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RESEARCH ARTICLE

The effect of roads on edge permeability and movement patterns for small mammals: a case study with Montane Akodont

Fernando Ascensão · **Priscila Silva Lucas** · **Aline Costa** · **Alex Bager**

Abstract

Context Increased edge density is among the main negative effects of habitat loss and fragmentation. Roads are linear infrastructures that may promote barrier effects due to disturbance and mortality effects. We hypothesized that edges of habitat patches bordered by roads are less permeable than roadless edges.

Objectives We tested whether edge permeability and avoidance are influenced by the presence of paved and dirt roads bordering habitat patches, relatively to roadless edges.

Methods We translocated 55 montane akodonts (*Akodon montensis*) from the interior of vegetation remnants to their edges, and tracked fine-scale movements using spool-and-line devices. Edges were bordered by dirt roads (n = 12 mice), paved roads (n = 21) or were not bordered by roads (n = 22). We assessed edge permeability by comparing the number of tracks with crossings, and by comparing the empirical data to simulated correlated random walks. We also assessed edge avoidance by comparing the net direction travelled and net displacement from edge.

Results No edge crossings were recorded in roaded edges, whereas 36% of tracks in roadless edges crossed the edge at least once. Simulations indicated a significantly lower permeability of roaded edges, while the observed number of crossings in roadless edges was within the expected range. We found no evidence of higher avoidance of roaded edges, as both net direction travelled and displacement were similar across edge types.

Conclusions Roads decreased edge permeability for the montane akodont. This is likely to increase population isolation among vegetation remnants by reducing the structural connectivity in the already fragmented landscape.

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Introduction

Habitat loss and fragmentation deriving from agriculture and urban sprawl are amongst the biggest threats for biodiversity conservation, converting once continuous areas into smaller and more isolated habitat patches (Fahrig 2003; Fischer et al. 2003). A major consequence of these landscape changes is the increasing density of habitat edges, that can have different biotic and abiotic conditions than those found in the interior of habitat patches (Laurance et al. 2001, 2011; Ries et al. 2004). Depending on species-specific responses, the contrast of such conditions may create a simple semi-permeable or complete barrier for animal movement. For example, forest edges can be permeable to habitat generalist species but can reduce or halt movements of forest specialists (Brodie et al. 2015). In fact, there is a vast body of literature showing that edge permeability, i.e. the propensity of individuals to cross the patch boundaries (Stamps et al. 1987), is a key element influencing the movement and distribution of species (Manson et al. 1999; Collinge and Palmer 2002; Uezu et al. 2005; Ewers et al. 2007; Baguette and Dyck 2007; Prevedello and Vieira 2010; Youngquist and Boone 2014). Additionally, certain species avoid the proximity of edges, which may further decrease the amount of available habitat and edge permeability (Murcia 1995; Zurita et al. 2012), thereby increasing the negative effects of habitat loss and fragmentation.

Roads are ubiquitous features worldwide, representing key elements for the transportation of people and goods. Several studies have shown that roads promote a panoply of negative effects on biodiversity (Forman et al. 2003; van der Ree et al. 2015), often leading to conflicts between human benefits and biodiversity (Laurance and Balmford 2013; Laurance et al. 2014). Amongst these are species-specific barrier effects for movement and gene flow, either due to road mortality, road avoidance behavior or by representing a physical obstacle (Rondinini and Doncaster 2002; McDonald and Clair 2004; Ford and Fahrig 2008; McGregor et al. 2008; Clark et al. 2010; Holderegger and Di Giulio 2010). In forest/habitat patches bordered by roads, the contrast in biotic and abiotic conditions tends to be very high, therefore, we hypothesized that edge permeability is lower in these patches. Furthermore, we expected this effect to be stronger in paved than in dirt roads as the former have an artificial substrate and higher traffic volume, potentially increasing disturbance and mortality risk, and thereby inhibiting crossing attempts.

Forest prey species are particularly affected by edge permeability as they generally avoid areas lacking vegetation cover, partially due to increased predation exposure. This has been described for several small mammals, including e.g. snowshoe hares (*Lepus americanus*) (Rohner and Krebs 1996) and prairie voles (*Microtus ochrogaster*) (Smith and Batzli 2006). Here, we analyzed the movement patterns of the montane akodont (*Akodon montensis*, Thomas 1913), a common small mammal species in southeast Brazil. The montane akodont inhabits semi-deciduous woodlands with relatively open upper canopy layers but denser vegetative cover near the ground (Umetsu and Pardini 2007; Puttker et al. 2008; Goodin et al. 2009; Antunes et al. 2010). Forest edges are unlikely to significantly hinder its movements as this species also occurs in a variety of other habitats, including agricultural land, Eucalyptus stands or pastures, although always in lower densities (Stevens and Husband 1998; Umetsu and Pardini 2007; Antunes et al. 2010; Martin et al. 2012; Galiano et al. 2013). The montane akodont thus represents a good model for small mammal species that prefer but are not limited to forest patches. From a conservation perspective, the montane akodont is an important prey item (Silva-Pereira et al. 2011) and seed disperser (Vieira et al. 2006). On the other hand, this species is a known vector for hantaviruses that can be fatal for humans (Goodin et al. 2009; Owen et al. 2010).

We analyzed the fine-scale movements of individuals tracked along the edges of forest patches embedded in a matrix of agriculture/pasture lands. The main goal was to test for a decrease in edge permeability and an increase in edge avoidance in sites bordered by paved or dirt roads relative to sites without roads. We defined edge avoidance as movements predominantly moving away from the edge and into the forest patch, with extreme avoidance characterized by a straight line into the forest and perpendicular to the patch edge. We expected lower permeability where patches were bordered by paved roads, intermediate permeability at edges bordered by dirt roads, and higher permeability of edges without roads. Our expectations were based on the assumptions that: (i) deforested areas without roads retain some cover that protects small mammals

from predation; (ii) dirt roads may hinder animal movements, but their lower traffic volume and speed, together with their natural substrate, represent a less restrictive feature for animal movement; and (iii) pavement is an artificial substrate, devoid of cover, that presents the highest mortality risk due to predation and roadkill. Moreover, as the road-effect zone is higher for paved relatively to dirt roads (Forman and Deblinger 2000), we expected highest edge avoidance on paved roads, followed by dirt roads, and lowest avoidance of edges without roads. Our null hypothesis was that neither permeability nor edge avoidance are related to road presence.

The study of edge permeability and movement patterns may provide valuable information on how functional connectivity can be affected by the presence of roads in already fragmented landscapes, thereby informing landscape management plans to increase their overall conservation (Uezu et al. 2005; Baguette and Dyck 2007; Fuentes-Montemayor et al. 2009; Porto Peter et al. 2013; Mimet et al. 2013). However, there is still limited data on how animal movement behavior is affected by roads. This study is therefore of primary interest to diverse research fields where the effects of roads on habitat fragmentation has implications for habitat connectivity, conservation biology and disease spread.

Materials and methods

Study area

This study was conducted in Minas Gerais, Brazil, near the city of Lavras, within Cerrado biome. Remnants of native forest are scattered across the region (Fig. 1), dominated by secondary regenerating forest. The climate is Cwa, with dry winters and rainy summers. Average annual temperature and rainfall are 20.4 °C and 1460 mm, respectively (Dantas et al. 2007). We selected eleven forest fragments with a minimum size of 240 ha for sampling procedures. Six of these fragments were bordered on one side by paved roads with regularly mown narrow grassy verges (1–5 m) (routes MG354 or MG335); three were bordered by dirt roads without verges; and two patches lacked bordering roads. These sampling site types are hereafter referred to as 'paved', 'dirt' and 'roadless' edges. The land cover beyond the edge (and road) and

near release points (see below) were fallow (paved, n = 4; dirt, n = 2; roadless, n = 1) or pasture (paved, n = 2; dirt, n = 1; roadless, n = 1).

Paved and dirt roads from surveyed patches had low nocturnal (1800–2400 h) traffic volumes, which is the main period of activity of the montane akodont (Graipel et al. 2003; Puttker et al. 2008). We monitored traffic volumes using PlotWatcher Pro cameras (AY6 Outdoors), which were active for five consecutive days during the fieldwork period. Photographs were taken every 5 s, allowing accurate enumeration of vehicles. Dirt roads had less than one vehicle per hour and paved roads had ca. 20 vehicles per hour during the night.

Capture and movement data

Trapping was performed using Sherman aluminum live traps (25 × 9 × 8 cm) set in a 6 × 6 trap grid with 20 m spacing, in the interior of the selected forest fragments. Where required, oral permission to access private land to conduct the study was obtained from the owners. A mixture of banana, ground peanuts, corn meal and commercial codfish oil was used as bait, and cotton-nesting material was placed inside each trap as bedding to protect captives from low temperatures. In addition, traps were hidden under vegetation to protect animals from adverse weather conditions and to avoid detection by predators. Traps were rechecked at dawn to minimize the time that animals were kept inside.

Captured individuals were weighed, measured, sexed and marked with two numbered earrings (National Band & Tag Co., Newport, KY, USA). All juveniles, pregnant and lactating females were released at the place of capture after measurements. Only individuals >27 g were kept for translocation and tracking procedures. The selected individuals were then transported to a field tent, in an opaque, wooden nest box (45 × 17 × 15 cm) herein referred to as the release device. Inside the tent the individuals were equipped with a spool-and-line device, which consisted of a cocoon of ca. 50–60 m white polyester thread 470/10 (Hiltex Indústria e Comércio de Fios Ltda., São Paulo, Brazil). Each cocoon was packed with transparent PVC film and duct tape (MSK 6140 19 mm) to ensure better adhesion to the skin of the animal and then bonded with instant cyanoacrylate glue (Super-Bonder®) to the back of each animal. The thread was not attached to the animal, and therefore
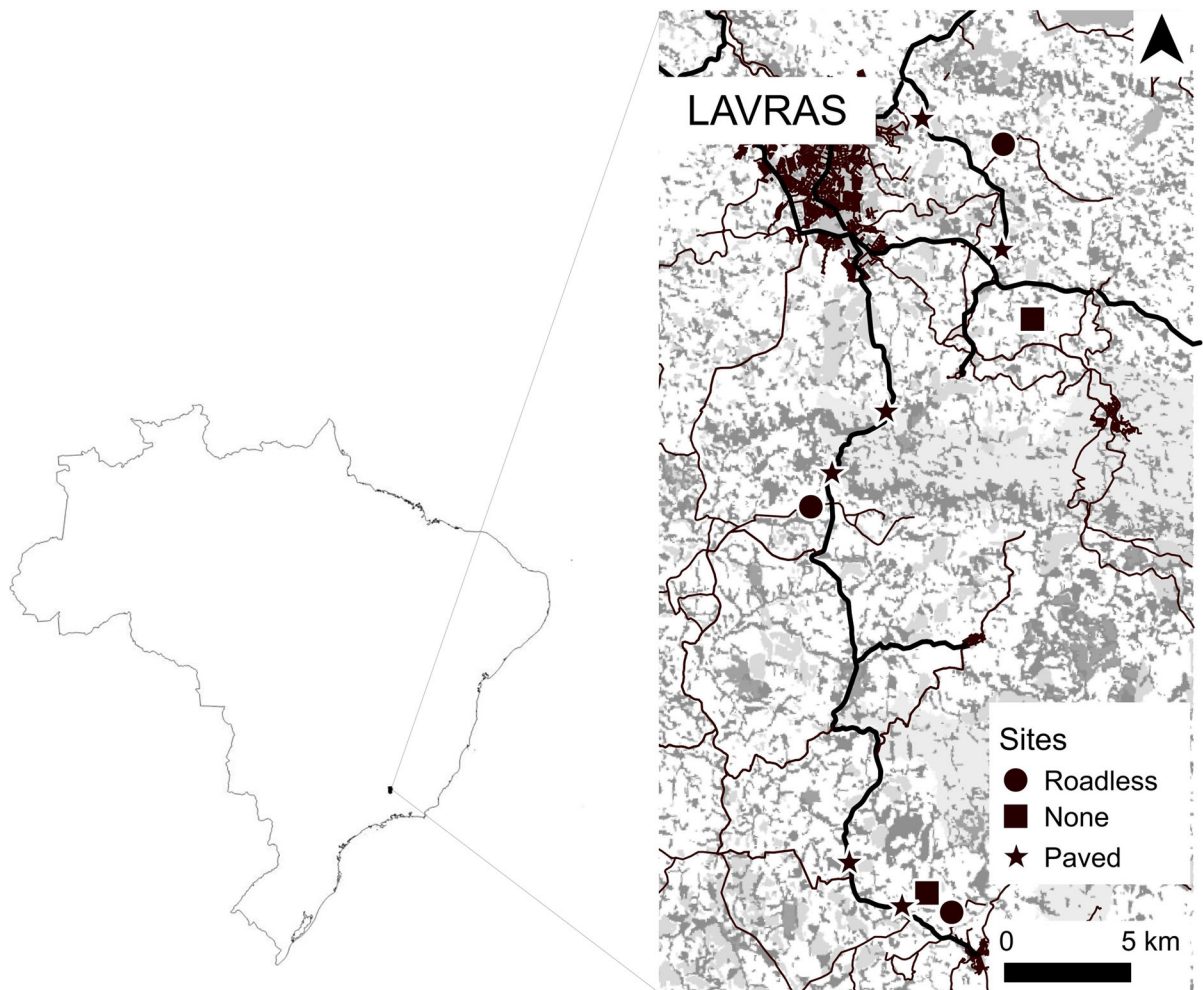
Fig. 1 Study area in Brazil (smaller image) and sampling sites for each edge type: patches bordered by paved or dirt roads, and roadless patches. *Dark grey areas* are vegetation remnants, *light grey* are rocky areas and *white* are agricultural areas. *Continuous lines* depict main paved roads, with *thicker lines* representing main roads and *thinner lines* secondary and dirt roads

when the line ends the animal could move freely. Cocoons weighed ca. 1.5 g (<5.5% of the animal's weight). Some individuals were recaptured at least once in subsequent months (data not shown), and all appeared to be in good condition and were no longer carrying the spool-and-line device. These observations suggest that our procedures do not affect the survival of the tracked individuals.

The field tent was placed in the shade, where animals were held inside the release device with food and water, and with minimal perturbation. In the evening they were released at the edge of the forest patch where they had been captured, as follows: the release device was placed at the release point, 1-5 m from the forest edge (inside the forest patch), and the loose end of the tracking thread was tied to a marker stake. One end of a 40-m rope was tied to the release device, passed through a tree branch above the release device, and the other end was held by observers at a distance of at least 20 m. After waiting in silence for 10 min, the end of the 40-m rope was slowly pulled, lifting the lid of the box directly upward. The release device allowed the animal to exit in any direction, while the lid was left ca. 20 cm above ground to provide the animal with a sense of security. We therefore reduced the biases related to observers' presence and device opening in animal movement directionality. Releases (up to three individuals per night, each placed 50 m apart) were carried out between 1700 and 1900 h. We avoided rainy nights

as it could potentially influence animal movement behavior. In the following morning, we monitored the line track using a tape measure and compass, identifying each turning point with a flag. We classified turning points as changes in the track line greater than 5° (0.087 rad). We considered the move angle as the direction of movement, and the turn angle as the angle of the current move step minus the angle of the previous move step.

Fieldwork was performed between April 2013 and March 2014, during which individuals from the three edge types were tracked concurrently. To complement the small sample size on roadless patches, another site was selected and sampled in June 2014 (see Supplementary Material S1 for tracking history and sample sizes, per edge type). Translocations among patches (including roadless areas) or across roads were not carried out, as data regarding the genetic structure of the populations or the disease implications of these translocations were not available.

Data analysis

Edge permeability

We tested if the number of tracks with at least one crossing were different across edge types using the Chi square goodness of fit test. To assess whether mice avoided or crossed the edges more than expected by chance, we compared the number of crossings from observed paths with those from simulated paths using correlated random walk (CRW) models, representing predicted movement without any behavioral response to the edges (e.g., Brehme et al. 2013). We parameterized CRW models with tracking data for each individual as follows: first, we estimated the concentration parameter (k) that determined the dispersion of a von Mises distribution. Second, we generated a sequence of turning angles using the von Mises distribution with a random mean turn angle, but the same value for k from the observed track, and with the same move-step lengths as in the observed track (hence, the total length for each simulated track was also the same as in the observed track). We simulated 1000 paths for each individual for which we derived a probability of crossing as being the proportion of simulations with at least one crossing. For each edge type, we considered the expected permeability to be the average probability of crossing of the simulated

paths. We then assessed the cumulative probability (p) of having observed the same number of tracks with at least one crossing (empirical data), given the expected permeability of the edge type (simulations). We assumed that values outside the 95% distribution would suggest a significant effect, with avoidance of edges if $p < 0.025$ or preference for surrounding habitat areas if $p > 0.975$. We parameterized and simulated all CRW models with a program written in R (R Development Core Team 2016).

Movement patterns

We analyzed movement patterns potentially describing edge avoidance behaviors, namely net direction traveled and net displacement from edges. Movement directions were standardized so that 0° represented the direction toward the nearest forest edge from the release points. We used Rayleigh's test of uniformity (general unimodal alternative with unknown mean direction and vector length) to determine whether net direction travelled deviated significantly from a random distribution. We also tested if the net direction travelled deviated significantly from 180°, i.e. the opposite direction from nearest edge, this fold using the Rayleigh test of uniformity with mean direction 180°. We used a p value of 0.025 in both tests to correct for multiple testing.

We compared if the net direction travelled differed across edge types using Analysis of Variance for Circular data with likelihood ratio test and an approximation to Chi squared distribution (Cordeiro et al. 1994). We further compared the net displacement from edges (straight-line distance from start to end location, perpendicular to edge) using the non-parametric Kruskal–Wallis test. Higher net displacement from edges suggests stronger avoidance of edge proximity.

We searched for potential bias due to time of year, by visually inspecting the plots of net direction travelled and net displacement from edge, for each edge type (see below) along sampling time, as well of body weight along sampling time. We also checked for a directional bias caused by a homing response. If individuals were released too close to their home ranges, we expected to observe a tendency to move towards the location where they were trapped, thus preventing inferences about edge effects. We therefore compared the pairs of bearings resulting from the

release point to the point where the pathway ended and to the trap location using circular–circular regression (Jammalamadaka and Sarma 1993). We further compared the translocation distances across edge types. All analyses and plots were made in R (R Development Core Team 2016). Circular statistics were run using the "circular" package in R (Agostinelli and Lund 2013).

Results

We captured 208 individuals (95F, 113M) of which 55 had the minimum weight required to install the spool-and-line device. Of these, 22 were tracked in roadless edges (10F, 12M); 12 in edges with dirt roads (6F, 6M); and 21 in edges with paved roads (9F, 12M). Tracks ranged between 16.4 and 58.9 m, averaging 39.0 ± 11.4 m. Translocations of these individuals averaged 200 ± 86 m (range = 68–492 m). We found no evidences of different response patterns or of significant changes in body condition of tracked individuals along time (Supplementary Information S1). Bearings of animal directionality and trap locations were not correlated (r = 0.23, p = 0.137), indicating that our results were not strongly influenced by homing behavior. The translocation distance was higher for mice tracked in dirt edges (258 ± 101 m), followed by paved (185 ± 40 m) and roadless edges (166 ± 78 m). Yet, these distances were not significantly different across edge types (Kruskal–Wallis test, K = 4.98, df = 2, p = 0.083).

Edge permeability

The number of observed road crossings was significantly different across edge types (Pearson's Chi squared test: 20.6; df = 2, p < 0.01). While we did not record any crossings on dirt or paved roads, or any signs of attempted crossings (e.g. line broken near the edge), 36% of the individuals (4M, 4F) tracked in roadless edges crossed the edges at least once, two of which (1M, 1F) ventured ca. 15 m into the matrix beyond the edge. The three edge types had a similar expected permeability, as derived from CRW simulations: 0.30 in roadless edges, 0.41 in dirt roads and 0.43 in paved edges. When comparing the observed proportion of individuals that crossed the edge to the proportion of simulated paths (i.e. assuming random

travel), we found that the probability of having no tracks with any crossings was <0.002 for both types of roaded edges, indicating low edge permeability. On the other hand, for roadless edges, the probability of having the same result as the one observed (8 tracks with at least one crossing) was within the expected range, suggesting a null edge effect (Fig. 2).

Movement patterns

We found no evidences that the net direction travelled was randomly distributed for any of the three edge types (roadless: Rayleigh test = 0.32, p = 0.102; dirt: Rayleigh test = 0.45, p = 0.083; paved: Rayleigh test = 0.34, p = 0.082). Likewise, we found no evidences that mice tend to moved away (180°) from roadless (Rayleigh test = 0.28, p = 0.029) or dirt
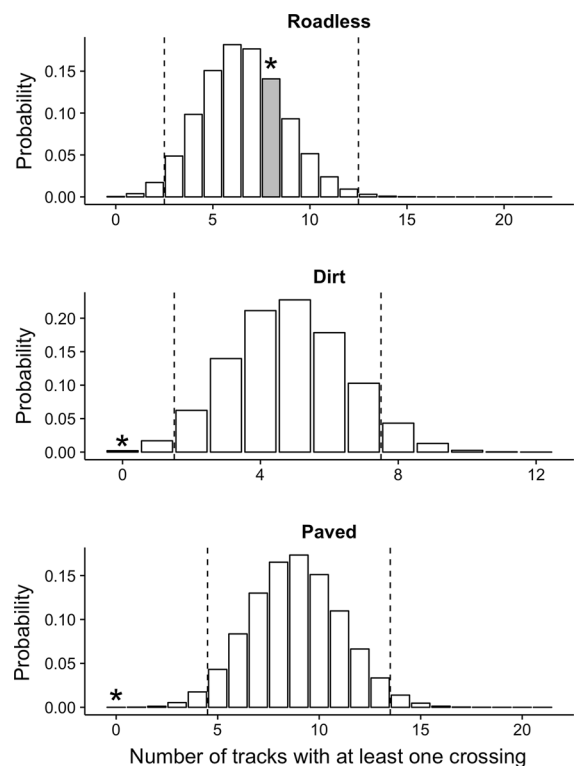

Fig. 2 Histograms showing the simulated (i.e., predicted) probability of obtaining the number of tracks with at least one crossing event across edge types. The observed number of tracks with at least one crossing is represented by "*Asterisk*" and a *grey bar*. *Dotted lines* enclose the 95% envelope of expected outcomes given a no edge effect scenario. Observed values outside of the envelope suggest that individuals avoid crossing edges (*left*), or search for matrix more often than expected (*right*)

edges (Rayleigh test = 0.36, p = 0.038). Conversely, mice tended to move away from paved edges (Rayleigh test = 0.33, p = 0.016). Nevertheless, we found no evidences that the net direction travelled differed significantly across edge types (Chi test = 0.26, df = 2, p = 0.88) (Fig. 3). We also found no differences in net displacement from edges across edge types (K = 0.34, df = 2, p = 0.84; Fig. 3).

Discussion

Our results support the hypothesis that roads decrease edge permeability, evidenced by the lack of individuals crossing the two road edge types. Nearly one-third of the individuals tracked in roadless edges crossed the edge at least once into the surrounding pasture or fallow lands, whereas no crossings occurred in edges bordered by dirt or paved roads. While we expected this outcome in edges bordered by paved roads, the lack of crossings at edges bordered by dirt roads was

rather unexpected, given the low perturbation and more natural substrate found therein. Furthermore, although we found no evidence of mice avoiding edge proximity, as the patterns of net direction travelled and net displacement from edge were similar across edge types, the individuals tracked near paved edges apparently tended to move away from edges more consistently. These results suggest an avoidance behavior from road proximity, and are in accordance with previous research reporting a lack or low number of road crossings by small mammals, even for narrow and unpaved roads (Oxley et al. 1974; Swihart and Slade 1984; Goosem 2002; Rico et al. 2007; McLaren et al. 2011).

Avoiding crossing roads, even unpaved ones, is probably related to the lack of overhead or complex ground cover, increasing predation risk (Rohner and Krebs 1996; Smith and Batzli 2006). This could explain the higher proportion of individuals that explored the agricultural and pasture areas after being released near roadless edges. Hence, individuals inhabiting edges bordered by both types of roads are

Fig. 3 a Net direction traveled of individuals after release, across edge types. Directions were standardized so that 0° symbolizes the nearest forest edge. The length of wedges represents the number of individuals whose direction fell within the designated bin. b Boxplots of net displacement from edges across edge types. *Boxplot upper* and *lower limits* represent the interquartile range (IQR), the thick line is the median and ''whiskers'' are the ±1.5 * IQR. *Dots* are the individual values. *Dotted line* indicates the release point (1–5 m from edge, inside the forest patch). *Negative/positive values* indicate that the individual moved toward/away the edge
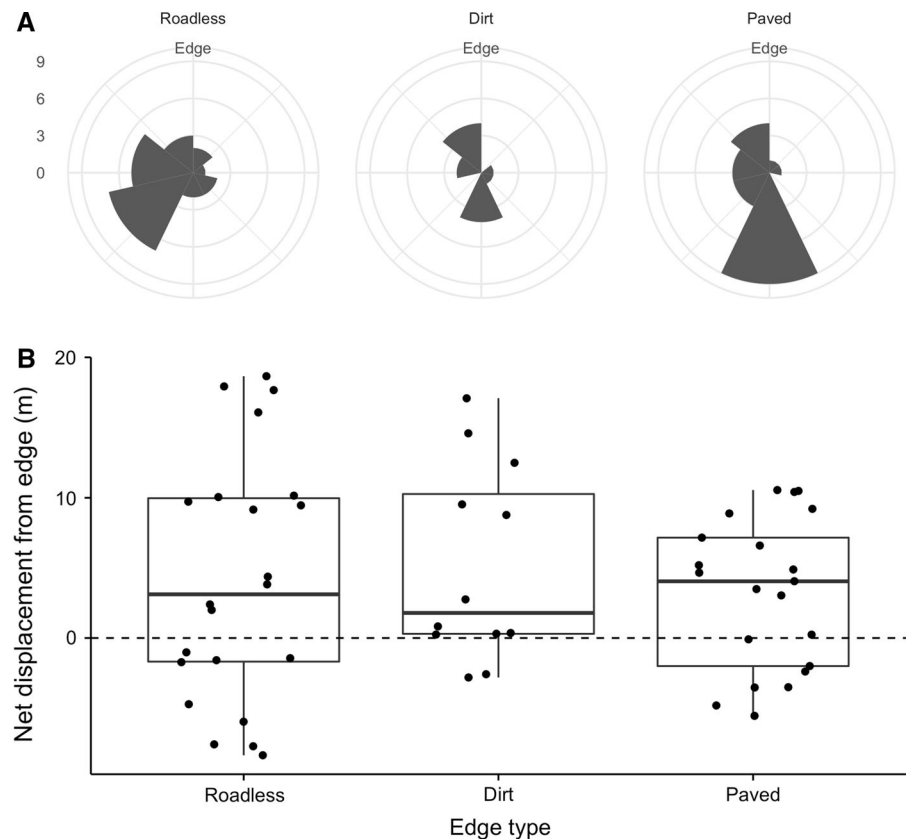
less likely to investigate these areas, apparently due to road presence. This suggests that, in certain circumstances, the barrier effect of roads may be more intense than initially expected. In particular, our study suggests that all roads might constitute a significant barrier when bordering forest edges. Moreover, because the montane akodont is a common species adapted to several different habitats (Umetsu and Pardini 2007; Antunes et al. 2010; Martin et al. 2012; Galiano et al. 2013), we anticipate that the effect of roads is more intense for forest specialists. If so, movement between patches for a multitude of other species may be significantly compromised, potentially destabilizing the entire ecosystem.

We acknowledge that these results should be read cautiously as we were only able to track individuals up to a limited distance (<60 m), therefore, the movement patterns may reflect initial orientation and reaction after release. However, we were very careful in minimizing the disturbance when releasing the animals, which should have reduced stress and abnormal movement reactions. Nevertheless, further research using other tracking methods (e.g. VHF collars) or genetic approaches (Manel et al. 2003) should be performed in order to evaluate if mice persistently avoid crossing roaded edges. It should be noted that these methods, despite providing large-scale movement information, do not allow for such fine-scale information as our approach.

It is important to maintain roaded edges more permeable in order to sustain functional connectivity across the landscape. This can be facilitated by installing new or improving existing crossing structures, such as culverts, thereby allowing animals to safely cross roads (Ascensão et al. 2015; Rytwinski et al. 2016). However, the adequate placement of such structures is crucial, requiring a landscape management perspective and particularly detailed knowledge of the role of habitat matrices and other edge types in animal movement and dispersal (Maciel and Lutscher 2013). This is particularly relevant for Brazil. The Brazilian road network is currently one of the most extensive transportation networks, consisting of 213,000 km of paved roads (National Agency of Terrestrial Transport—ANTT). This immense network bisects important habitats, including world biodiversity hotspots such as the Cerrado biome (Mittermeier et al. 1998; Costa et al. 2005; Klink and Machado 2005).

Despite its importance, Cerrado areas are rapidly disappearing, giving way to pasture and intensive agriculture (Brooks et al. 2002; Klink and Machado 2005; Silva et al. 2006). Many at-risk species are either endemic to Cerrado or found in higher densities there (Costa et al. 2005; Klink and Machado 2005; Strassburg et al. 2016). Moreover, habitat remnants are generally scattered throughout the landscape and roads often contour those remnants. Hence, roads may represent a severe driver of isolation for several species, leading to genetic structuring (Gerlach and Musolf 2000; Riley et al. 2006; Mendez et al. 2011; Lesbarreres and Fahrig 2012), which in turn may diminish population persistence (Balkenhol and Waits 2009; Holderegger and Di Giulio 2010; McCall et al. 2010). Therefore, further research should focus on structural connectivity for multiple species in order to improve road permeability and landscape connectivity.

Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.

References

Antunes PC, Campos MAA, Oliveira-Santos LGR, Graipel ME (2010) Population dynamics of Akodon montensis (Rodentia, Cricetidae) in the Atlantic forest of Southern Brazil. Mamm Biol 75:186–190

Ascensão F, LaPoint S, van der Ree R (2015) Roads, traffic and verges: big problems and big opportunities for small mammals. In: van der Ree R, Smith D, Grilo C (eds) Handbook of road ecology. Wiley, New York, pp 325–333

Baguette M, Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecol 22:1117–1129

Balkenhol N, Waits LP (2009) Molecular road ecology: exploring the potential of genetics for investigating transportation impacts on wildlife. Mol Ecol 18:4151–4164

Brehme CS, Tracey JA, McClenaghan LR, Fisher RN (2013) Permeability of roads to movement of scrubland lizards and small mammals. Conserv Biol 27:710–720

Brodie JF, Giordano AJ, Ambu L (2015) Differential responses of large mammals to logging and edge effects. Mamm Biol 80:7–13

Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. Conserv Biol 16:909–923

Clark RW, Brown WS, Stechert R, Zamudio KR (2010) Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conserv Biol 24:1059–1069

Collinge SK, Palmer TM (2002) The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. Landscape Ecol 17:647–656

Cordeiro GM, Paula GA, Botter DA (1994) Improved likelihood ratio tests for dispersion models. Int Stat Rev 62:257

Costa LP, Leite YLR, Mendes SL, Ditchfield AD (2005) Mammal conservation in Brazil. Conserv Biol 19:672–679

Dantas AAA, de Carvalho LG, Ferreira E (2007) Climatic classification and tendencies in Lavras region, MG. Ciênc Agrotecnol 31:1862–1866

Ewers RM, Thorpe S, Didham RK (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. Ecology 88:96–106

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fischer J, Lindenmayer DB, Fahrig L (2003) Landscape modification and habitat fragmentation: a synthesis. Glob Ecol Biogeogr 34:487–515

Ford AT, Fahrig L (2008) Movement patterns of eastern chipmunks (Tamias striatus) near roads. J Mammal 89:895–903

Forman RTT, Deblinger RD (2000) The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conserv Biol 14:36–46

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC (2003) Road ecology: science and solutions. Island Press, Washington, DC

Fuentes-Montemayor E, Cuaron AD, Vazquez-Dominguez E, Benítez-Malvido J, Valenzuela-Galván D, Andresen E (2009) Living on the edge: roads and edge effects on small mammal populations. J Anim Ecol 78:857–865

Galiano D, Kubiak BB, Marinho JR, de Freitas TRO (2013) Population dynamics of Akodon montensis and Oligoryzomys nigripes in an Araucaria forest of southern Brazil. Mammalia 77:173–179

Gerlach G, Musolf K (2000) Fragmentation of landscape as a cause for genetic subdivision in bank voles. Conserv Biol 14:1066–1074

Goodin DG, Paige R, Owen RD, Ghimire K, Koch DE, Chu YK, Jonsson CB (2009) Microhabitat characteristics of Akodon montensis, a reservoir for hantavirus, and hantaviral seroprevalence in an Atlantic forest site in eastern Paraguay. J Vector Ecol 34:104–113

Goosem M (2002) Effects of tropical rainforest roads on small mammals: fragmentation, edge effects and traffic disturbance. Wildl Res 29:277–302

Graipel ME, Miller PRM, Glock L (2003) Padrão de atividade de Akodon montensis e Oryzomys russatus na reserva volta velha, santa catarina, sul do brasil. Mastozool Neotrop 10:255–260

Holderegger R, Di Giulio M (2010) The genetic effects of roads: a review of empirical evidence. Basic Appl Ecol 11:522–531

Jammalamadaka SR, Sarma YR (1993) Circular regression. In: Matusita K, Puri ML, Hayakawa Y (eds) Statistical sciences and data analysis. VSP, Utrecht, pp 109–128

Klink CA, Machado RB (2005) Conservation of the Brazilian Cerrado. Conserv Biol 19:707–713

Laurance WF, Balmford A (2013) A global map for road building. Nature 495:308–309

Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, Bruna EM, Stouffer PC, Williamson GB, Benítez-Malvido J, Vasconcelos HL, Van Houtan KS (2011) The fate of Amazonian forest fragments: a 32-year investigation. Biol Conserv 144:56–67

Laurance WF, Clements GR, Sloan S, O'Connell CS, Mueller ND, Goosem M, Venter O, Edwards DP, Phalan B, Balmford A, Van Der Ree R (2014) A global strategy for road building. Nature 513:229–232

Laurance WF, Didham RK, Power ME (2001) Ecological boundaries: a search for synthesis. Trends Ecol Evol 16:70–71

Lesbarreres D, Fahrig L (2012) Measures to reduce population fragmentation by roads: what has worked and how do we know? Trends Ecol Evol 27:374–380

Maciel GA, Lutscher F (2013) How individual movement response to habitat edges affects population persistence and spatial spread. Am Nat 182:42–52

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197

Manson RH, Ostfeld RS, Canham CD (1999) Responses of a small mammal community to heterogeneity along forest-old-field edges. Landscape Ecol 14:355–367

Martin PS, Gheler-Costa C, Lopes PC, Rosalino LM, Verdade LM (2012) Terrestrial non-volant small mammals in agro-silvicultural landscapes of southeastern Brazil. For Ecol Manag 282:185–195

McCall SC, McCarthy MA, van der Ree R, Harper MJ, Cesarini S, Soanes K (2010) Evidence that a highway reduces apparent survival rates of squirrel gliders. Ecol Soc 15(3):27

McDonald WR, Clair CCS (2004) The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. Oikos 105:397–407

McGregor RL, Bender DJ, Fahrig L (2008) Do small mammals avoid roads because of the traffic? J Appl Ecol 45:117–123

McLaren AAD, Fahrig L, Waltho N (2011) Movement of small mammals across divided highways with vegetated medians. Can J Zool 89:1214–1222

Mendez M, Tella JL, Godoy JA (2011) Restricted gene flow and genetic drift in recently fragmented populations of an endangered steppe bird. Biol Conserv 144:2615–2622

Mimet A, Houet T, Julliard R, Simon L (2013) Assessing functional connectivity: a landscape approach for handling

multiple ecological requirements. Methods Ecol Evol 4:453–463

Mittermeier RA, Myers N, Thomsen JB, Da Fonseca GA, Olivieri S (1998) Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conserv Biol 12:516–520

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10:58–62

Owen RD, Goodin DG, Koch DE, Chu YK, Jonsson CB (2010) Spatiotemporal variation in *Akodon montensis* (Cricetidae: Sigmodontinae) and hantaviral seroprevalence in a subtropical forest ecosystem. J Mammal 91:467–481

Oxley DJ, Fenton MB, Carmody GR (1974) The effects of roads on populations of small mammals. J Appl Ecol 11:51–59

Porto FP, Molina-vacas G, Rodriguez J, Grilo C (2013) Effects of roads on spatial behaviour and abundance of small mammals: gaps in knowledge. Oecol Aust 17:63–76

Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19:1205–1223

Puttker T, Pardini R, Meyer-Lucht Y, Sommer S (2008) Responses of five small mammal species to micro-scale variations in vegetation structure in secondary Atlantic Forest remnants, Brazil. BMC Ecol 8:9

Rico A, Kindlmann P, Sedlacek F (2007) Barrier effects of roads on movements of small mammals. Folia Zool 56:1–12

Ries L, Robert J, Fletcher J, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35:491–522

Riley SPD, Pollinger JP, Sauvajot RM, York EC, Bromley C, Fuller TK, Wayne RK (2006) A southern California freeway is a physical and social barrier to gene flow in carnivores. Mol Ecol 15:1733–1741

Rohner C, Krebs C (1996) Owl predation on snowshoe hares: consequences of antipredator behaviour. Oecologia 108:303–310

Rondinini C, Doncaster CP (2002) Roads as barriers to movement for hedgehogs. Funct Ecol 16:504–509

Rytwinski T, Soanes K, Jaeger JAG, Fahrig L, Findlay CS, Houlahan J, Van Der Ree R, van der Grift EA (2016) How effective is road mitigation at reducing road-kill? A meta-analysis. PLoS ONE 11:e0166941

Silva JF, Farinas MR, Felfili JM, Klink CA (2006) Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. J Biogeogr 33:536–548

Silva-Pereira JE, Moro-Rios RF, Bilski DR, Passos FC (2011) Diets of three sympatric Neotropical small cats: food niche overlap and interspecies differences in prey consumption. Mamm Biol 76:308–312

Smith JE, Batzli GO (2006) Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment. Oikos 112:209–217

Stamps JA, Buechner M, Krishnan VV (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. Am Nat 129:533–552

Stevens SM, Husband TP (1998) The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. Biol Conserv 85:1–8

Strassburg BBN, Latawiec A, Balmford A (2016) Brazil: urgent action on Cerrado extinctions. Nature 540:199

Swihart RK, Slade NA (1984) Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. J Mammal 65:357–360

Uezu A, Metzger JP, Vielliard JME (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic forest bird species. Biol Conserv 123:507–519

Umetsu F, Pardini R (2007) Small mammals in a mosaic of forest remnants and anthropogenic habitats—evaluating matrix quality in an Atlantic forest landscape. Landscape Ecol 22:517–530

van der Ree R, Grilo C, Smith DJ (2015) Handbook of road ecology. Wiley, Chichester

Vieira EM, Paise G, Machado PHD (2006) Feeding of small rodents on seeds and fruits: a comparative analysis of three species of rodents of theAraucaria forest, southern Brazil. Acta Theriol (Warsz) 51:311–318

Youngquist MB, Boone MD (2014) Movement of amphibians through agricultural landscapes: the role of habitat on edge permeability. Biol Conserv 175:148–155

Zurita G, Pe'er G, Bellocq MI, Hansbauer MM (2012) Edge effects and their influence on habitat suitability calculations: a continuous approach applied to birds of the Atlantic forest. J Appl Ecol 49:503–512