

Does land use affect perceptual range? Evidence from two marsupials of the Atlantic Forest

J. A. Prevedello^{1,2}, G. Forero-Medina³ & M. V. Vieira²

¹ Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil

² Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro, RJ, Brazil

³ Nicholas School of the Environment, Duke University, Durham, NC, USA

Keywords

body mass; dispersal; functional connectivity; habitat fragmentation; matrix type; search behaviour.

Correspondence

Jayme Augusto Prevedello, Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Ilha do Fundão, Rio de Janeiro, RJ, CEP 21941-590, Brazil.
Email: ja_prevedello@yahoo.com.br

Editor: Andrew Kitchener

Received 29 June 2010; revised 28 October 2010; accepted 9 November 2010

doi:10.1111/j.1469-7998.2010.00783.x

Abstract

Perceptual range is one of the main determinants of dispersal success in fragmented landscapes, which are composed of scattered remnants of original habitat in a matrix of variable composition. How perceptual range varies according to land use is essential information to estimate the functional connectivity of landscapes. We determined for the first time how different types of land use affect the perceptual range of a species, using as model organisms two neotropical marsupials endemic to the Atlantic Forest in Brazil (*Philander frenatus* and *Didelphis aurita*). We released and tracked the movements of 196 individuals in three types of land use commonly found in fragmented landscapes: manioc plantation, mowed pasture and abandoned pasture. We also determined how orientation to the nearest forest fragment is affected by distance to the fragment, wind speed, body mass and sex using a model selection approach. The type of land use affected the perceptual ranges of both marsupials. The estimated perceptual ranges for *P. frenatus* and *D. aurita* were 100 and 200 m in the mowed pasture, respectively, 50 and < 30 m in the abandoned pasture and 30 and 50 m in the plantation. The orientation of both species decreased with increasing distance to the fragment, but for *D. aurita* orientation also increased with the wind speed and body mass. These results agree with previous studies depicting a general pattern of increased perceptual range with lower vegetation obstruction in the matrix and larger body mass and wind speed, depending on the use of visual versus olfactory cues by animals. Our findings allow more realistic estimates of functional connectivity in fragmented landscapes based on basic information on the biology of each species and the type of matrix.

Introduction

Perceptual range, defined as the maximum distance from which an animal can perceive landscape elements (Lima & Zollner, 1996), is one of the main determinants of dispersal success in fragmented landscapes (Zollner & Lima, 1999a; Zollner & Lima, 2005). Perceptual range defines the fraction of the landscape that is detectable and thus the spatial scale at which an animal interacts with the landscape (Lima & Zollner, 1996; Olden *et al.*, 2004). The ability to detect habitat patches at distance will determine the time an animal spends in the matrix searching for habitat and the related predation risks it faces (Lima & Zollner, 1996; Zollner & Lima, 1999a, 2005). Perceptual range has been studied in small mammals (e.g. Zollner & Lima, 1997; Schooley & Branch, 2005; Forero-Medina & Vieira, 2009), turtles (Yeomans, 1995; Caldwell & Nams, 2006) and insects (Schooley & Wiens, 2003). Perceptual range affects movement behaviour (Schooley & Wiens, 2003; Prevedello, Forero-Medina & Vieira, 2010), the occurrence of species in isolated habitat

fragments (Zollner, 2000) and the rate of interfragment movements (Forero-Medina & Vieira, 2009), providing important inferences on the functional connectivity of a landscape for a given species (Pe'er & Kramer-Schadt, 2008).

Perceptual range depends on body size (Mech & Zollner, 2002), habitat use (Zollner, 2000), and orienting mechanisms of animals (Forero-Medina & Vieira, 2009). Besides, perceptual range may be context-dependent (Olden *et al.*, 2004), varying with luminosity (Zollner & Lima, 1999b), cloud cover (Yeomans, 1995; Flaherty *et al.*, 2008) and wind direction (Schooley & Wiens, 2003; Forero-Medina & Vieira, 2009). An important but rarely considered factor affecting perceptual range is the type of matrix surrounding habitat patches. Different types of land use such as pastures, plantations or buildings offer different conditions for the navigation of dispersing animals (e.g. Schooley & Wiens, 2003; Haynes & Cronin, 2003), and probably affect their ability to perceive habitat patches. Differences in perceptual range among habitat types might

be one of the causal mechanisms explaining the strong influence of matrix type on population dynamics (review in Prevedello & Vieira, 2010a). The influence of matrix structure on perceptual range was evaluated in earlier studies, but always within the same type of land use with varying vegetation height, such as plantation (Zollner & Lima, 1997), pasture (Forero-Medina & Vieira, 2009) and grassland (Schooley & Wiens, 2003). No study to date has compared the perceptual ranges of a given species across different types of land use, which is important to assess the impacts of different economic activities on the persistence of fragmented populations. Estimates of habitat-specific perceptual abilities would be valuable to parameterize and to increase the predictive power of models of functional connectivity and dispersal success (Zollner & Lima, 1999a, 2005; Pe'er & Kramer-Schadt, 2008).

We determined for the first time how different types of land use affect the perceptual range of a species. We used as model organisms two neotropical marsupials, the grey four-eyed opossum *Philander frenatus* (Olfers, 1818) and the black-eared opossum *Didelphis aurita* Wied-Neuwied, 1826, both endemic to the highly fragmented Atlantic Forest in Brazil. Populations of these species persist in small forest fragments surrounded by a mosaic of land-use types including urban areas, pastures, plantations and paved roads (Vieira *et al.*, 2009). *P. frenatus* and *D. aurita* move only occasionally between fragments (Pires *et al.*, 2002; Lira *et al.*, 2007), are absent from some fragments (Vieira *et al.*, 2009) and do not live in the matrix where exposure to predators is high (Lira *et al.*, 2007). For these reasons, these species are good models to understand the factors that allow the persistence of populations in small forest fragments. Both marsupials are nocturnal, solitary and omnivores with subtle differences in food habits (Astúa de Moraes *et al.*, 2003). *D. aurita* is semi-terrestrial using mainly the ground and the understorey, but also the canopy occasionally (Cunha & Vieira, 2002). *P. frenatus* is also semi-terrestrial, moving on the ground and in the understorey, but never in the canopy (Cunha & Vieira, 2002). *D. aurita* is one of the

largest neotropical marsupials (mean \pm SD: 760 \pm 351 g in the present study), and *P. frenatus* is considered to be of medium size (mean \pm SD: 405 \pm 151 g).

Materials and methods

Study site

Animals were captured in 14 fragments and one site of continuous forest in the municipalities 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 is mild-humid mesothermal (Nimer, 1989), and vegetation is classified as dense evergreen forest (IBGE, 1991). The landscape is composed by small Atlantic Forest remnants (<100 ha) structurally isolated by a matrix of urban and rural areas (Vieira *et al.*, 2009).

To determine perceptual ranges, animals were released into two types of land use: manioc plantation and abandoned pasture (Fig. 1). To analyse the variables affecting orientation ability, we also used data from individuals released in mowed pasture in the same landscape (Fig. 1), whose perceptual ranges were reported by Forero-Medina & Vieira (2009). Pastures and plantations are the predominant types of land use in the landscape studied (Vieira *et al.*, 2009), commonly found in other tropical landscapes. Mowed and abandoned pastures had only one release site each, but for manioc plantation, we used three release sites because of harvesting regimes. We released individuals in the site that best represented an abandoned pasture and in the site that best represented a mowed pasture. The use of more than one release site in each category would introduce uncontrolled variation because potential replicates always had more than one type of land use or were too close to roads, rivers or human buildings. The sites chosen differed structurally only in terms of land-use type, with similar visible height and breadth of the closest fragment. All sites were located in the vicinities of a forest fragment and at >1 km from other fragments including the fragment of

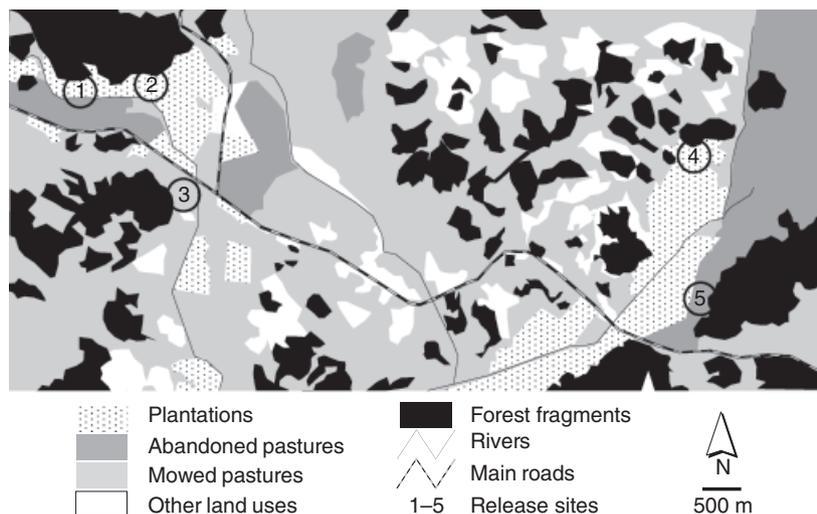


Figure 1 Schematic representation of the studied landscape located in Rio de Janeiro, Brazil. The different types of land use and the five sites where marsupials were release are indicated.

capture. The three manioc plantations (*Manihot esculenta*, Euphorbiaceae) were fully grown (c. 185 cm high) and arranged in parallel rows spaced c. 160 cm. The mowed pasture was dominated by grasses periodically mowed by farm managers, resulting in a low grass height (mean \pm SD = 14.2 \pm 5.2 cm), with some variation during the study due to cattle grazing. The abandoned pasture was also dominated by grasses, but the absence of grazing and mowing resulted in taller grasses (45.0 \pm 13.5 cm) and the presence of shrubs. To better characterize the vegetation structure of the three matrix types, we also measured vegetation obstruction at the ground level. Measures were taken in five release points located at 100 m from the edge of the fragment in each release site. This 100 m distance is intermediate among those used during the releases of animals, and it is representative of the entire release site because each matrix type was very homogeneous. Visual obstruction was measured using a 0.50 \times 0.50 m square wood frame divided into 100 open squares, with the number of squares visually obstructed by matrix vegetation representing the percentage of vegetation obstruction. This was estimated as 77 \pm 19% (mean \pm SD) in manioc plantation, 66 \pm 16% in abandoned pasture and 31 \pm 9% in mowed pasture. Release experiments were performed 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.

Field methods

Animals were captured in the forest sites using Tomahawk and Sherman traps (details in Vieira *et al.*, 2009). Captured animals were placed in individual cages, fed and left in a protected place for 3–72 h before release. No biases in orientation ability related to length of captivity were detected. Individuals were released using a standard mechanism, which consisted of an inverted box with a 20 m string attached to the bottom of the box (Forero-Medina & Vieira, 2009). The box could be lifted by an observer at a distance, minimizing influence on animal movements (Forero-Medina & Vieira, 2009). When the box was lifted, animals had almost 360° to choose a direction. Individuals were released at five distances from the fragment's edge: 30, 50, 100, 200 and 300 m. Only healthy adult and subadult individuals were used, excluding lactating females. Individuals released on the same day were positioned 20 m apart from each other to minimize possible interferences (Forero-Medina & Vieira, 2009). Because the species studied are nocturnal, releases were carried out at dusk, between 1730 and 1930 h depending on the month, with up to five animals released at the time in the same area. In general, animals were asleep when the box of the mechanism was lifted, taking a few minutes to become active, without any sign of stress or escape behaviour. Wind speed and direction were measured immediately after release using a compass and an anemometer. However, there was no wind current during most releases in manioc plantation and abandoned pasture precluding the determination of wind direction, which was not included in the analyses.

Before release, animals were equipped with a spool-and-line device to record movements. Individual paths were mapped by taking the distance and bearings between two points of directional change ($>10^\circ$). Paths were tracked either until the animal reached the forest, the line was broken or up to 170 m, resulting in 77 \pm 32 m (mean \pm SD) of thread tracked for each path. Each individual was released and tracked only once. We assumed that animals perceived the three matrix types as inhospitable and searched for a refuge after being released in all sites, because the three matrix types had lower vegetation cover and probably offered a high risk of predation by domestic dogs or raptors (Lira *et al.*, 2007). Also, captures of these species in these types of matrix are rare (Umetsu & Pardini, 2007; Vieira *et al.*, 2009).

Data analysis

To estimate the perceptual ranges, the mean vector for the initial 20 m of the path was calculated (Goodwin *et al.*, 1999; Forero-Medina & Vieira, 2009). This 20 m initial path was sufficient to determine at what distance from the fragment animal paths became non-oriented. At short distances from the fragment, animals oriented themselves right after the first steps, with directed and linear movements along the entire path. As the distance increased, the initial portions of the path became more tortuous (Prevedello *et al.*, 2010), indicating that animals progressively lost their perception of the fragment, eventually losing it completely at larger distances. Orientation towards the fragment was determined at each of the five distances using *V*-tests (Zar, 1999). The maximum distance with significant orientation to the forest was the estimate of perceptual range for the species. *V*-tests were also used to test if animals oriented towards the fragment where they were captured. The mean vectors and other circular statistic tests were calculated using Oriana 2.0 (RockWare Inc., Golden, CO, USA).

Orientation ability was measured by angular divergence, the absolute difference between the direction of the nearest fragment and the direction of the mean vector of each individual (Schooley & Wiens, 2003; Forero-Medina & Vieira, 2009). We evaluated the effects of land-use type, distance to the fragment, wind speed, body mass and sex on orientation ability using a multiple regression design and a model selection approach (Burnham & Anderson, 2002). All possible subsets of the five independent variables were used to build models, and their fit to the data was compared by the modified Akaike information criteria (AICc; Burnham & Anderson, 2002). For each model, we determined Δ_i (= AICc_{*i*} – minimum AICc) and w_i , which indicates the probability that the model is the best model. The weight of evidence in favour of a given variable was estimated by summing w_i of the models containing the variable (Burnham & Anderson, 2002). A null model, composed only by the intercept and residual errors as parameters, was also included to compare the explanatory power of measured variables relative to other unaccounted sources of variation in data.

Results

Perceptual range estimates at different land-use types

We successfully tracked a total of 109 paths from *P. frenatus*, 50 in mowed pasture (31 males and 19 females), 37 in manioc plantation (22 males and 15 females) and 22 in abandoned pasture (13 males and nine females). A total of 87 paths of *D. aurita* were tracked, 35 in mowed pasture (20 males and 15 females), 28 in manioc plantation (18 males and 10 females) and 24 in abandoned pasture (eight males and 16 females). There was no tendency of individuals orienting towards the fragment where they had been captured.

In the manioc plantation, individuals of *P. frenatus* oriented significantly towards the nearest fragment at 30 m ($u = 2.34$; $P = 0.007$; $N = 5$), but not at 50 m ($u = 0.28$; $P = 0.39$; $N = 8$), 100 m ($u = 1.33$; $P = 0.09$; $N = 14$) and 200 m ($u = -0.30$; $P = 0.61$; $N = 10$; Fig. 2). Individuals of *D. aurita* oriented towards the nearest fragment at 30 m ($u = 2.28$; $P = 0.007$; $N = 3$) and at 50 m ($u = 2.07$; $P = 0.02$; $N = 8$), but not at 100 m ($u = -0.87$; $P = 0.80$; $N = 9$) and 200 m ($u = 0.70$; $P = 0.26$; $N = 8$; Fig. 2).

In the abandoned pasture, individuals of *P. frenatus* oriented towards the nearest fragment at 50 m ($u = 2.07$; $P = 0.02$; $N = 7$), but not at 100 m ($u = 1.23$; $P = 0.11$; $N = 8$) and 200 m ($u = 1.22$; $P = 0.11$; $N = 7$; Fig. 3). Individuals of *D. aurita* did not orient towards the nearest fragment at any distance tested (50 m: $u = 0.83$; $P = 0.21$; $N = 9$; 100 m: $u = 0.52$; $P = 0.30$; $N = 10$; 200 m: $u = 1.09$; $P = 0.14$; $N = 7$; Fig. 3). Perceptual ranges in the mowed pasture were estimated in a previous study as 100 m for *P. frenatus* and 200 m for *D. aurita* (Forero-Medina & Vieira, 2009).

Variables affecting orientation ability

The most plausible model explaining the degree of orientation of *P. frenatus* towards the fragment included only the distance of release ($w_i = 0.29$; Table 1). Distance also appeared in the remaining 15 top models, with larger distances indicating larger angular divergences and thus lower orientation [coefficient estimate (mean \pm SE) = 0.34 ± 0.09]. Sex and body mass also appeared in models with $\Delta_i < 2$, but the addition of these variables did not improve the fit of models, judging from their almost identical likelihoods (Table 1). The null model was implausible ($\Delta_i = 12.35$, $w_i \leq 0.01$).

For *D. aurita*, the most plausible model included wind speed, body mass and distance ($w_i = 0.26$; Table 1). Wind speed and body mass had similar importance (sum of $w_i = 0.88$ and 0.84 , respectively), but distance had a smaller relative importance (sum of $w_i = 0.54$). Angular divergence decreased with wind speed and body mass, but increased with distance [coefficient estimates (mean \pm SE): wind speed = -22.95 ± 9.61 ; body mass = -0.04 ± 0.02 ; distance = 0.12 ± 0.08]. Thus, large animals were more oriented than small ones, individuals close to the fragment were more oriented and high wind speeds also favoured orientation. The null model was less plausible ($\Delta_i = 7.98$, $w_i = 0.02$).

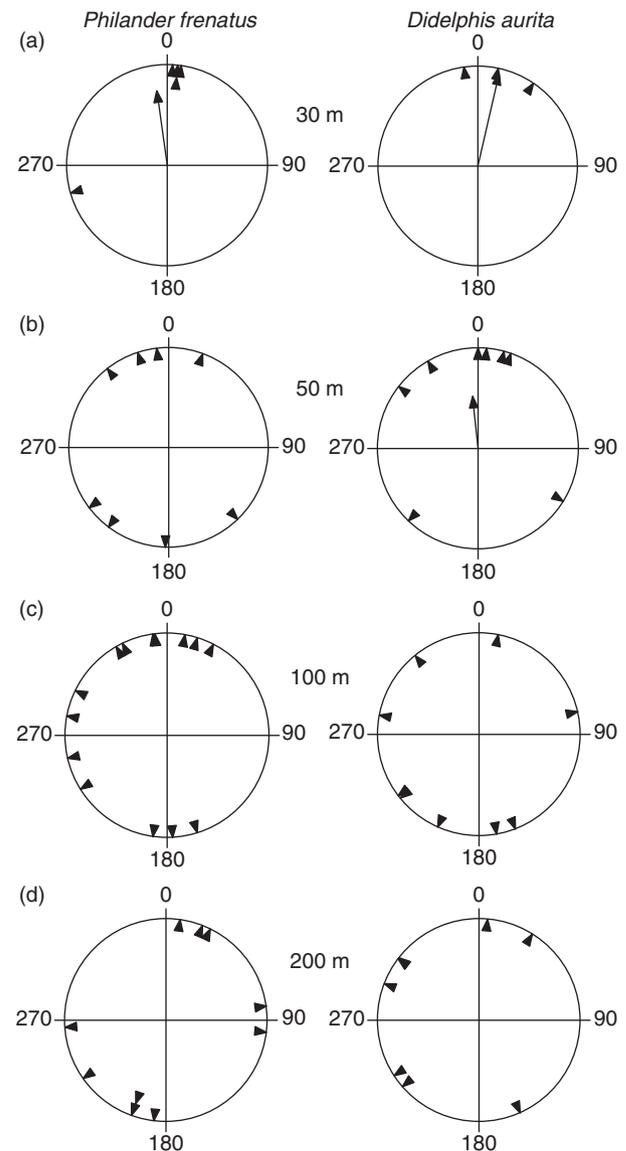


Figure 2 Angular orientations of *Philander frenatus* and *Didelphis aurita* released in manioc plantations at 30 m (a), 50 m (b), 100 m (c) and 200 m (d) from the nearest forest fragment. The centre of the circle indicates the release site, and the zero indicates the forest direction. Each triangle represents the mean angle for the initial 20 m of movement of one individual. Vectors indicate the mean angle and concentration of the group of animals and are only shown when there was a significant orientation to the forest.

Discussion

Perceptual ranges of both marsupials differed among the three types of land use studied. The two species had higher perceptual ranges in the mowed pasture compared with the abandoned pasture and manioc plantation. These findings agree with previous studies confirming that perceptual range and matrix obstruction are inversely related. Forero-Medina & Vieira (2009) showed that grass height in the same

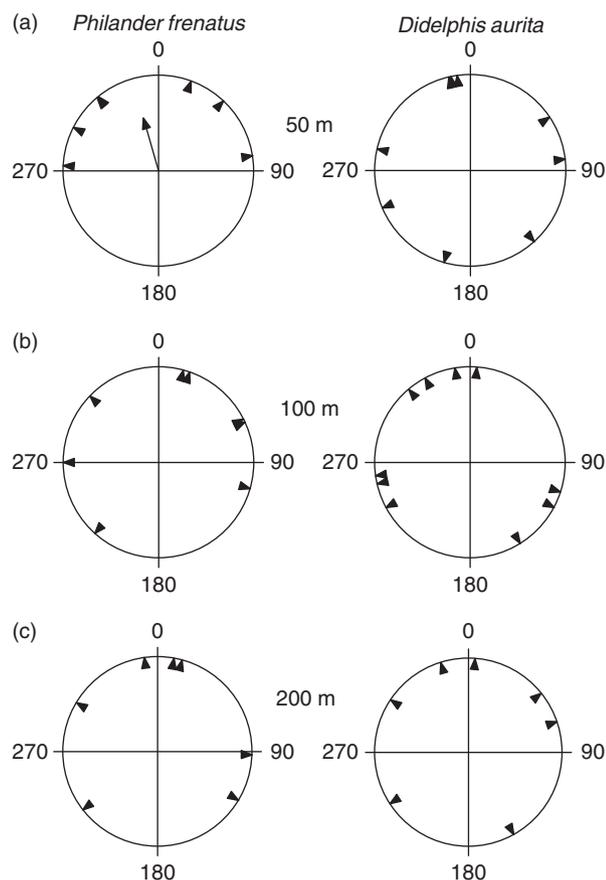


Figure 3 Angular orientations of *Philander frenatus* and *Didelphis aurita* released in the abandoned pasture at 50 m (a), 100 m (b) and 200 m (c) from the forest fragment. All symbols as in Fig. 2.

mowed pasture we studied affected negatively the perception of forest fragments by *P. frenatus* and *D. aurita*. Similarly, white-footed mice oriented better after the harvest of soy plantation (Zollner & Lima, 1997), northern-flying squirrels oriented better in clearcut habitats compared with second-growth stands (Flaherty *et al.*, 2008) and cactus bugs oriented better when grass height was lower (Schooley & Wiens, 2003). Thus, considering perceptual range alone, the functional connectivity of fragments surrounded by pasture is higher because animals can perceive habitat at longer distances and reach it more quickly (Lima & Zollner, 1996; Zollner & Lima, 1999a).

It is reasonable to assume that animals released in the three land-use types are all similarly attracted to the forest fragment. These marsupials rarely use the matrix (Umetsu & Pardini, 2007; Lira *et al.*, 2007) and immediately go to the nearest perceived forest patch after being released in the three matrix types, as evidenced by the straight and oriented paths of individuals released within their perceptual ranges (Prevedello *et al.*, 2010). Abandoned pastures and manioc plantations may apparently offer more vegetative cover than mowed pastures, but animals are still under a higher predation risk compared with the forest, its primary habitat.

Once in an inhospitable matrix, the animal will look for the closest forest fragment as quickly as possible. When there are no fragments within perceptual range, animals may prefer the matrix that more resembles its forest habitat to use as a dispersal route. Beyond perceptual range, an open pasture probably presents higher predation risks and may be less attractive to animals leaving a fragment than a plantation, given the low vegetative cover. For example, red squirrels *Tamiasciurus hudsonicus* were more likely to move across the landscape when vegetative cover was present in

Table 1 Performance of models predicting the degree of orientation of *Philander frenatus* and *Didelphis aurita* towards the nearest forest fragment in three matrix types

Model	Variables	K	Log-likelihood	AICc	Δ_i	w_i
<i>Philander frenatus</i>						
1	Distance	3	-595.78	1197.79	0.00	0.29
2	Distance, sex	4	-595.26	1198.90	1.11	0.17
3	Distance, body mass	4	-595.67	1199.72	1.94	0.11
4	Distance, wind speed	4	-595.71	1199.81	2.02	0.10
5	Distance, sex, wind speed	5	-595.19	1200.96	3.17	0.06
6	Distance, sex, matrix	6	-594.70	1202.22	4.44	0.04
17	None	2	-603.01	1210.14	12.35	<0.01
<i>Didelphis aurita</i>						
1	Body mass, wind speed, distance	3	-464.83	940.41	0.00	0.26
2	Body mass, wind speed	4	-466.27	941.03	0.62	0.19
3	Body mass, wind speed, distance, sex	6	-464.73	942.51	2.10	0.35
4	Body mass, wind speed, sex	5	-466.27	943.28	2.87	0.06
5	Wind speed, distance	4	-467.46	943.41	3.00	0.06
6	Body mass, wind speed, distance, matrix	7	-464.06	943.53	3.12	0.05
22	None	2	-472.12	948.39	7.98	0.02

The model without variables represents the null model.

K, number of parameters of the model; AICc, Akaike information criteria corrected for small ratio sample size/number of parameters; Δ_i =AICc_i-minimum AICc; w_i , Akaike weight.

the matrix, probably due to a decrease in the perceived risk of predation (Goheen *et al.*, 2003). However, within perceptual range, this tradeoff may disappear as animals are able to maintain straight and oriented movements, quickly reaching a nearby fragment reducing predation risk (Prevedello *et al.*, 2010). Indeed, in 88 animals we released within the perceptual range and followed up to the forest fragment, only one (*D. aurita*) was predated.

Manioc plantation and abandoned pasture affected the perceptual ranges of *P. frenatus* and *D. aurita* differently, probably reflecting the different orienting mechanisms used by these species. The orientation of *P. frenatus* apparently has an important visual component, as it was negatively affected by distance to the fragment and grass height, but not by wind speed or direction, which are more likely to affect olfactory ability (Forero-Medina & Vieira, 2009; this study). Manioc plantation was the most visually obstructed matrix type studied and, accordingly, the most detrimental to the orientation of *P. frenatus*. On the other hand, *D. aurita* appears to rely mainly on olfaction using wind currents to orient its movements (anemotactic behavior), as can be inferred from the strong effects of wind direction (Forero-Medina & Vieira, 2009) and speed (this study) on the orientation of individuals. The orientation of *D. aurita* apparently is hampered by the dense vegetation at the ground level in tall pasture, which blocks and diffuses wind currents (J. A. Prevedello, pers. obs.). This would hamper perception of the forest fragment by *D. aurita* using odour cues, as apparently occurs with cactus bugs (Schooley & Wiens, 2003). Therefore, despite the tendency of reducing perceptual range with increasing vegetation obstruction, the actual effects of matrix type on perceptual range also depend on the orienting mechanisms of each species.

In manioc plantations *D. aurita* and *P. frenatus* frequently moved parallel to plantation rows, as evidenced by the bimodal distribution of the angular orientations of individuals (see Figs. 2b and d; Prevedello & Vieira, 2010b). This effect was clear in the three plantation sites studied, which differed in the orientation of plantation rows relative to the position of the fragment. The main reason is that vegetation obstruction along plantation rows is much reduced compared with routes oriented perpendicular to the row (Prevedello & Vieira, 2010b). However, it was possible to determine perceptual ranges even with this bias in movement directionality: at short distances from the fragment, almost all animals moved in its direction, clearly perceiving it, whereas at longer distances, a bimodal distribution appeared, animals moving towards the fragment or in opposite direction with the same frequency, hence non-oriented (Prevedello & Vieira, 2010b). Once vegetation obstruction is reduced along plantation rows, the perceptual range of these species in manioc plantations is probably anisotropic, that is, different directions of the landscape are perceived differently (Olden *et al.*, 2004).

The strong intraspecific effect of body mass on the orientation ability of *D. aurita* indicates that body size may be a stronger determinant of perceptual range than considered previously. Previous effects of body size on perceptual

range were detected only in interspecific comparisons, hence considering a large range of body size variation (Zollner, 2000; Mech & Zollner, 2002; Forero-Medina & Vieira, 2009). For *D. aurita*, body mass was the main determinant of habitat perception, probably because of the large intraspecific variation in body mass among the released individuals (from 145 to 1635 g). Larger animals oriented better than smaller ones possibly because of the elevated position relative to the ground of sensory organs (vision, olfaction and hearing) and also because visual acuity apparently increases with body size (Mech & Zollner, 2002). One prediction of this result is that dispersal success is higher for adults than for young individuals of *D. aurita*.

Our findings have important implications for evaluating landscape connectivity and managing land use for conservation in fragmented landscapes. First, the dynamic behaviour of perceptual range reported here demonstrates the need for the use of a functional rather than a structural approach to study landscape connectivity. Models of landscape connectivity frequently consider only structural parameters of the landscape, such as patch size and isolation, with no information on movement behaviour or perceptual abilities of organisms (Taylor, Fahrig & With 2006). This is clearly inadequate for the marsupials studied because orientation ability varied both within and between species, and for *D. aurita* it also depended on wind speed. Second, the effects of different land-use types on the orientation of a given species must be explicitly considered. The habitat-specific perceptual ranges reported in this study allow estimates of functional connectivity in real, heterogeneous landscapes based on empirical data, improving previous simulations based on assumed values (Pe'er & Kramer-Schadt, 2008). Such estimates will provide guidelines to identify gaps in functional connectivity and to identify strategic forest remnants that maintain the overall connectivity of the landscape.

Acknowledgements

We thank students and staff of the Laboratório de Vertebrados – UFRJ for assistance in the fieldwork, particularly Ana C. Delciellos and Antonio A. Menezes. We are grateful to Renata Pardini, Marcelo Passamani and two anonymous reviewers for comments on the paper. This study was part of the MSc thesis of Jayme A. Prevedello in the PPG-Ecologia (UFRJ) and was supported by CNPq, CAPES, FAPERJ, PDA/MMA and FNMA/MMA (Brazil).

References

- Astúa de Moraes, D., Santori, R.T., Finotti, R. & Cerqueira, R. (2003). Nutritional and fiber contents of laboratory established diets of Neotropical opossums (Didelphimorphia, Didelphidae). In *Predators with pouches: The biology of carnivorous marsupials*: 225–233. Jones, M., Dickman, C. & Archer, M. (Eds). Melbourne: CSIRO Publishing.

- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer-Verlag.
- Caldwell, I.R. & Nams, V.O. (2006). A compass without a map: tortuosity and orientation of eastern painted turtles (*Chrysemis picta picta*) released in unfamiliar territory. *Can. J. Zool.* **84**, 1129–1137.
- Cunha, A.A. & Vieira, M.V. (2002). Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. *J. Zool.* **258**, 419–426.
- Flaherty, E.A., Smith, W.P., Pyare, S. & Ben-David, M. (2008). Experimental trials of the northern flying squirrel (*Glaucomys sabrinus*) traversing managed rainforest landscapes: perceptual range and fine-scale movements. *Can. J. Zool.* **86**, 1050–1058.
- Forero-Medina, G. & Vieira, M.V. (2009). Perception of a fragmented landscape by Neotropical marsupials: effects of body mass and environmental variables. *J. Trop. Ecol.* **25**, 53–63.
- Goheen, J.R., Swihart, R.K., Gehring, T.M. & Miller, M.S. (2003). Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos* **102**, 95–103.
- Goodwin, B.J., Bender, D.J., Contreras, T.A., Fahrig, L. & Wegner, J.F. (1999). Testing for habitat detection distances using orientation data. *Oikos* **84**, 160–163.
- Haynes, K.J. & Cronin, J.T. (2003). Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology* **84**, 2856–2866.
- IBGE. (1991). *Manual Técnico da Vegetação Brasileira*, Rio de Janeiro: IBGE.
- Lima, S.L. & Zollner, P.A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* **11**, 131–135.
- Lira, P.K., Fernandez, F.A.S., Carlos, H.S.A. & Curzio, P.L. (2007). Use of a fragmented landscape by three species of opossum in south-eastern Brazil. *J. Trop. Ecol.* **23**, 427–435.
- Mech, S.G. & Zollner, P.A. (2002). Using body size to predict perceptual range. *Oikos* **98**, 47–52.
- Nimer, E. (1989). *Climatologia do Brasil*. Rio de Janeiro: IBGE/Departamento de Recursos Naturais e Estudos Ambientais.
- Olden, J.D., Schooley, R.L., Monroe, J.B. & Poff, N.L. (2004). Context-dependent perceptual range and their relevance to animal movements in landscapes. *J. Anim. Ecol.* **73**, 1190–1194.
- Pe'er, G. & Kramer-Schadt, S. (2008). Incorporating the perceptual range of animals into connectivity models. *Ecol. Model.* **213**, 73–85.
- Pires, A.S., Lira, P., Fernandez, F.A.S., Schittini, G.M. & Oliveira, L.C. (2002). Frequency of movements of small mammals among Atlantic Coastal Forest fragments in Brazil. *Biol. Conserv.* **108**, 229–237.
- Prevedello, J.A., Forero-Medina, G. & Vieira, M.V. (2010). Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. *J. Anim. Ecol.* **79**, 1315–1323.
- Prevedello, J.A. & Vieira, M.V. (2010a). Does the type of matrix matter? A quantitative review of the evidence. *Biodivers. Conserv.* **19**, 1205–1223.
- Prevedello, J.A. & Vieira, M.V. (2010b). Plantation rows as dispersal routes: a test with didelphid marsupials in the Atlantic Forest, Brazil. *Biol. Conserv.* **143**, 131–135.
- Schooley, R.L. & Branch, L.C. (2005). Limited perceptual range and anemotaxis in marsh rice rats *Oryzomys palustris*. *Acta Theriol.* **50**, 59–66.
- Schooley, R.L. & Wiens, J.A. (2003). Finding habitat patches and directional connectivity. *Oikos* **102**, 559–570.
- Taylor, P., Fahrig, L. & With, K.A. (2006). Landscape connectivity: back to the basics. In *Connectivity conservation*: 29–43. Crooks, K. & Sanjayan, M.A. (Eds). Cambridge: Cambridge University Press.
- Umetsu, F. & Pardini, R. (2007). Small mammals in a mosaic of forest remnants and anthropogenic habitats – evaluating matrix quality in an Atlantic forest landscape. *Landsc. Ecol.* **22**, 517–530.
- Vieira, M.V., Olifiers, N., Delciellos, A.C., Antunes, V.Z., Bernardo, L.R., Grelle, C.E.V. & Cerqueira, R. (2009). Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. *Biol. Conserv.* **142**, 1191–1200.
- Yeomans, R.S. (1995). Water-finding in adult turtles: random search or oriented behaviour? *Anim. Behav.* **49**, 977–987.
- Zar, J.H. (1999). *Biostatistical analysis*, 4th edn. New Jersey: Prentice-Hall Inc.
- Zollner, P.A. (2000). Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landsc. Ecol.* **15**, 523–533.
- Zollner, P.A. & Lima, S.L. (1997). Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* **80**, 51–60.
- Zollner, P.A. & Lima, S.L. (1999a). Search strategies for landscape-level interpatch movements. *Ecology* **80**, 1019–1030.
- Zollner, P.A. & Lima, S.L. (1999b). Illumination and the perception of remote habitat patches by white-footed mice. *Anim. Behav.* **58**, 489–500.
- Zollner, P.A. & Lima, S.L. (2005). Behavioral trade-offs when dispersing across a patchy landscape. *Oikos* **108**, 219–230.