads is especially important for long-lived, *K*-selected species (Sih, Ferrari & Harris, 2011; Montgomery, Macdonald & Hayward, 2020) that take longer to reach sexual maturity and have longer interbirth intervals than short-lived species (De Magalhaes & Costa, 2009). Yet, the extent to which individuals modify their movement behaviour and space use to roads is largely unknown for most taxa—despite such information being critical in both the delineation of species and landscape management programs and for the planning and mitigation of transportation infrastructures (D'Amico *et al*., 2016).

Here, we address this research gap by identifying facets of animal behaviour that might exhibit plasticity in response to roads. We base our study on giant anteaters *Myrmecophaga tridactyla*, the largest extant anteater. Giant anteaters reach over 2 m and weigh up to 50 kg (McNab, 1984) and are distributed throughout Central and South America (Gardner, 2008). Giant anteater populations have suffered severe reductions with local and regional extirpations and are currently classified as vulnerable to extinction (Miranda *et al*., 2014). Moreover, WVCs are a major threat to giant anteaters, as they are commonly reported as one of the top mammals recorded in systematic roadkill surveys, reaching an annual rate of ~17 ind. 100 $km^{-1}$ $year^{-1}$ in Mato Grosso do Sul (MS), Brazil (Ascensão *et al*., 2021). Such high non-natural mortality is thought to reduce the viability of populations (Desbiez *et al*., 2020), given their low recruitment (about one pup per year; Gaudin, Hicks & Di Blanco, 2018) and low densities (generally <1 ind. $km^{-2}$) (Bertassoni, Bianchi & Desbiez, 2021). Consequently, reducing WVC-induced mortality is recognized as a conservation priority for the species (Miranda, Bertassoni & Abba, 2014). Despite this recognition, as for most mammals, there is no information on whether roadside residents regularly cross highways, or if dispersing individuals make up the bulk road-killed animals, nor how giant anteaters respond to different types of roads and traffic volumes. Similarly, giant anteaters are known to use road passage structures (Abra *et al*., 2020), but there is no evidence as to whether they search for existing structures to safely cross roads, or if these are only used opportunistically.

Understanding how the movement of giant anteaters responds to roads and its relationship with roadkill can thus provide valuable information for landscape and road management. Such information is even more pressing given the increasing agribusiness expansion, infrastructure development and low legal protection for this species' habitat (Strassburg *et al*., 2017), which may worsen the persistence of local populations in road vicinity areas (Desbiez *et al*., 2020). Moreover, reducing the number of WVCs also reduces the number of human injuries and material damage, with great benefits for people (Ascensão *et al*., 2021). We carried out the most extensive telemetry study on giant anteaters to date to fill these critical knowledge gaps. In particular, we aimed to address four over-arching questions: $Q_1$ – Does the movement behaviour of giant anteaters differ with distance to paved roads? $Q_2$ – Does traffic volume influence giant anteater crossing behaviour? $Q_3$ – Do giant anteaters prefer to cross the roads via passage structures? and $Q_4$ – Do anteaters respond to roads differently than to natural barriers?

Currently, little is known about the movement ecology of giant anteaters (Medri & Mourão, 2005; Giroux *et al*., 2021), but because of the high number of giant anteaters found in roadkill surveys (Ascensão *et al*., 2021) relative to their low population densities (Bertassoni *et al*., 2021), our underlying hypothesis was that roads do not significantly deter giant anteaters. As such, we expected to observe no differences in movement behaviour with road proximity or traffic volumes and similar road crossing rates across the different types of roads and natural linear features such as streams. Likewise, the use of road passage structures (e.g. culverts, viaducts, etc.) was expected to be opportunistic. Findings are directly applicable to developing road and landscape management plans for giant anteaters as well as for other medium–large mammals that occupy road-side habitats.

# Materials and methods

## Study area

The study was conducted at three sites in the state of MS, in the Cerrado biome (savannah) of Brazil (Fig. 1). The climate throughout MS is wet from October to March and dry from April to September (Koppen's Aw), with mild year-round temperatures (range 21–32°C). Average annual rainfall ranges between 1000–1500 mm. The land use bordering all roads was dominated by pasture, with sparse remnants of native forest and savanna, and some areas of eucalyptus plantation. Streams bordered with native riparian vegetation were common throughout the study area, mostly accompanying native savanna vegetation. Three paved, two-lane highways of different ages and traffic volumes cross the study area (Table 1). Speed limits for the highways varied between 80 and 100 km $h^{-1}$. Traffic volume information for BR262 and BR267 was obtained from official counts (DNIT, 2020). MS040 counts were obtained using a similar methodology used by governmental authorities (DNIT, 2020), that is vehicle counting throughout 5 consecutive days, 24 h $day^{-1}$. A network of unpaved roads was also present, linking main roads and ranches. These roads had significantly lower traffic volumes (<1 car $h^{-1}$) in comparison with paved roads (pers. observations when using the roads to access the study areas). Each study area had 9–11 passages (culverts, box culverts and viaducts) near the territories of the tracked giant anteaters (Table 1; Supporting Information Appendix S1). This study was performed under License No. 53798 (Chico Mendes Institute for Biodiversity Conservation) that granted

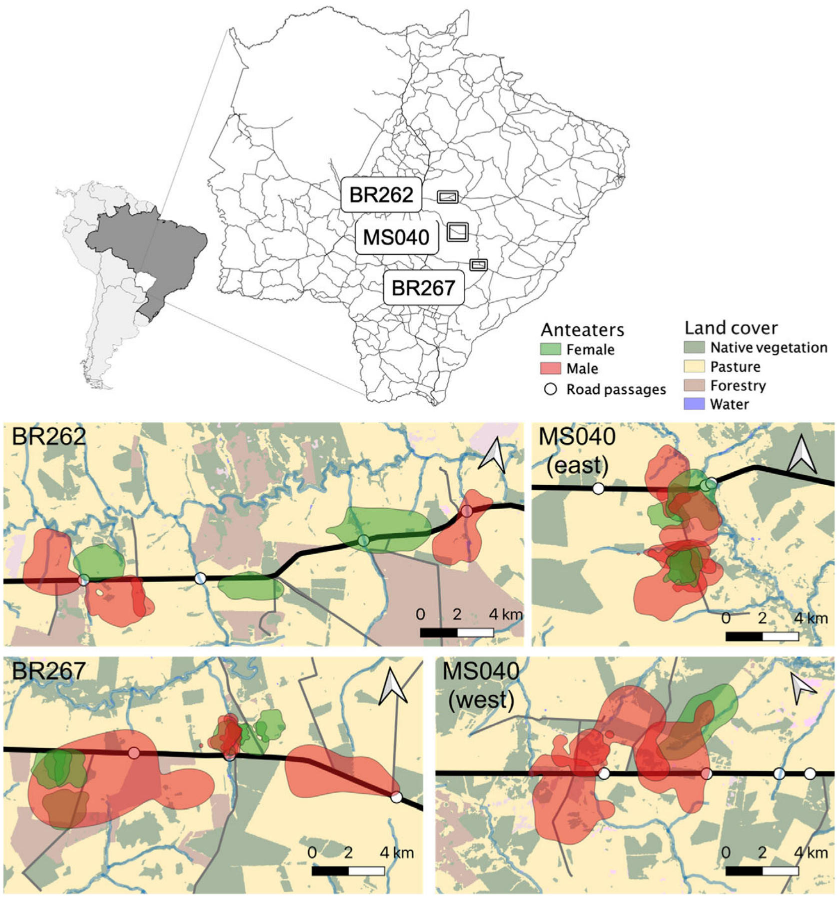


**Figure 1** Map showing the location of the three study areas (BR262, MS040 and BR267) in Mato Grosso do Sul, Brazil (top), with state main road network (black lines). In each study area, home ranges are in red for males and green for females (see text for details); the main paved road is depicted in thick black line and other unpaved roads are in thinner black lines and road passage locations are white circles (some circles indicate more than one passage). Blue lines indicate streams. Land cover classes were from MapBiomas (2018 version).

**Table 1** Age and mean daily traffic volume (MDT) for the three main roads present in the study area. Traffic volume information for BR262 and BR267 was obtained from official counts (DNIT, 2020). MS040 counts were obtained using a similar methodology used by governmental authorities (DNIT, 2020), that is vehicle counting throughout 5 consecutive days, 24 h day$^{-1}$. The 'passages' column indicates the type of passage structures in the study areas (numbers in parentheses are the mean width and the mean height of the passages, in m). Full details on the passages are provided in Supporting Information Appendix S1

| | | | Passages | | |
|---|---|---|---|---|---|
| Study area | Road age (years) | MDT | Culvert | Box-culvert | Viaduct |
| MS040 | 6 | 603 | 2 (1.0 × 1.0 m) | 6 (2.4 × 2.4 m) | 1 (30 × 10 m) |
| BR262 | 34 | 3206 | 3 (2.4 × 2.4 m) | 7 (2.0 × 2.0 m) | 1 (35 × 10 m) |
| BR267 | 34 | 4285 | 9 (1.3 × 1.3 m) | – | – |

permission to capture, immobilize and manipulate giant anteaters and collect/store biological samples. All procedures followed the Guidelines of the American Society of Mammologists for the use of wild mammals in research (Sikes & Animal Care and Use Committee of the American Society of Mammalogists, 2016).

## Giant anteater GPS data collection

Wild giant anteaters were captured between 2017 and 2018, in the vicinity of the three paved highways of the study area, >15 km from urban areas and equipped with GPS tracking collars. The capture team was always comprised of two veterinarians and a biologist, minimum. To capture giant anteaters, we searched open areas for individuals foraging, during colder months (May–August) when individuals are known to exhibit greater diurnal activity (Camilo-Alves & Mourão, 2006). When an adult was spotted, two members of the capture team approached the individual by foot and captured it using two long-handled dip nets (handle 1.5 m; hoop 0.7-m diameter) to restrain it (Kluyber *et al.*, 2021). The veterinarian was then able to safely apply an intramuscular combination anaesthetic injection of butorphanol tartrate (0.1 mg $kg^{-1}$), detomidine hydrochloride (0.1 mg $kg^{-1}$) and midazolam hydrochloride (0.2 mg $kg^{-1}$) into its hind limbs (Kluyber *et al.*, 2021). After anaesthetic induction, the front claws were first wrapped and completely immobilized using tape. Physical exams were then performed to evaluate health conditions and included measuring weight, pregnancy detection (palpation), general appearance, hydration status, mucous membrane colour, respiratory auscultation and presence of scars or wounds (Kluyber *et al.*, 2021). Only adult individuals considered in good health by the veterinarians were fitted with the GPS harness (TGW-4570-4 Iridium GPS) and VHF transmitters (MOD 400; Telonics, Mesa, Arizona). For anaesthetic reversal procedures, all individuals received a combination of three antagonists: naloxone hydrochloride (0.02 mg $kg^{-1}$), yohimbine hydrochloride (0.125 mg $kg^{-1}$) and Flumazenil (0.01 mg $kg^{-1}$) (Kluyber *et al.*, 2021). After the procedure, the animal was maintained in a wooden ventilated crate until complete recovery and was then released at its capture location. Collared giant anteaters were recaptured *c.* 1 year after for harness removal and data download, but each animal was visually inspected at a distance through binoculars at least once every 2 weeks for a general health check without disturbing the animals. The trackers took GPS fixes with 20-min intervals.

We deployed collars on 43 individuals out of a total of 45 total captures (two were deemed too young to collar). These 43 individuals were considered in good health and no signs of infection or diseases were observed during clinical exams performed upon captures and recaptures. Importantly, no health differences were noted between individuals regardless of how far they lived from the highway. Six of the collared giant anteaters were found dead in the course of the study period, four of which were road-killed and two due to unknown causes (see Supporting Information Table S3.1 in Appendix S1). Two of the collared animals had insufficient data due to collar malfunctions and were excluded from our analyses. Furthermore, three of the individuals dispersed over the study period and were therefore excluded from our analyses as we were interested primarily in understanding typical behaviour from range-resident individuals. We therefore present results for 38 range-resident giant anteaters. Trackers operated for a median of 11.2 months across all tagged giant anteaters. The final GPS dataset comprised 847 683 GPS fixes collected over 12 761 individual days (Supporting Information Appendix S2).

## Data analysis

### Movement data preprocessing

Before analysis, we performed a data cleaning process in order to calibrate the GPS measurement error and filter outliers using the methods implemented in the R package 'ctmm' (Calabrese, Fleming & Gurarie, 2016; Fleming & Calabrese, 2020, see Supporting Information Appendix S2). For each location estimate, the GPS trackers recorded a unitless Horizontal Dilution of Precision (HDOP) value which is a measure of the accuracy of each positional fix. We converted the HDOP values into calibrated error circles by estimating an equivalent range error from 6948 calibration data points where a tag had been left in a fixed location (Fleming *et al.*, 2020). For each individual dataset, we then removed outliers based on error-informed distance from the median location, and the minimum speed required to explain each location's displacement.

### Movement metrics

For each of the collared giant anteaters, we quantified key movement metrics and home range–related characteristics that allowed us to test for an effect of road proximity, traffic volume and natural linear features on giant anteater movement behaviour. First, using the R package 'ctmm', we fitted a series of continuous-time movement models (hereafter 'CTMM') to the track data, using perturbative-hybrid residual maximum likelihood (pHREML; Fleming *et al.*, 2019), and identified the best CTMM via small sample-sized corrected Akaike's information criterion ($AIC_c$).

From each CTMM, we estimated both the mean *daily movement speed* (in km $day^{-1}$) and the *instantaneous movement speed* (in m $s^{-1}$) using continuous-time speed and distance estimation (Noonan *et al.*, 2019). This approach is insensitive to the sampling schedule and corrects for GPS measurement error, enabling robust comparisons across individuals.

We next estimated the *home range* for each animal, as the polygon delimited by the 95% isopleth of the utilization distribution using autocorrelated Kernel density estimation (AKDE) (Fleming *et al.*, 2015). AKDE home-range estimates were conditioned on the autocorrelation structure of the CTMM and we implemented the small sample size bias correction of Fleming & Calabrese (2017). For each individual, we quantified the land cover within their home-range polygon to control for possible confounding effects related to habitat quality that could influence movement behaviour. Land cover was obtained from MapBiomas (Souza & Azevedo, 2017) for 2018. We compared the proportion of cover of the two main classes occurring within home ranges, namely pasture and native vegetation. Because of a strong negative correlation between the proportion of pasture and native vegetation in an individual's home range (Pearson correlation = −0.92), only the proportion of pasture cover was included in our analyses. We also calculated the Euclidean distance between each individual's home-range centroid and the nearest paved road.

We further estimated the *total number of crossings* across the highways, unpaved roads and streams for each giant anteater. For this, we used each animal's tracking data and their CTMM to reconstruct the most likely path that they travelled through the landscape. We identified the total number of intersections (crossings) between the most likely path and the different linear features.

## Movement pattern comparisons

We used the information obtained from each animal's GPS location data to address each of our four core research questions. The R code required to reproduce these analyses is presented in Supporting Information Appendix S3.

### $Q_1$: Does the movement behaviour of giant anteaters differ with distance to paved roads?

In order to answer $Q_1$, we tested for any relationship between the distance individuals lived from roads and (1) individual home-range areas, (2) daily movement speeds and (3) instantaneous movement speeds. We also looked at whether there were any differences in these measures across each of the three paved roads to test for an effect of traffic volume. Home-range areas and daily movement speeds were analysed using the meta-regression model implemented in the R package 'metafor' (Viechtbauer, 2010), which allowed uncertainty in each individual estimate to be propagated into the population level estimate when making comparisons. Instantaneous speeds were analysed using a Gaussian mixed-effects model that included the quadratic effects of distance to road and time of day (to control for circadian rhythms) and the identity of the nearest paved road (to control for traffic volume). We also included a random intercept for each individual and a random slope for the relationship between movement speed and the distance to the road for each individual giant anteater. Finally, we applied a first-order auto-regressive correction to the residuals to account for autocorrelation in instantaneous movement speeds. The final model structure was confirmed using likelihood ratio tests and $AIC_c$-based model selection. We therefore modelled instantaneous speed as follows:

$$\text{Speed}_i \sim N(\mu, \sigma^2), \tag{1}$$

$$\begin{aligned}\mu = \alpha_{j[i]} + \beta_{1j[i]}(\text{Dist}) + \beta_{2j[i]}\left(\text{Dist}^2\right) \\ + \beta_3(\text{hour}) + \beta_4\left(\text{hour}^2\right) + \beta_4(\text{Road})\end{aligned}, \tag{2}$$

$$\begin{pmatrix}\alpha_j \\ \beta_{1j}\end{pmatrix} \sim \left(\begin{pmatrix}\gamma_0^\alpha + \gamma_1^\alpha(\text{Road}_{\text{BR262}}) + \gamma_2^\alpha(\text{Road}_{\text{MS}-040}) \\ \mu_{\beta_{1j}}\end{pmatrix}, \begin{pmatrix}\sigma^2_{\alpha_j} & \rho_{\alpha_j\beta_{1j}} \\ \rho_{\beta_{1j}\alpha_j} & \sigma^2_{\beta_{1j}}\end{pmatrix}\right), \quad \text{for ID} j = 1, \ldots, J. \tag{3}$$

Where equation (1) defines the model's stochastic component, equation (2) the models fixed effects structure and equation (3) the model's random effects structure. For the instantaneous speed analyses, all individuals that lived >2 km from a paved road were excluded. This cut-off was selected as animals that lived >2 km from a paved road did not interact with roads over the course of the study period, making it unlikely that they would be modifying their behaviour with respect to how close/far they were from a road at any given point in time.

### $Q_2$: Does traffic volume influence giant anteater crossing behaviour?

To answer $Q_2$, we modelled the relationship between the number of road crossings according to the nearest highway as a proxy for traffic volume. We also included the variables related to the home-range location (distance of home-range centroid to nearest paved road), sampling duration, sex and weight. The road crossing data were zero-inflated, where only 26 of the 38 range-resident individuals (see below) were actually observed to have crossed a road. As a result, we analysed these data using a hurdle model (Zuur *et al.*, 2009) that modelled individual crossing/not crossing information according to a logistic regression model, and the individual number of crossings for those individuals that did cross according to a zero-truncated negative binomial generalized linear model. This formulation allowed us to distinguish between the factors governing whether giant anteaters crossed paved roads or not, and the factors driving the crossing rate for those individuals that did cross, allowing us to capture both ecological processes in a single model. For both processes, we started with the following global model:

$$\begin{aligned}\mu_i = \beta_0 + \beta_1\text{Road} + \beta_2\text{Distance to Road} + \beta_3\text{Sex} \\ + \beta_4\text{Weight} + \beta_5\%\text{Pasture} + \beta_6\text{Sampling uration}.\end{aligned} \tag{4}$$

From this global model, we specified a subset of candidate models comprising of all possible combinations of fixed effects using the R package 'MuMIn' (Bartoń, 2016) and used the $AIC_c$ for model selection to identify the best-fit model for the data. As $AIC_c$ has been shown to under/overfit models on small sample sizes (Brewer, Butler & Cooksley, 2016), we confirmed our selected model via block cross-validation using the methods implemented in the R package 'DAAG' (Maindonald, Braun & Braun, 2015). We also tested if the time of day for each road crossing event was related to the hourly traffic volume variation, using simple linear regression.

### $Q_3$: Do giant anteaters prefer to cross the roads via passage structures?

To address $Q_3$, we identified the crossings on each highway that were within 20 m (the median GPS measurement error) of a road passage. These were classified as crossings where a giant anteater could potentially have used that structure to move across the road. This allowed us to search for evidence that giant anteaters preferred to cross the roads through existing passages using a chi-square test.

### $Q_4$: Do giant anteaters respond to roads differently than to natural barriers?

Finally, to answer $Q_4$, we compared the number of crossings across paved roads to those across unpaved roads and streams using paired *t*-tests. In a complementary approach, we used simulations to generate a null model of the number of crossings across all linear features that would be expected by chance. For each giant anteater tracked, we used their CTMM to simulate 1000 movement datasets with sampling times that matched the empirical data. We then quantified the number and time of day of road and stream crossings in the simulated movement and averaged the results for each individual. This provided an estimate of the number of road crossings that would be expected by random movement within individuals' home ranges that we could compare our empirical results against. Observed and expected crossings across paved roads, unpaved roads and streams were compared using paired *t*-tests.

# Results

## Movement data summary

The 38 range-resident individuals occupied stable home ranges, with an average 95% area of 6.8 $km^2$ (4.6–9.0 $km^2$, 95% CIs reported hereafter). We found that males had significantly larger home-range areas than females (8.8, 5.9–11.6 vs. 4.4, 1.2–7.6 $km^2$, respectively; $Z = 2.01$, $P = 0.045$). There was no evidence for a relationship between home-range area and body size ($Z = -1.95$, $P = 0.052$), however, we did find a negative relationship between home-range area and the proportion of pastureland that it contained ($Z = -3.8$, $P < 0.001$). We found partial evidence that high traffic volumes seemed to inhibit some giant anteaters from establishing territories on both sides of the roads, but small sample sizes and substantial interindividual variation limited the power of these analyses (Supporting Information Appendix S4). Notably, we found no significant differences in habitat composition across the three study sites nor when comparing habitat on one side of a road versus the other (detailed in Supporting Information Appendix S3).

## $Q_1$: Does the movement behaviour of giant anteaters differ with distance to paved roads?

Overall, we found little evidence that giant anteaters modified their home-ranging behaviour in response to paved roads. When comparing giant anteaters between the three study sites, there were no differences in home-range sizes ($\mathscr{L} = 0.38$; $P = 0.83$; Fig. 2a) nor did we find a relationship between the distance that individuals lived from a paved road and their home-range sizes ($Z = 0.15$; $P = 0.88$; Fig. 2 b). There were also no differences between their mean daily speeds and the distance that individuals lived from a paved road ($Z = -0.08$; $P = 0.94$; Fig. 2c) nor any evidence that giant anteaters' mean daily movement speed differed when living near paved roads with differing traffic volumes ($\mathscr{L} = 3.87$; $P = 0.14$; Fig. 2d).

Interestingly, however, we did find evidence that individuals modified their instantaneous movement speed depending on how far they were from roads (Table 2A). This relationship was non-linear and, all else being equal, individuals tended to move slowly when close to or on roads, speed up at intermediate distances and then slow down again as they moved further away from roads. The interclass correlation was relatively low (14.5%), suggesting that this general pattern was fairly consistent across all of the giant anteaters we collared, but with some amount of interindividual variation in how the movement changed with distance to roads (Supporting Information Appendix S3).

## $Q_2$: Does traffic volume influence giant anteater crossing behaviour?

We also found little evidence that traffic volume influenced giant anteater crossing behaviour. Of the 27 giant anteaters with home-range centroids <2 km from the nearest paved road (i.e. those individuals with home ranges bordering or intersecting the nearest paved road), 22 crossed roads, with a median of 2 crossings per animal per day (range 1–15). Across all individuals, the selected model (<$AIC_c$) predicting whether a giant anteater would cross a road or not (Table 2 B) included the distance an animal lived from the nearest paved road, the animal's sex and the road it was crossing. Using these three terms alone, we found that a logistic regression model could predict crossings on a hold-out sample with a mean accuracy of 84.0% (83.8–84.3%, 95% CIs). Unsurprisingly, the closer an animal lived to a road, the more likely it was to cross. Males were ~3.7 times more likely to cross the roads than females, all else being equal. The model further suggests an overall similarity in crossing events across roads.

The selected model section relating the number of crossings per individual for those giant anteaters that did cross a paved road (Table 2B) included the distance to the nearest paved road, sex and the amount of pasture contained within their home ranges. Here again, individuals that lived closer to paved roads tended to cross them significantly more often, all else being equal (Fig. 3a). However, males tended to cross the roads more frequently than females (Fig. 3b), and the more pastureland that was in an individual's home range, the less it crossed paved roads (Fig. 3c).

Giant anteaters tended to cross paved roads more frequently at night, when the traffic volume was lowest, but this also coincided with when they were more active (Fig. 4). We found a significant negative correlation between mean hourly road crossings and traffic volume ($F_{1,22} = -17.0$, $P < 0.001$, adjusted $R^2 = 0.41$). Circadian

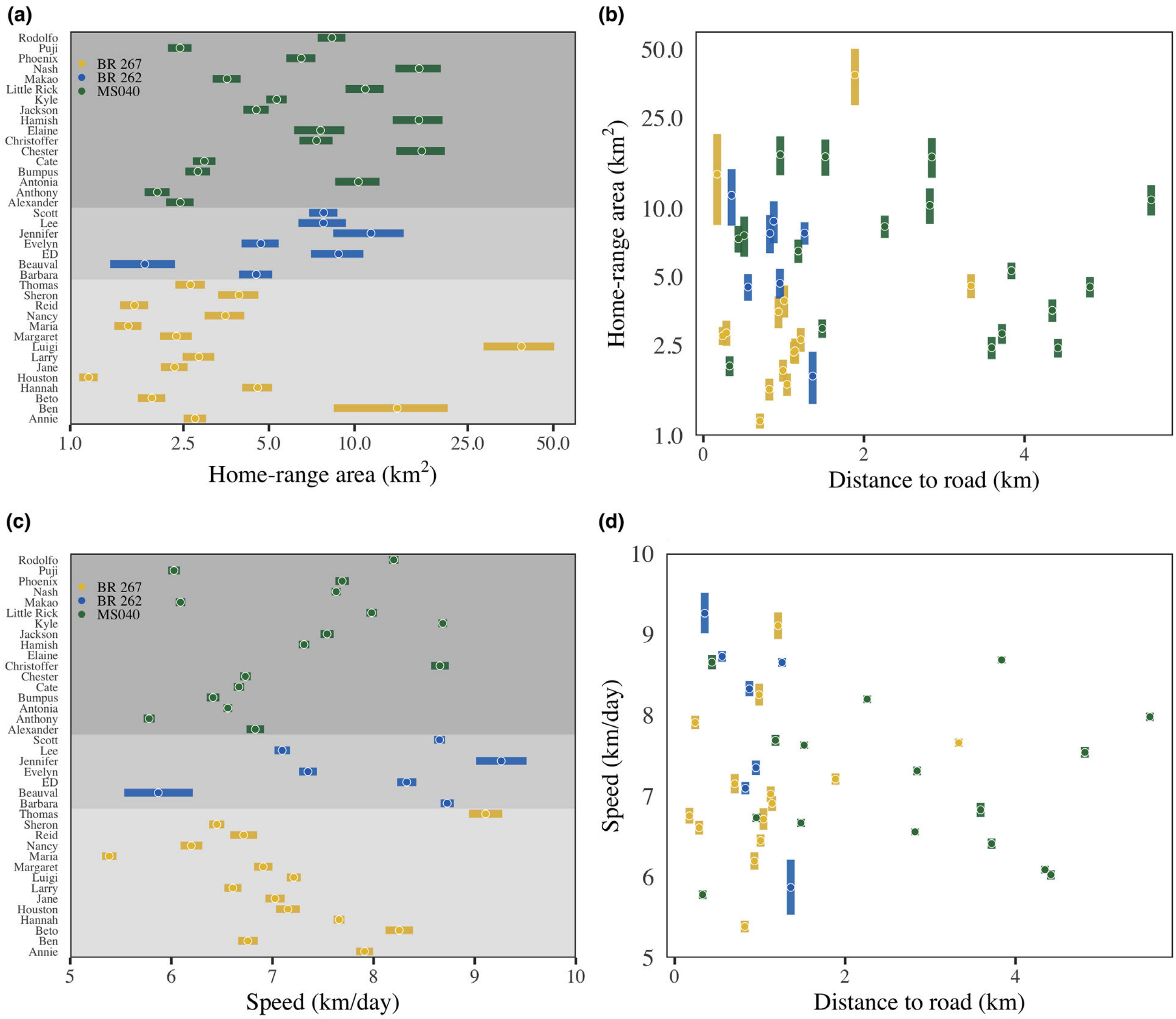


**Figure 2** Scatter plots summarizing information for each tracked giant anteater, including the home-range area (a), distance of the home-range centre to the nearest paved road (b), mean daily movement speed (c) and mean daily movement speed with distance to the road (d). Colours and grey shading indicate the three study areas. Circles and bars depict the estimates and the 95% confidence intervals, respectively. Note how there are no clear differences in the home-range area or movement speed across sites nor with distances to roads.

patterns in traffic volume were also consistent across all three roads (see Supporting Information Appendix S3).

## $Q_3$: Do giant anteaters prefer to cross the roads via passage structures?

We found no evidence that giant anteaters searched for road passages (culverts or viaducts) to cross the roads. The median distance of road crossings from the nearest road passage was 1720 m (1710–1730 m, 95% CIs), and individuals preferred to cross without the use of a structure ($\chi^2_{[1]} = 1494.9$, $P < 0.0001$). Only 19 crossing events (1.2%) were within 20 m of a passage, thus potentially utilizing it, and all of these were from the same animal living near BR267.

## $Q_4$: Do giant anteaters respond to roads differently than to natural barriers?

We found significant differences when comparing the number of crossings of giant anteaters across paved roads to that across unpaved roads and streams (i.e. natural linear features). Individuals crossed paved roads significantly fewer times than they crossed both unpaved roads ($t_{[37]} = -3.7$, $P < 0.001$) and streams ($t_{[37]} = -3.4$, $P < 0.005$; Fig. 5). This is also supported by the movement simulations results in which the observed number of paved road crossings was ~3.3 times lower than would have been expected by random chance ($t_{[37]} = -3.6$, $P < 0.001$). In contrast, the observed number of unpaved road crossings

**Table 2** Summary of models relating (A) instantaneous movement speed and (B) crossing events with different predictors. (A) Parameter estimates ($\hat{\beta}$), 95% CI, *t*-values and *P*-values for the best (<AIC$_c$) mixed-effects regression model fit to individual instantaneous movement speeds. The model included a first-order auto-regressive correlation structure with $\rho = 0.51$. (B) Parameter estimates ($\hat{\beta}$), 95% CI, *Z* values and *P*-values for the best (<AIC$_c$) zero altered negative binomial model fit to the number of times each individual crossed a paved road. Significant predictors ($P < 0.05$) are highlighted in bold

| | $\hat{\beta}$ | Lower 95% CI | Upper 95% CI | *t*-value | *P* |
|---|---|---|---|---|---|
| (A) | | | | | |
| Intercept | $1.01 \times 10^{-1}$ | $9.38 \times 10^{-2}$ | $1.00 \times 10^{-1}$ | 28.06 | <0.001 |
| **Distance to road** | $\mathbf{1.84 \times 10^{-3}}$ | $\mathbf{3.60 \times 10^{-4}}$ | $\mathbf{3.31 \times 10^{-3}}$ | **2.44** | **0.015** |
| **Distance to road$^2$** | $\mathbf{-2.28 \times 10^{-4}}$ | $\mathbf{-3.89 \times 10^{-4}}$ | $\mathbf{-6.77 \times 10^{-5}}$ | **−2.79** | **0.005** |
| **Time of day** | $\mathbf{-5.00 \times 10^{-3}}$ | $\mathbf{-5.13 \times 10^{-3}}$ | $\mathbf{-4.88 \times 10^{-3}}$ | **−77.06** | **<0.001** |
| **Time of day$^2$** | $\mathbf{2.09 \times 10^{-4}}$ | $\mathbf{2.03 \times 10^{-4}}$ | $\mathbf{2.14 \times 10^{-4}}$ | **75.52** | **<0.001** |
| Road – BR262 | $1.05 \times 10^{-2}$ | $-1.27 \times 10^{-3}$ | $2.23 \times 10^{-2}$ | 1.83 | 0.078 |
| Road – MS040 | $3.09 \times 10^{-3}$ | $-7.78 \times 10^{-3}$ | $1.40 \times 10^{-2}$ | 0.58 | 0.564 |

| | $\hat{\beta}$ | Lower 95% CI | Upper 95% CI | *Z*-value | *P* |
|---|---|---|---|---|---|
| (B) | | | | | |
| Zero hurdle model coefficients (binomial with logit link) | | | | | |
| **Intercept** | **1.97** | **0.06** | **3.87** | **2.03** | **0.043** |
| **Distance to road** | **−1.22** | **−2.32** | **−0.12** | **−2.17** | **0.030** |
| **Sex (male)** | **3.66** | **0.38** | **6.95** | **2.18** | **0.029** |
| Road (BR262) | 17.01 | −11 339.11 | 11 373.1 | 0.00 | 0.998 |
| Road (MS040) | −1.66 | −4.39 | 1.07 | −1.19 | 0.233 |
| Count model coefficients (truncated negative binomial with log link) | | | | | |
| **Intercept** | **16.08** | **9.22** | **22.29** | **4.59** | **<0.001** |
| **Distance to road** | **−2.51** | **−3.55** | **−1.48** | **−4.75** | **<0.001** |
| **Sex (male)** | **1.33** | **0.26** | **2.40** | **2.44** | **0.015** |
| **Pasture** | **−0.13** | **−0.20** | **−0.06** | **−3.50** | **<0.001** |

AIC$_c$, corrected Akaike's information criterion.

was only ~2.0 times lower than would have been expected by random chance ($t_{[37]} = 4.5$, $P < 0.001$), while the number of stream crossings was not significantly different than would have been expected by random chance ($t_{[37]} = 0.6$, $P = 0.57$).

# Discussion

A key step in reducing negative effects of roads on wildlife is to understand how individuals behave on and around roads of varying traffic volumes. From detailed tracking of 38 non-dispersing giant anteaters, we found that while individuals did tend to reduce their movement speed when approaching roads, they otherwise showed few signs of adapting their movement when living near paved roads of varying traffic volumes. High traffic volumes seem to inhibit some giant anteaters from establishing territories on both sides of the roads (Fig. 1), and alongside this, we found that individuals crossed paved roads less often than would be expected by random chance, whereas there was no difference between the number of observed stream crossings and what would have been expected by chance. In other words, this inhibition was not due to linear features functioning as home-range boundaries (Riley *et al.*, 2006), but rather that traffic may occasionally deter giant anteaters from crossing roads. This was also reflected in our finding that giant anteaters reduced their movement speeds as they approached paved roads, suggesting that some level of caution is taken when in the immediate vicinity of high traffic roads. Nevertheless, none of the highways we monitored was impervious to giant anteaters, and a high proportion (>80%) of tracked giant anteaters living near the paved roads (<2 km) did cross them regularly. It is important to note that we detected no significant differences in habitat composition on either side of the roads. As such, it was unlikely that the high rates of crossings we observed were due to giant anteaters needing access to resources contained on one side of the road or the other. Overall, traffic volume and associated noise and light pollution did not appear to significantly affect their behaviour one way or another. In fact, it is possible to observe giant anteaters foraging at the edge of major highways, and one of the individuals tracked in this study even slept regularly in the native vegetation near the road, but he was eventually a victim of a collision (Supporting Information Appendix S3). We also found no evidence that giant anteaters actively sought out road passages for safe crossings. Although we regularly find giant anteater footprints inside road passages (e.g. 0.02 crossings per passage per day; Abra *et al.*, 2020), our results suggest that few individuals actually make use of such passages, and those that do probably only do so opportunistically (e.g. when traveling along streams).

Collectively, these results demonstrate that giant anteaters do not change their movement behaviour and space use near

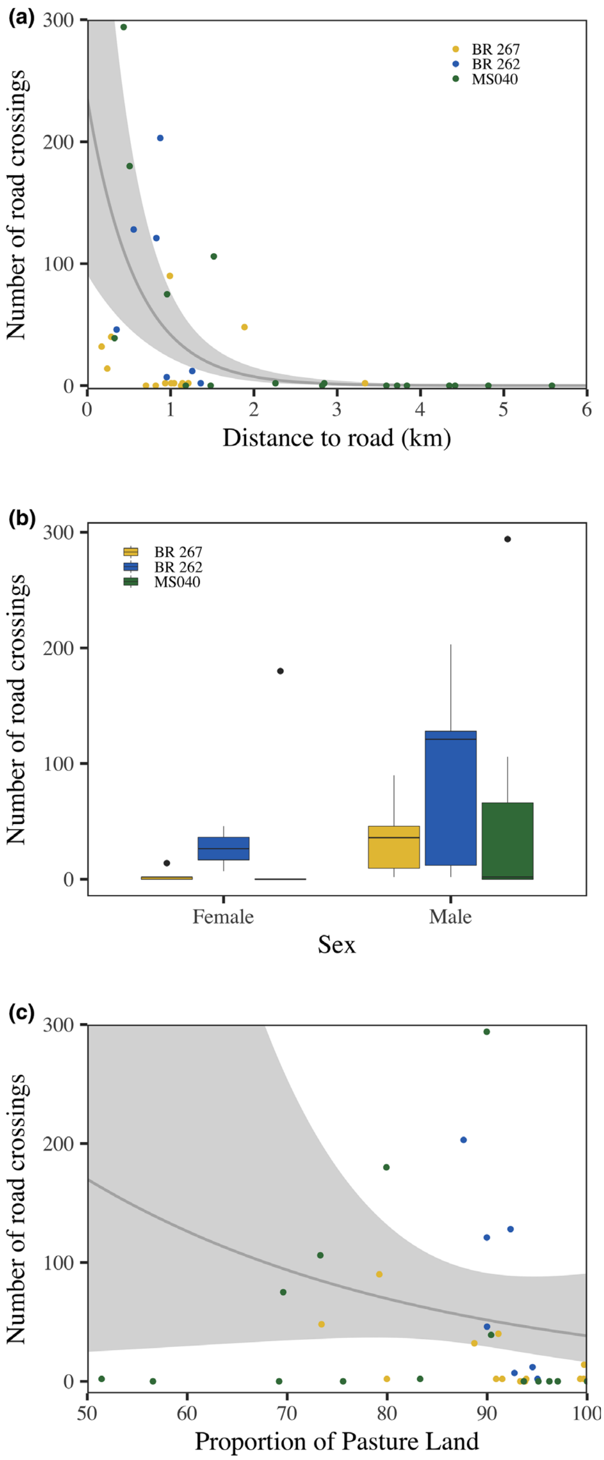


**Figure 3** Summary of the crossing results. In panel a, Scatter plots relating the total number of road crossings that each giant anteater performed in relation to the distance of their home-range centroid to the nearest paved road. In panel b, boxplots depicting the number of road crossings for males and females across the three study sites. In panel c, the relationship between the number of road crossings and the proportion of pastureland in each individual's home range is shown. In panels a and c, the grey lines depict the fitted negative-binomial regression model and shaded area the 95% confidence intervals.

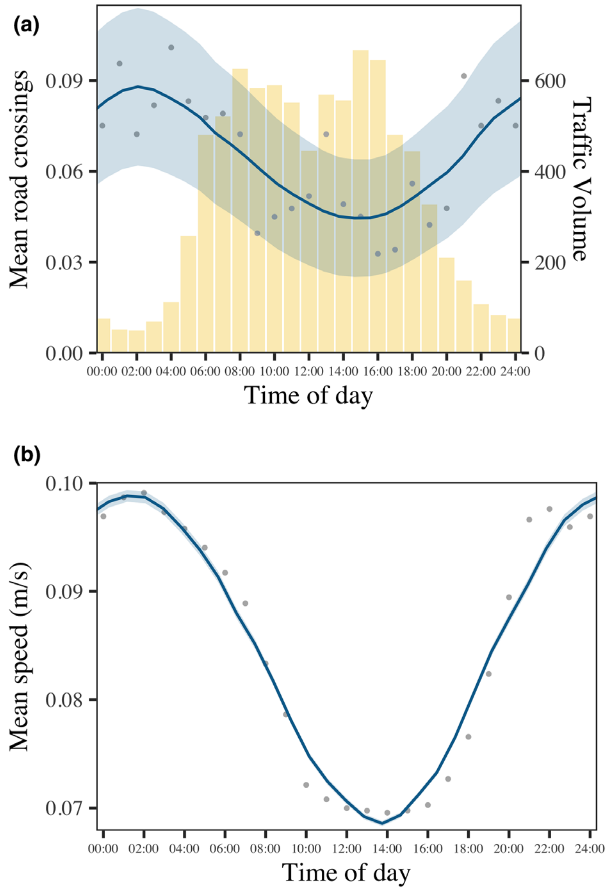


**Figure 4** (a) Relation between the mean number of crossings per hour (dots, left *Y* axis) and the hourly mean traffic volume across all roads in a total number of cars (bars, right *Y* axis). (b) Mean speed per time of day over the total duration of the study period. The blue lines depict loess smoothed regression curves fit the hourly means and the shaded area the 95% confidence intervals on hourly means. Note how most road crossings occurred at night when traffic volume was lowest and when giant anteaters are more active.

paved roads, nor search for safe crossing structures, which is probably the cause of the high roadkill rates (Ascensão *et al.*, 2021). This contradicts previous research suggesting that the barrier to movement and population redistribution was the most important road impact on giant anteaters and further emphasizes the need to obtain sound empirical data on animal movement when planning and managing transportation networks (Ascensão *et al.*, 2019).

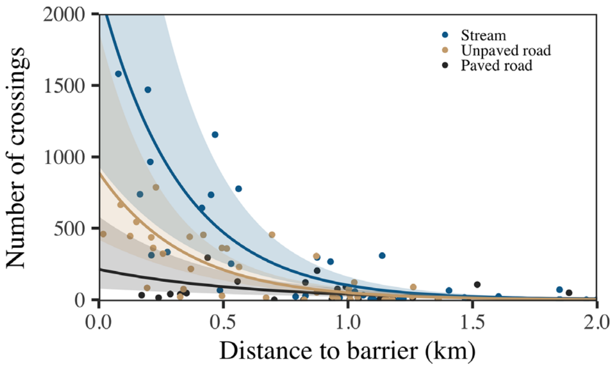


**Figure 5** Scatterplot of the relationship between the number of crossings across barriers and the distance the individual lived from that barrier. The solid lines depict fitted negative-binomial regression models and shaded areas the 95% confidence intervals.

## Roads as ecological traps

When species fail to recognize and avoid suboptimal sink habitats, the result can be a decrease in population sizes and an increased extinction risk (Pulliam & Danielson, 1991). To this end, no differences in clinical exams, clinical signs or body scores were noted between individuals living near or far from the paved roads, therefore eliminating the alternative hypothesis that territories near roads are suboptimal, and those giant anteaters that occupy such areas were likely to be more debilitated. Indeed, the best model for predicting how far a giant anteater lived from a road was the intercept only model (Supporting Information Appendix S3). Our results suggest that a large proportion of road-killed giant anteaters are roadside residents and not dispersing animals, as six of the individuals monitored in this study eventually died from vehicle collisions (~15%; Supporting Information Appendix S3). The three individuals that dispersed during this study (distances: 35, 50 and 100 km), crossed roads but survived and all established themselves. Because roadside habitats apparently offer good foraging opportunities that allow giant anteaters to remain healthy, the feedback that giant anteaters receive about the quality of roadside habitat may be misguiding. This makes it unlikely that they will learn that roadsides are mortality sinks that should be avoided. Hence, habitat near roads may function as an ecological trap where healthy individuals occupy the territories nearby or bisected by roads but eventually are road-killed given their regular crossings, leaving the territory vacant for subsequent occupation.

This dynamic is a worst-case scenario for this already threatened species that is likely to negatively impact the long-term population viability (Miranda *et al*., 2014). Moreover, giant anteaters live at low population densities and have low recruitment (Gaudin *et al*., 2018; Desbiez *et al*., 2020; Bertassoni *et al*., 2021), making them particularly vulnerable to WVC (Miranda *et al*., 2014). Indeed, population viability analysis showed how giant anteaters deaths due to vehicle collisions decrease the stochastic growth rate of populations by half, making them drastically less resilient to other threats, and slows their recovery time from catastrophic events (Desbiez *et al*., 2020). The sex ratios of roadkill (Barragán-Ruiz *et al*., 2021) and our results on road crossing rates are consistent, both suggesting that males are more threatened by roadkill due to their higher crossing rates relatively to females. The fact that males are the most affected by roadkill is less critical than if it were females (Desbiez *et al*., 2020). This is especially so given that females care for newborn pups for at least the first 6–12 months (Jerez & Halloy, 2003; Desbiez *et al*., 2020). Yet, there may be other unforeseen downstream genetic effects resulting from the high mortality of males, which may further imperil population persistence, and further study is clearly warranted.

## Conservation implications

As the transportation networks in South-Central America continue to expand, the impact of road, and most probably railway (Dasoler *et al*., 2020), induced mortality is likely going to be worsen. This may severely limit population persistence throughout the giant anteater's distribution, calling for immediate road mitigation actions. Because giant anteaters are mostly indifferent to roadside habitat and do not actively seek out road passages, it is unlikely that establishing a network of crossing structures alone will provide an effective solution. Fencing, leading to existing passages, has been suggested as a cost-effective mitigation measure, for both conservation purposes as well for human safety, as it allows separating giant anteaters and other large animals from traffic, thus significantly reducing the likelihood of collisions (Clevenger *et al*., 2001; Jaeger & Fahrig, 2004; Spanowicz, Teixeira & Jaeger, 2020; Ascensão *et al*., 2021). Another complementary approach is to manage traffic speed in some road sections (via, e.g. stop signs, speeds bumps, speed limits and/or animal crossing signs) in order to decrease the likelihood of drivers hitting animals.

The application of such management measures throughout the entire road network is unfeasible. One possible approach is to implement mitigation measures in locations with the highest WVC rates (Ascensão *et al*., 2021) and in road sections that clearly bisect areas of higher landscape connectivity (Grilo *et al*., 2011). Furthermore, the similarity of crossing events across the three roads suggests that the probability of giant anteaters incurring collisions is traffic volume dependent. In fact, a systematic roadkill survey in this same study area recorded three times as many cases on high-traffic roads (BR262 and BR267) as on the lower traffic MS040 (Ascensão *et al*., 2021). Given that we currently lack sound estimates on local giant anteater abundance in the three study sites, we cannot affirm if such differences in mortality rates were due to different population sizes or different probability of being road-killed. Yet, given the similarity in land cover across the three study areas, it is reasonable to assume that the abundance of giant anteaters across them is similar. As such, the mitigation of high-traffic roads should be prioritized. Also, given that the giant anteaters' activity peaks at night, similar to other large mammals recurrently involved in

WVC, notably tapirs *Tapirus terrestris*, reducing the overall amount of night-time driving would most likely result in fewer collisions and, consequently, fewer human injuries (Hobday & Hobday, 2010).

## Conclusion

Coupling detailed movement information with contemporary data from systematic road surveys allowed us to disentangle the main effects of roads on giant anteaters. Roads did not affect the movement behaviour and space use of giant anteaters, nor were substantial barriers for their displacements. In turn, giant anteaters did not search for passages for safe crossings and readily occupied the areas near the roads. Consequently, roadside areas are sink habitats due to the high roadkill rates, which may threaten the population persistence at the local scale. Such information is critical in the development of road and landscape management strategies, including the planning of future transportation infrastructures.

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## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Passage structures in study area.
**Appendix S2.** Workflow used to analyses the giant anteater GPS data.
**Appendix S3.** Descriptive analyses of movement metrics and road interactions.
**Appendix S4.** Home range establishment on roads of different traffic volumes.