

Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass

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Summary

1. For animal species inhabiting heterogeneous landscapes, the tortuosity of the dispersal path is a key determinant of the success in locating habitat patches. Path tortuosity within and beyond perceptual range must differ, and may be differently affected by intrinsic attributes of individuals and extrinsic environmental factors. Understanding how these factors interact to determine path tortuosity allows more accurate inference of successful movements between habitat patches.

2. We experimentally determined the effects of intrinsic (body mass and species identity) and extrinsic factors (distance to nearest forest fragment and matrix type) on the tortuosity of movements of three forest-dwelling didelphid marsupials, in a fragmented landscape of the Atlantic Forest, Brazil.

3. A total of 202 individuals were captured in forest fragments and released in three unsuitable matrix types (mowed pasture, abandoned pasture and manioc plantation), carrying spool-and-line devices.

4. Twenty-four models were formulated representing *a priori* hypotheses of major determinants of path tortuosity, grouped in three scenarios (only intrinsic factors, only extrinsic factors and models with combinations of both), and compared using a model selection approach. Models were tested separately for individuals released within the perceptual range of the species, and for individuals released beyond the perceptual range.

5. Matrix type strongly affected path tortuosity, with more obstructed matrix types hampering displacement of animals. Body mass was more important than species identity to determine path tortuosity, with larger animals moving more linearly. Increased distance to the fragment resulted in more tortuous paths, but actually reflects a threshold in perceptual range: linear paths within perceptual range, tortuous paths beyond.

6. The variables tested explained successfully path tortuosity, but only for animals released within the perceptual range. Other factors, such as wind intensity and direction of plantation rows, may be more important for individuals beyond their perceptual range.

7. Simplistic scenarios considering only intrinsic or extrinsic factors are inadequate to predict path tortuosity, and to infer dispersal success in heterogeneous landscapes. Perceptual range represents a fundamental threshold where the effects of matrix type, body mass and individual behaviour change drastically.

Key-words: functional connectivity, matrix permeability, matrix resistance, movement patterns, movement tortuosity

Introduction

In heterogeneous landscapes, dispersal between habitat patches is one of the main determinants of population

dynamics and persistence (Moilanen & Hanski 1998; Schooley & Wiens 2005). The success of an individual crossing the non-habitat matrix and colonizing new habitat patches is determined by an interaction between its behaviour, life-history traits and the composition of the matrix surrounding habitat patches (Goodwin & Fahrig 2002; Gardner &

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Gustafson 2004; Schooley & Wiens 2004; Walters 2007). Some matrix types allow animals to freely move between habitat patches, while others may function as complete barriers to movement (e.g. Jonsen, Bouchier & Roland 2001; Ricketts 2001; Schooley & Wiens 2003; Stevens *et al.* 2004; review in Prevedello & Vieira 2010a).

The interaction between life-history traits and matrix composition will determine the perceptual range (*sensu* Lima & Zollner 1996), and the tortuosity of the movement path, which is directly related to its effectiveness at finding habitat patches (Dusenbery 1989; Zollner & Lima 1999, 2005). The perception of habitat patches by individuals should result in oriented movements (Lima & Zollner 1996; Nams 2006; Forero-Medina & Vieira 2009), hence movement paths within the perceptual range should be straight and directed to a habitat patch. However, even within perceptual range other factors may affect path tortuosity, such as body size and vegetation obstruction. The same environment presents more obstacles to small animals, requiring more tortuous paths to circumvent (With 1994; Mech & Zollner 2002; Bowne & White 2004; Snider & Gilliam 2008), and matrix types with denser vegetation should also present more obstacles, hence result in more tortuous paths.

Beyond perceptual range, individuals may still try to maintain straight paths as a more efficient strategy to find unknown habitat patches, reducing the time and energy spent in the risky environment of the matrix (Zollner & Lima 1999). However, to keep on a straight path without a perceived target may be a more difficult task, when body size and vegetation obstruction may become more determinant of path tortuosity, or other strategies may be adopted, such as use of plantation rows (Prevedello & Vieira 2010b) or anemotactic behaviour (Schooley & Wiens 2003; Forero-Medina & Vieira 2009). These strategies may differ among species depending on their particular morphological, behavioural and locomotory adaptations.

Few studies analysed the shape of movement paths of individuals moving in the matrix to infer dispersal success of a species (Bowne & White 2004; Schooley & Wiens 2004; Selonen & Hanski 2004; Caldwell & Nams 2006; Haynes & Cronin 2006), or evaluated the relative importance of life-history traits vs. environmental features as determinants of path efficiency (Schooley & Wiens 2004). Besides, most studies evaluating matrix effects on movements focused on insects in micro-landscapes (e.g. Wiens, Schooley & Weeks 1997; Jonsen, Bouchier & Roland 2001; Goodwin & Fahrig 2002; Baum *et al.* 2004; Bender & Fahrig 2005; Cronin 2007), whereas little information is available for vertebrates in larger landscapes (Doerr & Doerr 2004, 2005). Vertebrates may respond differently to matrix type considering their large scale of movement, and the variety of matrix elements they interact (Lima & Zollner 1996; Doerr & Doerr 2005). The relative importance of matrix structure and type compared with species-specific traits as determinants of movement tortuosity of dispersing vertebrates is unknown.

Here we use path tortuosity of individuals within and beyond perceptual ranges to determine factors that affect

potential dispersal success of a species. We assumed that straighter paths are more efficient to cross the matrix and find habitat patches, and compared three sets of *a priori* explanatory models of path tortuosity: one containing only intrinsic factors potentially affecting path tortuosity (species identity and body mass), one containing only extrinsic factors (matrix type and distance from nearest habitat patch), and another containing simultaneously intrinsic and extrinsic factors.

The plausibility of models was compared by field experiments with three species of didelphid marsupials (*Didelphis aurita*, *Philander frenatus* and *Micoureus paraguayanus*) in three matrix types in a fragmented Atlantic Forest landscape. These species are endemic to the Atlantic Forest inhabiting forest remnants, moving only occasionally between fragments (Pires *et al.* 2002; Lira *et al.* 2007). They are absent of some fragments (Vieira *et al.* 2009), and do not live in the matrix (Lira *et al.* 2007; Umetsu & Pardini 2007). Our main goal was to determine the relative importance of species identity, body mass, distance from nearby forest fragment and matrix type on path tortuosity of these species. We expected a decrease in path tortuosity with body mass and an increase with distance from the nearest fragment and matrix obstruction. Body mass and species identity were tested as alternative hypothesis to check if behavioural and locomotory adaptations of each species are more important to determine movement tortuosity than differences in body size among individuals.

Materials and methods

STUDY SITE

Animals were captured in 14 Atlantic Forest fragments, with the exception of six individuals of *D. aurita* that were captured in a large stretch of continuous forest in the Macacu River watershed, in the cities of Guapimirim (22°2'S, 42°59'W) and Cachoeiras de Macacu (22°28'S, 42°39'W), Rio de Janeiro State, Brazil. The climate on the region is mild-humid-mesotermic (Nimer 1989), and vegetation is classified as dense evergreen forest (IBGE 1991). The region of the Macacu River was first occupied by the end of the XVI century, but the fragmentation process was significantly intensified in the 1960s, following the construction of a major highway (Cabral & Fiszson 2004). Nowadays, the landscape is characterized mainly by small Atlantic Forest remnants (< 100 ha) structurally isolated by a matrix of urban areas, pastures, plantations and paved roads (Cabral & Fiszson 2004; Vieira *et al.* 2009).

Experiments were conducted in three matrix types: manioc plantation, mowed pasture and abandoned pasture. These are the predominant types of land use in the landscape studied (Vieira *et al.* 2009), also occurring in other landscapes in the Atlantic Forest. Mowed and abandoned pastures had only one release site each, but for manioc plantation we had to use three release sites during the study because of harvesting, with no differences detected in movements among sites. All five release sites were located in the vicinities of a forest fragment, and located at > 1 km from other fragments, including the fragment where animal was captured. This distance should minimize the chance of homing behaviour affecting the movement of released animals (Zollner & Lima 1997; Forero-Medina & Vieira 2009). Maximum distance between release sites was 7.5 km. Manioc (*Manihot*

esculenta, Euphorbiaceae) plantations were fully grown (c. 185 cm high) and arranged in parallel rows spaced c. 160 cm. The mowed pasture matrix was dominated by grasses periodically mowed by farm managers, resulting in a low grass height (mean = 14.27, SD = 5.23 cm), with some variation during the study due to cattle grazing. The abandoned pasture matrix was also dominated by grasses, but the absence of grazing and mowing for more than 1 year prior to the beginning of the experiments resulted in denser and taller grasses (mean height = 45.00, SD = 13.50 cm) and occasional presence of shrubs. Visual vegetation obstruction at ground level was measured at 100 m from the fragment, using a 0.50 × 0.50 m square wood frame divided in to 100 open squares (Freitas, Cerqueira & Vieira 2002), and estimated as 77 ± 19% (mean ± SD) in manioc plantation, 66 ± 16% in abandoned pasture and 31 ± 9% in mowed pasture. Release experiments were done from August 2005 to August 2006 in the mowed pasture, from May 2007 to May 2008 in the manioc plantation and from March 2008 to July 2008 in the abandoned pasture. The proximity of the release sites both in space and time made climatic differences unlikely, and the nearest fragment (target) was similar in size and vegetation height among matrix types.

STUDIED SPECIES

The three species studied were the most abundant marsupials in forest fragments of the region (Vieira *et al.* 2009). The black-eared opossum *D. aurita* (Wied-Neuwied 1826) has semi-terrestrial habits (Cunha & Vieira 2002) and is the largest of the studied species (body mass for studied individuals: mean = 770, SD = 355 g). Movements between fragments and captures in the matrix were reported for this species in other areas of Atlantic forest (Pires *et al.* 2002). *Didelphis aurita* is considered to be tolerant to fragmented landscapes due to its high vagility and presence in fragments of different sizes and degree of disturbance by timber extraction, hunting and cattle raising (Fernandez & Pires 2006). The grey four-eyed opossum, *Philander frenatus* (Olfers 1818), it is also semiterrestrial (Cunha & Vieira 2002). Body mass for studied individuals was 410 ± 155 g. Movements between fragments and captures in the matrix also were reported in the Atlantic Forest (Pires *et al.* 2002; Lira *et al.* 2007). The opossum *Micoureus paraguayanus* (Moojen 1943) is the smallest among the studied species (115 ± 40 g for studied individuals), has more arboreal habits (Grelle 2003), and it was also reported to cross open grassland matrix, but only movements of males were detected (Pires *et al.* 2002).

FIELD METHODS

Animals were captured in the forest fragments using Tomahawk traps (40.6 × 12.7 × 12.7 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin) and Sherman traps (7.6 × 9.5 × 30.5 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida). Captured animals were placed into individual cages, fed, and left in a protected place for 3–72 h before release. Individuals were released using a standard mechanism, which consisted of an inverted box with a string attached to the bottom of the box (Forero-Medina & Vieira 2009). The string passed through two pulleys on top of a cross-shaped stake. The first pulley was at the end of one arm of the cross, positioned right above the box, and the second on top of the upper arm of the cross, from which the string was extended to a distance of at least 20 m. The box could then be lifted by an observer at a distance, minimizing influences on animal movements.

Individuals were released at five distances from the fragment's edge: 30, 50, 100, 200 and 300 m (Forero-Medina & Vieira 2009;

Prevedello 2009). Only healthy adult and sub-adult individuals (based on Macedo *et al.* 2006), excluding lactating females, were used in the experiments. Release points of individuals released on the same day were positioned 20 m apart from each other to minimize possible interferences. All releases were done in the late afternoon (between 17.30 and 19.30 h depending on the month of release) because these species are nocturnal, with up to five animals released simultaneously in a day at a same site.

Before release, animals received a spool-and-line device to record their fine-scale movements (Cunha & Vieira 2002). Individual paths were mapped by taking the distance and azimuth between two points of direction change (changes greater than 10°). We preferred to define points of direction change to preserve the actual step lengths used by animals, which should provide a more realistic description of path shape than fixed lengths of measurement. Each individual was released and tracked only once. It was assumed that animals perceived the three matrix types as inhospitable and searched for their primary habitat after release, their movements representing habitat search behaviour. This is reasonable because the three matrix types had lower vegetative cover and probably offered a high risk of predation by domestic dogs or raptors (Forero-Medina & Vieira 2009). Also, captures in the matrix were rare for the three species (Umetsu & Pardini 2007; Vieira *et al.* 2009). Wind intensity may affect orientation ability, hence path tortuosity, particularly for *D. aurita* (Forero-Medina & Vieira 2009). However, only in the mowed pasture was there a measurable wind current; there was no wind within the manioc plantation, and rarely in the abandoned pasture.

DATA ANALYSIS

Tortuosity of each path was measured by the fractal mean index, *D*, using Fractal v. 5.10 (Nams 2005). This index varies from 1 (a complete straight path) to 2 (a path that is as tortuous as to cover a plane), and is considered a good indicator of path efficiency of finding resources (Doerr & Doerr 2004). Tortuosity measures were transformed to log (*D*–1) to obtain normality as suggested by Caldwell & Nams (2006). Eighty-six percent of tested categories were normally distributed (*P* > 0.05 for Shapiro-Wilk's tests), and homogeneity of variances was not rejected in any test (*P* > 0.05 in Levene's test). Only paths longer than 30 m were used in the analyses.

To determine the relative effects of matrix type, species identity, body mass and distance to the nearest fragment on movement tortuosity, a model selection approach based on ANCOVA design and maximum likelihood parameter estimation was used (Burnham & Anderson 2002). Twenty-four models were formulated representing *a priori* hypotheses of major determinants of path tortuosity, grouped in three scenarios: only factors intrinsic to individuals, only factors extrinsic and models with both type of factors (Table 1). Interactions between explanatory variables were also included in some of these models; however, some possible models combining three variables and more than one interaction among them were not considered because of their complexity and low plausibility. Models did not include body mass and species identity simultaneously because of their redundancy (Vieira & Cunha 2008). Model performance was compared using statistics derived from the corrected Akaike Information Criterion (AICc), appropriate when the ratio of sample size to number of parameters is less than 40 (Burnham & Anderson 2002). The smaller the value of AICc, the less information a model loses relative to an incommensurable reality (Burnham & Anderson 2002). For each model two AIC statistics were determined, Δ_i (= AICc_{*i*} – minimum AICc) and w_i , which indicate the probability that the model is the best model. Values of $\Delta_i \leq 2$ were used as an

Table 1. Candidate models of factors affecting path tortuosity of three species of didelphid marsupials in three types of matrix (mowed pasture, abandoned pasture and manioc plantation)

Model	Variables
Scenario 1. Only factors intrinsic to individuals affect path tortuosity	
1	Species
2	Body mass
Scenario 2. Only factors extrinsic to individuals affect path tortuosity	
3	Distance
4	Matrix type
5	Distance, matrix type
6	Distance, matrix type, distance*matrix type
Scenario 3. Both factors intrinsic and extrinsic to individuals affect path tortuosity	
7	Species, distance
8	Species, distance, species*distance
9	Species, matrix type
10	Species, matrix type, species*matrix type
11	Body mass, distance
12	Body mass, distance, body mass*distance
13	Body mass, matrix type
14	Body mass, matrix type, body mass*matrix type
15	Species, matrix type, distance
16	Species, matrix type, distance, species*matrix type
17	Species, matrix type, distance, species*distance
18	Species, matrix type, distance, matrix type*distance
19	Species, matrix type, distance, species*matrix type*distance
20	Body mass, matrix type, distance
21	Body mass, matrix type, distance, body mass*matrix type
22	Body mass, matrix type, distance, body mass*distance
23	Body mass, matrix type, distance, matrix type*distance
24	Body mass, matrix type, distance, body mass*matrix type*distance

Models combine different subsets of four explanatory variables (distance to nearest fragment, matrix type, species identity and body mass), as well as interactions between them (indicated by an asterisk), considering three different scenarios.

initial criterion to select the best models, but models with $2 \leq \Delta_i \leq 10$ were also considered, which have less support from the data but cannot be disregarded (Burnham & Anderson 2002, p. 170). A null model was also included for comparison, which included only the intercept and residual errors as parameters. All analyses were carried out with the Generalized Linear Models module of STATISTICA (Statsoft Inc., Tulsa, OK, USA).

Two separate analyses were carried out to assess how matrix type affects movement tortuosity. First, comparing tortuosity among the three matrix types, thus treating matrix type as a categorical variable with three levels (mowed pasture, abandoned pasture and manioc plantation). This was only possible for *P. frenatus* and *D. aurita* because paths of *M. paraguayanus* were recorded in the mowed pasture only. Second, testing the association between grass height in the mowed pasture and tortuosity for the three species, thus treating matrix type as a continuous variable. The first analysis evaluates the effects of different types of human land use in the matrix, whereas the second determine more fine-scale effects of matrix type related to livestock activity. These analyses were done first using all individuals, and also using only individuals released within or beyond the perceptual ranges of these species. Perceptual ranges were estimated for *P. frenatus* and *D. aurita* as 100 and 200 m, respectively, in mowed pasture, 50 and < 30 m in the abandoned pasture and 30 and 50 m in

the manioc plantation (Forero-Medina & Vieira 2009; Prevedello 2009). Perceptual ranges differed among matrix types and species depending on vegetation obstruction, body mass and the use of visual vs. olfactory cues by the species (Forero-Medina & Vieira 2009; Prevedello 2009). Perceptual range of *M. paraguayanus* in the mowed pasture was estimated as 100 m (Forero-Medina & Vieira 2009). Distance was not included as an explanatory variable in these analyses because few distances of release were used for animals within or beyond the perceptual ranges.

Results

We tracked a total of 202 paths, 100 from *P. frenatus* (47 in mowed pasture, 37 in manioc plantation and 16 in abandoned pasture), 79 from *D. aurita* (34 in mowed pasture, 24 in manioc plantation and 21 in abandoned pasture) and 23 from *M. paraguayanus* (all in mowed pasture). There were no differences in the movements of males and females, therefore genders were pooled in all analysis.

DIDELPHIS AURITA AND *P. FRENATUS* IN THE THREE MATRIX TYPES

Considering all individuals of *D. aurita* and *P. frenatus* in the three matrix types, the most plausible model explaining tortuosity of movements included body mass, matrix type, distance to the nearest fragment and the interaction between matrix type and distance (Table 2a). This model was the only one with $\Delta_i < 2$ being clearly the most plausible ($w_i = 0.57$), and was therefore the only considered in the analysis of regression coefficients (Table 3a). Models with species identity were less plausible ($\Delta_i \geq 8.49$, $w_i \leq 0.01$), and the null model was implausible ($\Delta_i = 23.19$, $w_i < 0.01$). Tortuosity of movements increased with distance to the fragment, and it was higher in the abandoned pasture compared with the mowed pasture or manioc plantation (Table 3a). Tortuosity also increased as body mass decreased (Table 3a). Coefficients of continuous independent variables with large variation, such as distance and body mass, were very small because values of the dependent variable, tortuosity, has a small scale of variation. Therefore, one unit of variation in the independent variable had a small but plausible effect on tortuosity.

Considering only individuals released within the perceptual range of the species, matrix type and body mass were the main variables affecting tortuosity (Table 2b). The most plausible model included both variables ($w_i = 0.38$), and they were the only variables present in models with $\Delta_i < 2$. Models including species identity and the null model were less plausible ($w_i < 0.09$ and $w_i = 0.04$, respectively). The first two models had $\Delta_i < 2$ and were averaged for the analysis of regression coefficients (Table 3a). Tortuosity of movements increased as body mass decreased, and it was higher in the abandoned pasture compared with the mowed pasture or manioc plantation (Table 3a).

Considering only individuals released beyond the perceptual range of the species, the null model was the most

Table 2. Performance of models predicting path tortuosity of two didelphid marsupials (*Didelphis aurita* and *Philander frenatus*) in three matrix types (mowed pasture, abandoned pasture and manioc plantation)

Model	Variables	Log-likelihood	K	AICc	Δ_i	w_i
(a) All individuals						
1	Body mass, matrix type, distance, 1*2	-40.52	8	97.89	0.00	0.57
2	Body mass, matrix type, distance	-43.78	6	100.04	2.16	0.19
3	Body mass, matrix type, distance, 1*3	-43.48	7	101.61	3.73	0.09
4	Body mass, matrix type, distance, 1*2*3	-42.98	8	102.80	4.91	0.05
5	Body mass, matrix type, distance, 2*3	-43.28	8	103.40	5.51	0.04
6	Body mass, matrix type	-46.79	5	103.93	6.05	0.03
7	Matrix type, distance, species, 2*4	-44.76	8	106.38	8.49	0.01
23	None	-58.50	2	121.07	23.19	< 0.01
(b) Within the perceptual range						
1	Body mass, matrix type	-32.86	5	76.51	0.00	0.38
2	Body mass	-35.47	3	77.25	0.74	0.26
3	Matrix type	-35.05	4	78.61	2.10	0.13
4	Matrix type, species	-34.34	5	79.45	2.95	0.09
5	Species	-36.99	3	80.29	3.79	0.06
6	None	-38.40	2	80.96	4.45	0.04
(c) Beyond the perceptual range						
1	None	-9.41	2	22.96	0.00	0.19

Analyses were done including (a) all individuals, and only individuals released (b) within or (c) beyond the perceptual range of the species. K , number of parameters of the model; AICc, Akaike Information Criterion corrected for small ratio sample size/number of parameters; Δ_i , AICc_i - minimum AICc; w_i , Akaike weight.

Asterisks indicate interactions between variables, coded by numbers (distance to nearest fragment = 1, matrix type = 2, body mass = 3, species identity = 4). The model without variables represents the null model, including parameters only for the intercept and residual error. Models less plausible (greater AICc) than the null model are not shown.

plausible ($w_i = 0.19$; Table 2c). Therefore, none of the variables measured explained substantially variation in tortuosity.

DIDELPHIS AURITA, P. FRENATUS AND M. PARAGUAYANUS IN THE MOWED PASTURE

Considering data from all individuals released in the mowed pasture, the most plausible model included grass height, distance, body mass and the interaction between grass height and body mass ($w_i = 0.26$; Table 4a). These variables were also present in the second most plausible model. However, the third most plausible model included species identity and its interactions instead of body mass, with $w_i < 2$. Thus, it is not possible to discard body mass and species identity as important determinants of tortuosity. The null model was implausible ($\Delta_i = 22.70$, $w_i < 0.01$). Tortuosity of movements increased with increasing distance to the fragment and grass height, and decreased with body mass (Table 3b). Movements of *D. aurita* were straighter than movements of *M. paraguayanus* (Table 3b).

Considering only individuals released within the perceptual range of the species, tortuosity of movements was determined mainly by body mass and grass height (Table 4b). The two variables and their interaction were present in the most plausible model ($w_i = 0.44$), and grass height alone was the second most plausible model ($w_i = 0.34$). Models with species identity were less plausible than models with body mass (Table 4b). The null model was little plausible ($\Delta_i = 12.29$, $w_i < 0.01$). Tortuosity of movements increased with grass height and decreased with body mass (Table 3b).

For individuals released beyond the perceptual range of the species, grass height was present in the most plausible model ($w_i = 0.31$), but the null model was ranked as the second best model, thus the variables measured did not explain substantially variation in data (Table 4c).

Discussion

Both intrinsic and extrinsic factors affected tortuosity of movements in the marsupial species studied, regardless whether analyses considered only two species in the three matrix types, or three species in the mowed pasture. Scenarios considering only intrinsic or extrinsic factors were clearly incomplete and inadequate to explain movement tortuosity for these species. Therefore, future studies modelling movement behaviour, dispersal and functional connectivity in fragmented landscapes should include both kinds of factors for more realistic predictions.

Matrix type strongly influenced the movements of the didelphid marsupials, as reported previously mainly for invertebrates (e.g. Pither & Taylor 1998; Goodwin & Fahrig 2002; Schooley & Wiens 2004; Haynes & Cronin 2006). Few studies evaluated matrix effects on movements of vertebrates (e.g. Goheen *et al.* 2003; Bender & Fahrig 2005; Flaherty *et al.* 2008 see Prevedello & Vieira 2010a for a review), and this is the first study to empirically determine the relative importance of matrix type compared with other factors as determinants of movement tortuosity for vertebrates. The three matrix types studied, and even the varying height of the mowed pasture, created different degrees of resistance to

Table 3. Parameters of the most plausible models predicting path tortuosity of three species of didelphid marsupials in three types of matrix (mowed pasture, abandoned pasture and manioc plantation)

Model	Variables	Estimate	SE
(a) <i>Didelphis aurita</i> and <i>Philander frenatus</i> in the three matrix types			
(a1) All individuals			
1	Intercept	-0.902	0.064
	Distance	4×10^{-4}	3×10^{-4}
	Matrix type		
	Mowed pasture	-0.207	0.063
	Manioc plantation	-0.127	0.067
	Body mass	-2×10^{-4}	7×10^{-5}
	Matrix*distance		
	1	-7×10^{-4}	4×10^{-4}
	2	-9×10^{-4}	5×10^{-4}
	Scale	0.303	0.016
(a2) Within the perceptual range			
1 and 2	Intercept	-0.913	0.086
	Matrix type		
	Mowed pasture	-0.132	0.066
	Manioc plantation	-0.097	0.081
	Body mass	-3×10^{-4}	10^{-4}
Scale	0.364	0.027	
(b) <i>D. aurita</i> , <i>P. frenatus</i> and <i>Micoureus paraguayanus</i> in the mowed pasture			
(b1) All individuals			
1, 2 and 3	Intercept	-1.885	0.160
	Distance	0.002	0.001
	Grass height	0.037	0.008
	Body mass	-3×10^{-4}	10^{-5}
	Species		
	<i>D. aurita</i>	-0.003	0.090
	<i>P. frenatus</i>	0.204	0.082
	Body mass*grass height	-5×10^{-5}	2×10^{-5}
	Body mass*distance	-10^{-7}	10^{-7}
	*grass height		
	Species*distance*grass height		
	1	-7×10^{-5}	4×10^{-5}
	2	-8×10^{-5}	4×10^{-5}
Scale	0.319	0.022	
(b2) Within the perceptual range			
1 and 2	Intercept	-1.763	0.168
	Grass height	0.042	0.011
	Body mass	-10^{-3}	3×10^{-4}
	2*3	-10^{-4}	2×10^{-5}
	Scale	0.364	0.029
(b3) Beyond the perceptual range			
1	Intercept	-1.202	0.104
	Grass height	0.018	0.008
	Scale	0.187	0.028

Raw estimates are presented when only one model was clearly the most plausible, whereas only model-averaged estimates are presented when more than one model was considered plausible ($\Delta_i < 2$). Analyses considering only individuals released beyond the perceptual range in the three matrix types did not allow selection of any model, hence are not presented. In models where matrix type is present, abandoned pasture is the reference matrix type to which mowed pasture and manioc plantation are compared.

the movement of the marsupials. Movements were more linear in the mowed pasture, less so in the manioc plantation, and more tortuous in the abandoned pasture, following a gradient in increasing obstruction to movement. Also, movement tortuosity increased with grass height, as observed in

cactus bugs *Chelinidea vittiger* in grass matrix (Schooley & Wiens 2004). However, this response was apparent only when the marsupials were within their perceptual ranges. In such condition, individuals probably tried to reach the perceived fragment as quickly (or linearly) as possible, and its interaction with obstacles was the main determinant of movement tortuosity.

The perceptual ranges of *D. aurita* and *P. frenatus* were also higher in mowed pasture compared with the other two matrix types (Forero-Medina & Vieira 2009; Prevedello 2009), hence dispersal success could be higher in mowed pasture compared with the other matrix types. However, individuals will probably be more exposed to predators such as raptors and snakes when travelling on mowed pasture (Lira *et al.* 2007). For instance, squirrels were more likely to cross an agricultural matrix in the pre-harvest season, when vegetative cover was higher and perceived predation risk was presumably lower (Goheen *et al.* 2003). Since trade-offs between predation risk, speed of movement and perceptual range are difficult to predict (Zollner & Lima 2005; Flaherty *et al.* 2008), future research on predation rates is needed to determine the actual permeability of the studied matrix types to didelphid marsupials.

Beyond the perceptual range none of the variables measured had a plausible effect on path tortuosity, except for grass height in the mowed pasture; hence other non-measured factors are more important. In the manioc plantation, individuals of both species usually followed the direction of the plantation rows when released beyond the perceptual range, behaviour that decreased path tortuosity (Prevedello & Vieira 2010b). In the mowed pasture, some individuals of *D. aurita* and *M. paraguayanus* released beyond the perceptual range followed wind direction (Forero-Medina & Vieira 2009), and such anemotactic behaviour obviously affects tortuosity of movements (Schooley & Wiens 2003). Anemotactic behaviour was also detected in the mowed pasture for *D. aurita* but not for *P. frenatus* (Prevedello 2009). It was not possible to include the effects of plantation rows and wind direction in the models given the absence of wind in the interior of the manioc plantation, and absence of plantation rows in the other two matrix types.

Body mass generally was more plausible than species-specific effects as a determinant of path tortuosity. Thus, morphological, behavioural and locomotory adaptations of each species were less important than differences in body size among individuals. This is in agreement with intra and interspecific scaling of daily movements of didelphid marsupials within their primary habitat (Vieira & Cunha 2008). Part of the reason may be the large range of body mass considering the three species, from 50 to 1635 g, more than one order of magnitude. Vieira & Cunha (2008) suggested that when the difference in body mass approaches one order of magnitude it became more important than species-specific effects, a pattern that apparently also apply for movements of these animals in the matrix.

The effect of body mass rather than species identity also makes sense considering the similarity between *D. aurita* and

Table 4. Performance of models predicting path tortuosity of three didelphid marsupials (*Didelphis aurita*, *Philander frenatus* and *Micoureus paraguayanus*) in the mowed pasture matrix

Model	Variables	Log-likelihood	<i>K</i>	AICc	Δ_i	w_i
(a) All individuals						
1	Grass height, distance, body mass, 2*3	-30.32	6	73.50	0.00	0.26
2	Grass height, distance, body mass, 1*2*3	-30.63	6	74.14	0.64	0.19
3	Grass height, distance, species, 1*2*4	-28.36	8	74.23	0.73	0.18
4	Grass height, distance, species, 1*4	-29.10	8	75.72	2.22	0.08
5	Grass height, distance, species	-31.48	6	75.82	2.32	0.08
6	Grass height, distance, body mass	-32.99	5	76.60	3.10	0.05
7	Grass height, distance, species, 1*2	-31.08	7	77.33	3.83	0.04
23	None	-46.04	2	96.20	22.70	< 0.01
(b) Within the perceptual range						
1	Grass height, body mass, 2*3	-31.63	5	74.05	0.00	0.44
2	Grass height	-34.13	3	74.56	0.51	0.34
3	Grass height, body mass	-34.04	4	76.61	2.56	0.12
4	Grass height, species	-33.34	5	77.48	3.43	0.08
5	Grass height, species, 2*4	-32.62	7	80.77	6.72	0.02
6	None	-41.09	2	86.34	12.29	< 0.01
(c) Beyond the perceptual range						
1	Grass height	5.89	3	-4.53	0.00	0.31
2	None	3.55	2	-2.50	2.03	0.11

Analyses were done including (a) all individuals, and only individuals released (b) within or (c) beyond the perceptual range of the species. *K*, number of parameters of the model; AICc, Akaike Information Criterion corrected for small ratio sample size/number of parameters; Δ_i , AICci - minimum AICc; w_i , Akaike weight.

Asterisks indicate interactions between variables, coded by numbers (distance to nearest fragment = 1, grass height = 2, body mass = 3, species identity = 4). The model without variables represents the null model, including parameters only for the intercept and residual error. Models less plausible (greater AICc) than the null models are not shown.

P. frenatus in morphology, allometry and locomotory habit (semi-terrestrial; Vieira 1997; Cunha & Vieira 2002). A species effect appeared only when *M. paraguayanus* was present in the analysis, which may reflect the different morphology and the arboreal habits of this species (Grelle 2003). *Didelphis aurita* had more linear paths than the other two species probably because of its large body size, but also possibly because of its anemotactic behaviour (Forero-Medina & Vieira 2009; Prevedello 2009), which could be used to maintain straighter paths during habitat search (Schooley & Wiens 2003). The other two species are smaller and use different search strategies, judging by their more tortuous paths, probably relying more on vision (Forero-Medina & Vieira 2009; Prevedello 2009). More tortuous paths by the smaller species could result in reduced dispersal success. Indeed, Pires *et al.* (2002) evaluated inter-fragment movements by these species and observed the largest inter-fragment movement rate for the large *D. aurita* (19.4%) compared with *P. frenatus* (7.5%), and the smallest *M. paraguayanus* (1.2%). The higher perceptual range (Forero-Medina & Vieira 2009; Prevedello 2009) and more efficient search behaviour of *D. aurita* may explain its apparent tolerance to the fragmentation of the Atlantic Forest (Viveiros de Castro & Fernandez 2004; Fernandez & Pires 2006), and also why *D. aurita* is the most frequent small mammal in the landscape studied, occurring in 20 from the 21 forest fragments surveyed (Vieira *et al.* 2009).

Distance to the nearest suitable habitat patch has been frequently considered an important variable for dispersal

success because it should be proportional to time spent to reach the forest fragment, hence to mortality risks (Larsen & Boutin 1994; Bonnet, Naulleau & Shine 1999; Smith & Batzli 2006). Distance could be tested only when all individuals were considered, released within and beyond their perceptual range. In general, only one or two distances were tested within or beyond the perceptual range, limiting variation, but we suspect that the overall distance effect on path tortuosity may be nonlinear, with a threshold at the perceptual range. Animals released within their perceptual ranges, hence oriented, had linear paths, regardless of their distance to the forest fragment. Animals released beyond their perceptual ranges were not able to orient themselves to the forest fragment, and had more tortuous paths, regardless of the distance to the forest fragment. Thus, distance to the nearest habitat patch was not simply an extrinsic factor, but reflected an interaction between environmental and intrinsic factors that determine perceptual range.

Valuable insights on dispersal success in different matrix types are possible based on the tortuosity of animal paths. For individuals within their perceptual range both intrinsic and extrinsic factors must be considered: the efficiency to cross an inhospitable matrix and reach habitat patches for the marsupials studied depended on an interaction between their body size, distance to nearest patch, matrix type and vegetation obstruction; species-specific effects were less important than body mass. Beyond perceptual range path tortuosity was affected mostly by vegetation obstruction, and the use of guidelines, such as plantation rows and wind

direction, which would allow straight paths and function as dispersal venues in heterogeneous landscapes. Perceptual range becomes a central concept in estimates of successful movements and functional connectivity between habitat patches: it represents a threshold beyond which the effects of matrix type, body mass and individual behaviour change drastically.

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