



Plantation rows as dispersal routes: A test with didelphid marsupials in the Atlantic Forest, Brazil

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ARTICLE INFO

Article history:

Received 26 May 2009

Received in revised form 8 September 2009

Accepted 18 September 2009

Available online 12 October 2009

Keywords:

Anisotropy

Functional connectivity

Matrix permeability

Movement

Perceptual range

Row crops

ABSTRACT

Anecdotal observations suggest that some vertebrates follow plantation rows when crossing between habitat patches in fragmented landscapes, but the frequency of such behavior was never formally tested despite its potential implications for landscape management. We experimentally tested if the didelphid marsupials *Didelphis aurita* and *Philander frenatus* use plantation rows as guidelines when searching for habitat patches in a landscape of fragmented Atlantic Forest in Brazil. Thirty-seven individuals of *P. frenatus* and 24 of *D. aurita* were captured in forest fragments and released carrying spool-and-line tracking devices at four distances (30–200 m) from a forest fragment, in a matrix of manioc plantations. Animals of both species used plantation rows to orient their initial movements and used rows as guidelines along their paths for navigating in the matrix. By moving predominantly parallel to the plantation rows animals reduced the tortuosity of their paths and obtained an unobstructed view of the landscape ahead. These results demonstrate that the orientation of linear plantations can strongly influence functional connectivity between habitat fragments. Plantation rows should be oriented to maximize connection between nearby fragments, enhancing dispersal success of these species and probably many other terrestrial vertebrates in agricultural landscapes.

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1. Introduction

In fragmented landscapes, the composition of the matrix surrounding habitat patches can strongly influence dispersal of individuals and the persistence of populations (Moilanen and Hanski, 1998; Schooley and Wiens, 2005; Denoël and Lehmann, 2006; Haynes and Cronin, 2003; Pita et al., 2007). Some matrix types allow animals to freely move between habitat patches, while others may function as complete barriers to movement (Pither and Taylor, 1998; Goodwin and Fahrig, 2002; Haynes and Cronin, 2003). The structure and arrangement of elements within a given matrix type also can affect the flux of individuals in the landscape (Gustafson and Gardner, 1996; Bélisle and St. Clair, 2001; Ferreras, 2001; Ovaskainen, 2004; Vuilleumier and Metzger, 2006). For example, the orientation of movement barriers (Bélisle and St. Clair, 2001) or small variations in vegetal obstruction (Schooley and Wiens, 2003) can affect the ease of movement along different directions

in the landscape. The detection of such biases in the direction of movements would provide clear guidelines for theoretical modeling and conservation practices (Schooley and Wiens, 2003; Bélisle, 2005; Vuilleumier and Metzger, 2006).

Linear structures in the matrix may be used by dispersing vertebrates as guidelines for moving in the landscape, such as low-use roads and trails (Musiani et al., 1998; Brock and Kelt, 2004; Whittington et al., 2004), streambeds and washouts (Lemkau, 1970), and riverbanks and ditches (Vandewoestijne et al., 2004; Saekia et al., 2007). Animals using such structures could maintain nearly straight movement paths in the matrix, which is the most successful strategy to find habitat patches when the animal is unaware of their location (Zollner and Lima, 1999). Many plantations in agricultural landscapes are arranged in parallel lines, such as coffee, corn, soybean and sugar cane, with the potential to conduct animals to particular directions in the landscape. For instance, the white-footed mice *Peromyscus leucopus* exhibited a tendency to follow plantation rows both in soybean (Zollner and Lima, 1997) and corn fields (Rizkalla and Swihart, 2007). No single study, however, formally tested whether vertebrates use plantation rows as dispersal routes in fragmented landscapes. The existence of such behavioral pattern would provide a simple strategy to increase functional connectivity in agricultural landscapes, i.e. to manage

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the direction of plantation rows. Such strategy would be of large conservation value since plantations comprise a large portion of land surface on the planet (Foley et al., 2005).

In this study we experimentally tested the hypothesis that mammals use plantation rows as guidelines when searching for suitable habitat in the matrix. We used as model organisms the didelphid marsupials *Didelphis aurita* and *Philander frenatus* (Didelphimorphia), both endemic of the extensively fragmented Atlantic Forest in Brazil. These marsupials are considered to be tolerant to fragmentation due to their high vagility and presence in fragments of different sizes and degree of disturbance (Bonvicino et al., 2002; Viveiros de Castro and Fernandez, 2004; Fernandez and Pires, 2006). Both species are capable to move between fragments in areas of Atlantic Forest (Pires et al., 2002; Lira et al., 2007), but they may be highly exposed to predators in open matrices (Lira et al., 2007). Using experimental translocations, we answered three questions: (i) Do animals use the rows to decide the direction of their initial movements following release? (ii) Do animals move predominantly parallel to plantation rows? (iii) Does the behavior of following rows decrease path tortuosity? Positive answers for these questions would be expected if these species use the rows as guidelines when moving in plantations.

2. Methods

2.1. Study area and species

Animals were captured in five forest fragments and one large stretch of Atlantic Forest in the Macacu River watershed, 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-mesotermic (Nimer, 1989), and vegetation is classified as dense evergreen forest (IBGE, 1991). 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 and Fizon, 2004).

Animals were released in three fully-grown (ca 185 cm high) manioc plantations (*Manihot esculenta*, Euphorbiaceae) at least 1 km from the capture fragments. Each of the three release sites was located in the vicinities of a forest fragment and located >1 km from other fragments. Manioc plants grow side by side on parallel rows spaced ca. 160 cm and oriented usually following the longest unobstructed direction of the terrain. The use of three different plantations allowed variation in the orientation of plantation rows relative to the position of the fragment. This variation was increased by releasing animals at different points around the fragment, each point with row orientation differing from the mean direction of the fragment. Manioc plantations are presumably inhospitable environments for *D. aurita* and *P. frenatus* given the open canopy and the presence of domestic dogs or raptors. Animals released close to the fragment appeared strongly motivated to reach it, as indicated by the linearity and obvious orientation of their paths (Prevedello, 2009). Moreover, these species are rarely captured in this and other open matrices in the Atlantic Forest (Pires et al., 2002; Umetsu and Pardini 2006; M.V. Vieira unpublished data).

The black-eared opossum, *Didelphis aurita* Wied-Neuwied, 1826, and the grey four-eyed opossum *P. frenatus* (Olfers, 1818), are the most abundant marsupials in forest fragments of the region (Vieira et al., 2009). These species are nocturnal, solitary, semi-terrestrial (Cunha and Vieira, 2002), and are classified as omnivores with subtle differences in food habits (Astúa de Moraes et al., 2003). The individuals of *D. aurita* released

weighed about 840 g, and the individuals of *P. frenatus* weighed about 390 g.

2.2. Data collection

Animals were captured in the forest fragments using Tomahawk and Sherman type live traps (details in Vieira et al., 2009). 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 allowed the observer to release animals from a 20 m distance avoiding influences (Forero-Medina and Vieira, 2009). Individuals were released at four distances (30, 50, 100, and 200 m) from the fragment edge to estimate the perceptual range of the species (Prevedello, 2009). Only healthy adult and sub-adult individuals (classified based on Macedo et al., 2006) were used in the experiments, excluding lactating females. Individuals released in the same day were spaced 20 m from each other to minimize possible interferences. All releases were done in the late afternoon, between 17 h30 and 19 h30, with up to five animals released at a time. Experiments were conducted between May 2007 and May 2008.

Before release, animals received a spool-and-line device to record their fine-scale movements (Boonstra and Craine, 1986; Cunha and Vieira, 2002). Individual paths were mapped by taking the distance and azimuth to the next point of clear change in direction (> than 10°). The azimuth of the plantation rows was recorded, and each step along a path was classified as parallel (differences of 0–45°) or perpendicular (differences of 46–90°) to the rows.

2.3. Data analysis

We first investigated if animals used the plantation rows to decide the direction of movement following release. For each path, we calculated the mean direction in the initial 20 m, following the criterion used to estimate perceptual range and orientation for these species (Forero-Medina and Vieira, 2009; Prevedello, 2009). A possible bimodal distribution of mean angles, with individuals orienting towards the plantation rows, was tested using the doubling of angles procedure coupled with the V-test of circular statistics (Batschelet, 1981; Fisher, 1993; Schooley and Branch, 2005). Mean angles and V-tests were calculated with Oriana 2.0 (RockWare Inc., Golden, USA). We analyzed individuals released within and beyond the perceptual ranges of these species in this matrix, estimated as 30 m for *P. frenatus* and 50 m for *D. aurita* (Prevedello, 2009). We expected that animals released within the perceptual range would move directly towards the fragment, but not towards plantation rows. On the other hand, animals released beyond the perceptual range would orient toward the rows while trying to find suitable habitat.

We also determined if animals moved predominantly parallel to plantation rows along their entire paths, which would indicate that the rows are preferred routes when travelling in the matrix. We compared total amount of movement parallel and perpendicular to plantation rows for each path using paired *t*-tests (Zar, 1999). As in the first analysis, we separated animals released within and beyond perceptual ranges, expecting that the former would not use plantation rows given the orientation towards the fragment, contrary to individuals released beyond perceptual ranges. Finally, we tested if the behavior of following rows decreased path tortuosity using Pearson correlation between the proportion of parallel movement and the tortuosity of each path (Zar, 1999). Path tortuosity was calculated using the fractal mean index in the software Fractal v. 5.10 (Nams, 2005). Fractal mean index of each individual was transformed to log (fractal-1) as suggested by Caldwell and Nams (2006). Only paths longer than 30 m were used in analyses.

3. Results

We tracked a total of 37 *P. frenatus* (22 males and 15 females) and 24 *D. aurita* (15 males and nine females). There were no detectable differences between movements of males and females in any tests, therefore genders were pooled in subsequent analysis.

Both species oriented their initial movements bimodally towards plantation rows. The movements of *P. frenatus* were significantly oriented towards plantation rows both within ($n = 5$; $u = 1.99$; $P = 0.02$) and beyond ($n = 32$, $u = 4.65$; $P < 0.0001$) its perceptual range in this matrix (Fig. 1). Similarly, movements of *D. aurita* were significantly oriented towards plantation rows at distances within ($n = 10$; $u = 1.93$; $P = 0.03$) and beyond ($n = 14$; $u = 1.67$; $P = 0.05$) its perceptual range (Fig. 2).

Both species moved more parallel than perpendicular to plantation rows. *Philander frenatus* moved predominantly parallel to rows within (parallel: 42.92 ± 26.14 m; perpendicular: 20.57 ± 20.82 m; $n = 5$, $t = 2.60$, $P = 0.05$), and beyond its perceptual range (parallel: 54.74 ± 18.15 m; perpendicular: 22.91 ± 13.06 m; $n = 32$, $t = 7.05$, $P < 0.001$). Similarly, *D. aurita* moved mainly parallel to rows within (parallel: 42.19 ± 13.92 m; perpendicular: 18.45 ± 18.16 m; $n = 10$, $t = 3.81$, $P = 0.004$) and beyond its perceptual range (parallel: 52.36 ± 16.28 m; perpendicular: 27.67 ± 13.25 m; $n = 14$, $t = 4.12$, $P = 0.001$).

There was a significant negative correlation between percentage of movement parallel to plantation rows and tortuosity of paths, for both *P. frenatus* ($n = 37$, $r = -0.59$, $P = 0.0001$) and *D. aurita* ($n = 24$, $r = -0.63$, $P = 0.001$). Therefore, individuals travelling parallel to the rows moved more linearly.

4. Discussion

We confirmed the hypothesis that *D. aurita* and *P. frenatus* use plantation rows to guide their movements in manioc plantations. This behavior occurred independent if the fragment was near or out of perception, allowing animals to move straighter while trying to reach the forest fragment. Directional biases in movement were also observed in other vertebrates during habitat search, and are probably a strategy to reduce the time spent in the matrix (Selonen and Hanski, 2004; Caldwell and Nams, 2006; Bowne and White, 2004). Nearly straight paths allow animals to quickly explore a given area while searching for habitat, being more successful to locate unknown habitat patches than tortuous paths (Zollner and Lima, 1999, 2005). However, maintaining a straight path is not

an easy task in an environment full of obstacles, and for real animals, with limitations on their perceptual capabilities. In manioc plantations, the rows provide an effortless way for *D. aurita* and *P. frenatus* to maintain a straight path, given their conspicuous linearity and reduced number of obstacles.

Surprisingly, animals oriented towards plantation rows even when the fragment was detected. Some individuals preferred to follow such open and linear routes over more obstructed ones even when plantation rows were not directly oriented to the fragment. The main reason is that plantation rows have reduced vegetation obstruction compared to routes oriented perpendicularly to the direction of the plantation, facilitating the movement of animals. Moreover, plantation rows allow an open view of the landscape ahead, increasing perceptual range of animals and probably their success at finding the forest (Zollner and Lima, 1999; Pe'er and Kramer-Schadt, 2008). Animals could be more susceptible to predators when following such less obstructed paths, but it appears that they either do not perceive such increased risks or judge them less important than the benefits of using the rows. Perceptual ranges of *D. aurita* and *P. frenatus* in plantations can be therefore considered anisotropic, that is, different directions of the landscape are perceived differently (Olden et al., 2004).

The tendency to move along plantation rows is likely to be found in many species other than didelphid marsupials, and in many plantations other than manioc. The taxa most affected by plantation rows are probably terrestrial mammals and reptiles with life-history traits similar to didelphid marsupials, such as limited vagility, high risk of predation, and limited perceptual range. These characteristics probably result in a similar perception of obstacles and risks within the plantations, stimulating animals to favor unobstructed routes. Flying and arboreal vertebrates, amphibians, and most invertebrates are less likely to use rows as dispersal routes, because of their different locomotory habits, perception of obstacles and movement routes. Plantations around the world are frequently linearly arranged, being generally classified as row crops (Clay, 2004). These plantations may function as dispersal routes for many terrestrial vertebrates, resulting in an asymmetric flux of individuals, i.e. an anisotropic functional connectivity (Bélisle, 2005), in many agricultural landscapes.

Our results have clear implications for biodiversity conservation in agricultural landscapes around the world. If plantation rows are oriented to maximize connection between nearby fragments, it is possible to enhance dispersal success of *D. aurita*, *P. frenatus*, and probably many other terrestrial vertebrates. Properly oriented plantation rows would function as directional corridors, conduct-

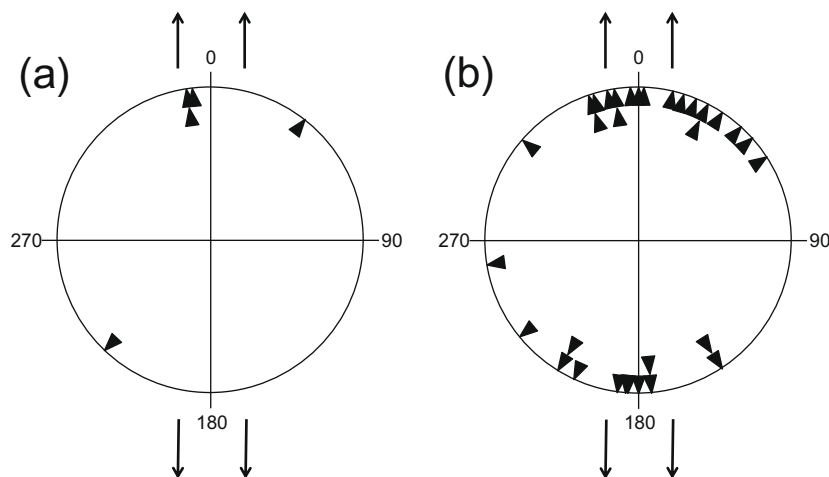


Fig. 1. Angular orientations of *Philander frenatus* released at 30 m (a) and ≥ 50 m and (b) from the forest fragment. The centre of the circle indicates the release point. Each triangle represents the mean angle for the first 20 m of movement of one individual. The arrows show the direction of the plantation row.

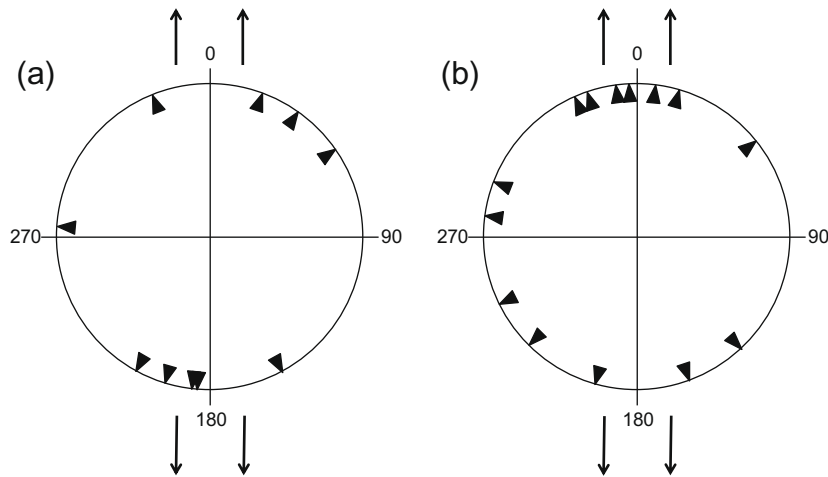


Fig. 2. Angular orientations of *Didelphis aurita* released at ≤ 50 m (a) and ≥ 100 m (b) from the forest fragment. Symbols as in Fig. 1.

ing individuals quickly between adjacent fragments. Even if some animals do not use plantation rows, it is unlikely plantation rows joining habitat patches will represent any threat to their populations. The manipulation of the direction of plantation rows is a simple and low cost management action which requires, in the case of manioc plantations, little more than awareness of farmers, with no prejudice to their productivity. Changes in plantation direction may be unfeasible in some hilly landscapes, where rows usually follow contour lines to minimize erosion and facilitate machine work. Moreover, in some landscapes the direction of the rows may influence light and wind incidence with significant effects on productivity (Karlen and Kasperbauer, 1989; Anda and Stephens, 1996). However, in most kinds of plantations in flat landscapes the direction of rows does not significantly affect productivity (Robinson, 1975; Steiner, 1986; Tsubo et al., 2003; Amateis et al., 2009). Therefore, we strongly recommend that farmers, whenever feasible, orient plantation rows to functionally connect as many fragments as possible. Such a simple guideline is likely to maximize dispersal success and population persistence of many terrestrial vertebrates in agricultural landscapes.

Acknowledgements

We thank to students of the Laboratório de Vertebrados – UFRJ for the invaluable assistance in the fieldwork, particularly to Ana Delciellos and Antonio Aisengart. Angela Marcondes and Nélio P. Barros provided logistical support. João Schaffer provided essential information on agronomic consequences of managing the direction of plantation rows. Renata Pardini, Marcelo Passamani, and two anonymous reviewers made valuable comments on the manuscript. This study was part of the MSc thesis of Jayme A. Prevedello in the PPG-Ecologia (UFRJ) and was supported by CNPq, CAPES, FA-PERJ, PDA/MMA, and FNMA/MMA.

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