

Conspecific and heterospecific attraction in assessments of functional connectivity

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Abstract Functional connectivity is known to have an important, positive influence on species persistence. Measurements of functional connectivity traditionally focus on structural attributes of landscapes such as the distance and matrix type between habitat patches as well as on how species interact with those structural attributes. However, we propose that the social behavior of a species, through conspecific and heterospecific attraction, will also impact connectivity by changing how dispersers move with respect to each other and occupied patches. We analyzed functional connectivity patterns using circuit and graph theory for golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Brazil under three scenarios. In the first scenario, we looked at connectivity without the effects of attraction under varying maximum dispersal distance and ecological movement cost thresholds. In the second scenario, we allowed dispersers to travel over more hostile matrix than they normally would to reach an occupied patch. In the final scenario, we allowed dispersers to move only to occupied patches. We found that, according to the first scenario, range-wide functional landscape connectivity for golden-headed lion tamarins is low at realistic maximum dispersal distance and movement cost thresholds. Incorporating

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the effects of conspecific or heterospecific attraction would increase functional connectivity, in the case of scenario two, or decrease functional connectivity, in the case of scenario three. Because conspecific/heterospecific attraction can have an impact on movement for some species, this factor should be incorporated in assessments of functional connectivity patterns for social species and others where patch occupancy is likely to influence the movements of dispersers.

Keywords Atlantic forest · Brazil · Circuit theory · Dispersal · Graph theory · Golden-headed lion tamarin · Wied's marmoset

Introduction

Functional habitat connectivity, defined as the “degree to which a landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993) for a given species, is often critical to the survival of populations and ultimately a species itself. Connectivity facilitates foraging across multiple habitats (Kozakiewicz 1995), resource supplementation and complementation (Dunning et al. 1992), recolonization of extirpated patches (Henderson et al. 1985), rescue effect of declining populations through immigration (Brown and Kodric-Brown 1977), and reduction of inbreeding depression (Richards 2000). Population persistence has been correlated with high levels of habitat connectivity for many species (e.g. Anzures-Dadda and Manson 2007; Fagan et al. 2002).

Given the value of connectivity for population and species persistence, understanding characteristics associated with potential movement pathways between habitat patches is important for managing populations, especially in fragmented landscapes. As the definition suggests, measurements of functional connectivity have traditionally focused on the structural attributes of landscapes and on how individuals move in response to those attributes given species-specific movement behaviors. In these measurements, important landscape features for functional connectivity have included inter-patch or nearest neighbor distance (Goodwin and Fahrig 2002; Radford and Bennett 2004) as well as the nature of the matrix between habitat patches (Anderson et al. 2007; Ricketts 2001). Finally, the degree to which patches can be considered functionally connected depends on species-specific traits such as vagility (D'Eon et al. 2002), perceptual range (Baguette and Van Dyck 2007), and degree of habitat specialization (With and Crist 1995).

We suggest that, in addition to structural landscape features and the behaviors of individuals in response to those features, measurements of functional connectivity patterns should also reflect social behaviors and/or information sharing to incorporate the motivation of individuals to disperse from and settle into a different habitat patch. In this paper, we focus specifically on the social behaviors conspecific and heterospecific attraction (Mönkkönen 1990; Stamps 1988) and on how these behaviors could impact measurements of connectivity.

Many species preferentially immigrate and settle into habitat patches that are already occupied by their own species (conspecific attraction; Danchin et al. 1998; Stamps 1988). In other cases, rates of settlement and colonization appear to be enhanced by the actions or presence of heterospecifics, in particular by individuals belonging to ecologically-similar species (heterospecific attraction; Mönkkönen and Forsman 2002; Parejo et al. 2004). Evidence suggests that individuals settle near conspecifics or ecologically-related heterospecifics because (1) the presence of others, a form of public social information (Wagner and Danchin 2010), acts as an indicator of habitat quality (Valone 1989) or (2) individuals

benefit in some way (e.g. increased mating opportunities, foraging success, predator protection) by settling near neighbors (Alleé et al. 1949). When dispersers use public information to assess habitat suitability, they spend less time in search of suitable habitat and thereby reduce search-related movement costs (Stamps et al. 2005). Theoretical models suggest that informed individuals should have higher fitness than individuals that disperse and settle at random (Boulinier and Danchin 1997; Fletcher 2006). Similarly, individual dispersers of species adapted to living in social groups should also benefit from moving directly into an occupied habitat patch provided they can successfully assimilate into a new group.

If conspecific or heterospecific attraction motivates dispersers to move toward an occupied habitat patch as opposed to an unoccupied one, occupied patches could act as magnets by drawing dispersers more often and perhaps over riskier matrix habitats, as seen in certain avian species (Sieving et al. 2004). We hypothesize that this would result in movement to occupied forest patches where connectivity might not otherwise be expected, thereby increasing the overall level of functional landscape connectivity (Fig. 1a).

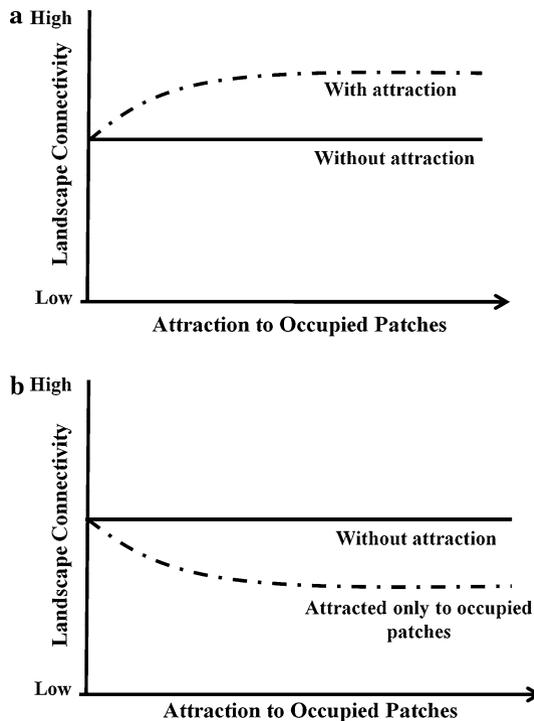


Fig. 1 If individuals change their dispersal behavior in response to conspecific/heterospecific attraction, we predict that connectivity would either increase or decrease depending on the specific dispersal pattern. In **a** we assume that individuals will disperse to any patch, regardless of occupancy in that destination patch, but that these individuals will be willing to travel over more hostile matrix or farther distances in order to reach other occupied patches (or other individuals). In this case, we hypothesize that landscape connectivity would be higher than expected, especially as the strength of that attraction to occupied patches increases, as compared to situations where dispersal is not impacted by attraction. Conversely, in **b** we assume that individuals disperse preferentially to occupied patches until, at the highest level of attraction, individuals only disperse to occupied patches. In this case, we hypothesize that connectivity would be lower than expected as compared to situations where dispersal is not driven by attraction to occupied patches

Conversely, dispersers may not be motivated to move to vacant, although suitable, habitat patches without conspecific or heterospecific cues (Seppänen et al. 2007). This may be especially true for species where information regarding the location of a neighboring patch is available through conspecific or heterospecific cues but is not otherwise available through visual cues (e.g. the potential disperser cannot see a neighboring patch but it is aware of its existence because it can hear calls from individuals on that neighboring patch; Fletcher and Sieving 2010). If dispersers are unmotivated to move to an unoccupied patch, we hypothesize that there may be no connectivity where movement might otherwise be expected, leading to lower overall landscape connectivity (Fig. 1b). In each case, measurements of functional connectivity patterns that include the effects of occupancy, information sharing, or social behavior could differ from measurements that simply incorporate landscape features.

The importance of conspecific attraction has been discussed briefly in relation to metapopulation colonization/extinction dynamics (Ray et al. 1991; Smith and Peacock 1990), but the importance of heterospecific attraction and the role of conspecific/heterospecific attraction in measurements of functional connectivity has not been examined in depth (but see Fletcher and Sieving 2010). Here, we measure range-wide functional connectivity using a traditional landscape-focused approach and hypothesize that conspecific/heterospecific attraction will alter these measurements for the endangered (IUCN 2010) golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*) in a fragmented environment. In this paper we conceptually discuss the role of information sharing and social behavior in connectivity analysis, and scenarios described here are not intended to explain the current distribution of this species.

Methods

Study system: GHLT

GHLTs are arboreal primates endemic to a 19,462 km² range of the Atlantic forest in southern Bahia, Brazil (Pinto and Rylands 1997; Fig. 2). Forest cover in this region is characterized by seasonal semi-deciduous tropical rainforest in the west and more contiguous coastal evergreen tropical rainforest in the east. GHLTs preferentially use primary and secondary/regenerating forest as well as cabruca agroforests (Raboy et al. 2004) below 500 m elevation (Pinto and Rylands 1997).

GHLTs are cooperatively breeding primates that live in family groups typically consisting of a single reproductive female, one to three adult males, and their juvenile offspring (Dietz et al. 1994). GHLTs have also been observed associating with groups of Wied's marmosets (*Callithrix kuhlli*; Rylands 1989) more often and longer than expected by chance (Raboy 2002) for both foraging benefits (Raboy 2002) and predator protection (Oliveira 2010; Oliveira and Dietz 2011). In one instance, a dispersing GHLT joined a group of Wied's marmosets where it lived for over 4 months (Oliveira, unpublished data). Such associations are prevalent for primates, especially between species within the family Callitrichidae which includes marmosets and tamarins (Buchanan-Smith 1990; Heymann and Buchanan-Smith 2000; Terborgh 1983). Like GHLTs, Wied's marmosets are cooperatively breeding with groups averaging 4.3 individuals (Raboy et al. 2008). Both species subsist on a diet of ripe fruits, insects, and small vertebrates (Rylands 1989). In addition, Wied's marmosets also eat plant exudates (Rylands 1989).

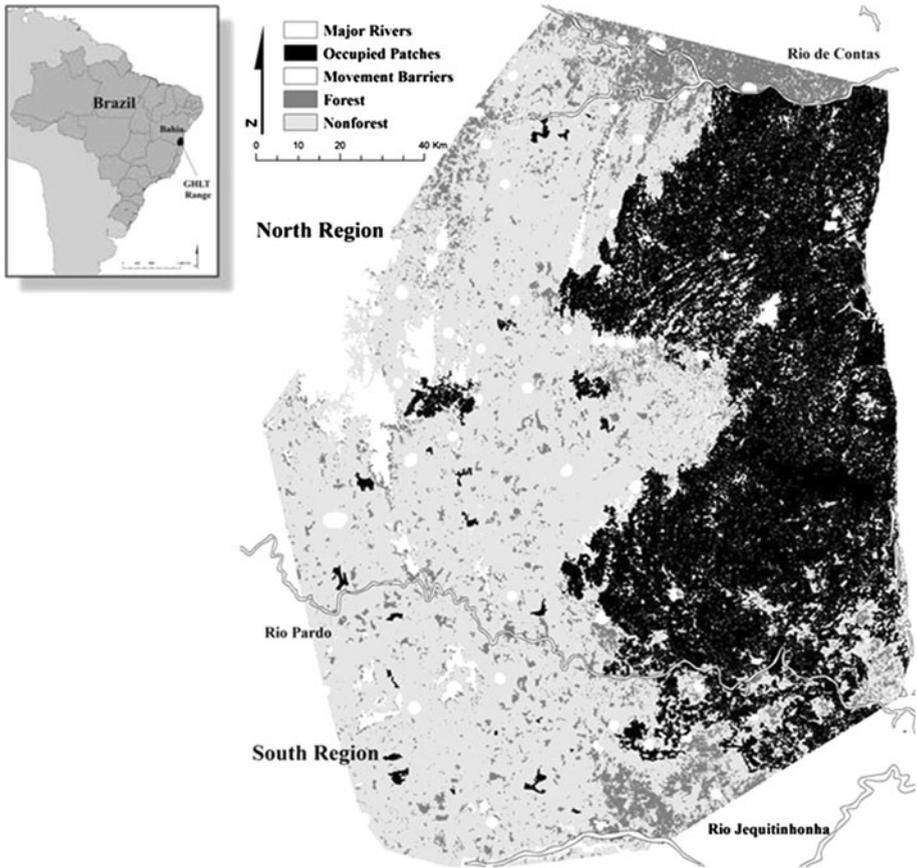


Fig. 2 Resistance (ecological cost) map used in Circuitscape ver3.5 to predict the movement of GHLTs between habitat patches. Forest (*dark gray*) had the lowest movement resistance and non-forest (*light gray*) had the highest movement resistance. Areas above 500 m elevation, large rivers, and urban areas acted as barriers to movement (*white*). Patches displayed in *black* were occupied by GHLTs or Wied's marmosets according to a 2005–2008 survey by Neves (2008) and Raboy et al. (2010)

In cooperatively breeding species such as GHLTs, where typically only a single male and female breed per group, the need to find mating opportunities may drive a non-breeding individual's decision to disperse from its natal territory. This is supported by the fact that GHLTs exhibit prospecting behaviors before making permanent dispersal decisions (Oliveira unpublished data). Although observed group-level immigration and emigration rates are relatively low (0.61 and 0.53 individuals/group/year, respectively), most GHLTs leave their natal territories between 2 and 4 years of age (Raboy 2002). Males and females are equally likely to disperse from their natal territories, but males are more likely to successfully immigrate into new groups (Raboy 2002). Dispersing GHLTs have been documented traveling alone (56% of time) or in same sex pairs or trios (44%; Raboy 2002).

Less is known about how far dispersing GHLTs will travel. GHLTs spend 43% of their daily activity budget on locomotion, moving on average 1.4–2.2 km per day (Raboy and Dietz 2004; Rylands 1989); however, these movements were confined to the territorial ranges of those particular groups. The majority of evidence for long-distance dispersal

movements consists of a few anecdotal observations by field researchers. Individuals have been observed on two occasions traveling 4–5 km (straight line distance; Raboy 2002; Oliveira, unpublished data) through forest from their natal territories. A group of GHLTs was also observed crossing an open field, which is the landcover type separating the majority of habitat patches in this system, over a distance of 1.8 km (Raboy, unpublished data) while a pair of golden lion tamarins (*L. rosalia*) were seen dispersing through open field over a distance of 1 km (Grativol et al. 2001). However, GHLTs are rarely seen moving through open pasture (Raboy et al. 2010; Guidorizzi, unpublished data), and experts estimate that consistent movements between patches more than 100 m apart are possible but unlikely for most lion tamarins (J. Mickelberg, personal communication).

Analysis of habitat

A binary map of forest/non-forest habitat within the GHLT geographic range served as the foundation of our study of functional connectivity. This map was created through a supervised classification of Landsat 5TM remotely-sensed imagery from 2004 to 2008 (Zeigler et al. 2010 for further details on how this map was created). To overcome processing limitations and to facilitate computations in programs used to analyze connectivity patterns, we resampled the cell size of the forest map from 30 to 200 m and divided the GHLT range into regions north and south of the Rio Pardo (Fig. 2). Large rivers such as the Rio de Contas and Rio Jequitinhonha, which mark the northern and southern boundaries of the species' range, as well as the Rio Pardo likely serve as barriers to GHLT movement (Rylands 1989). Therefore, it is unlikely that dividing the GHLT range at the Rio Pardo affected the results of the range-wide connectivity analysis. These two regions were considered separately for all subsequent analyses in our study.

From these range-wide maps of forest cover for the regions north and south of the Rio Pardo, we selected patches 36 ha or larger in area to serve as source patches in assessments of functional connectivity. This is the smallest recorded GHLT home range size (Rylands 1989) and represents the smallest patch size that a group of GHLTs will likely inhabit with any permanence. Smaller forest patches, while not serving as source patches, were incorporated by reducing movement costs between source patches.

Assessment of movement patterns

We examined pathways of potential GHLT movement among forest patches using Circuitscape ver3.5 (McRae 2006). Circuitscape uses circuit theory to model animal movement and considers matrix landscape features separating patches, multiple pathways between patches, and the width of those pathways to predict the likelihood that an animal will move between any two habitat patches (McRae 2006; McRae et al. 2008).

We input a patch identification file and a raster landscape resistance map into Circuitscape, both of which were ASCII files exported from raster maps in ArcGIS ver9.3 (ESRI). The patch identification file contained the location and unique identification code for the 769 individual habitat patches 36 ha or larger in the landscape. In the landscape resistance map, each cell was given a resistance value associated with how easily an individual could move through that cell/landscape type with values equaling 1 (low resistance) for forest cells, 50 (high resistance) for non-forest cells, and no data (barrier to movement) for urban areas, areas of elevation greater than 500 m, and rivers (Fig. 2).

“Urban areas” consisted of the area within the boundary of each major city in the region, as delineated by Fonseca et al. (1999), plus a 1 km buffer completely surrounding each boundary to account for sprawl. The entire area (area within boundary plus 1 km buffer) was given a value of “no data”.

Absolute resistance values were chosen arbitrarily and reflect the reduced movement (and increased resistance) for individuals in non-forest matrix. Observations and expert opinion suggest that predation of GHLTs is higher in open pasture as compared to forest and that GHLTs, as arboreal primates, are much less likely to move through this open pasture that dominates the matrix throughout the species’ range (Raboy et al. 2010; Guidorizzi unpublished data; Raboy personal communication). Studies assessing the sensitivity of least-cost routes of animal movement found that such models are most sensitive to the relative values of landcover types in the matrix and not the values distinguishing habitat and inhospitable matrix types (Rayfield et al. 2010). Similarly, Lee-Yaw et al. (2009) found that models of connectivity for wood frogs were most sensitive to absolute dispersal barriers, not the resistance values given to landscape variables. Because we incorporated movement barriers and only a single matrix type, we do not believe that absolute resistance values arbitrarily chosen here will greatly impact connectivity results as long as these values reflect higher resistance in non-forest as compared to forest.

The final output of our analysis in Circuitscape was a unitless ‘resistance distance’ between every pair of patches. The resistance distance is a composite of Euclidean distance, number of possible pathways, width of those pathways, and ecological cost of traveling between a given pair of forest patches (McRae 2006). Thus, patches with low resistance distance values (values approaching 0) are close together, have multiple wide movement pathways, and have little hostile matrix between them. Resistance distance values were used as inputs in all three connectivity modeling scenarios (see below).

We also examined movement pathways in terms of Euclidean distance between patches in Circuitscape for one of the scenarios (see below). Methods described above were repeated in Circuitscape, but the analysis of movement pathways was capped at distance thresholds of 50 m, 100 m, 500 m, 1 km, and 5 km while the cost of those pathways was ignored (e.g. at a distance threshold of 50 m, movement between patches occurred only between pairs of patches separated by an edge-to-edge distance of 50 m or less). The resulting output from Circuitscape indicated whether any pair of patches was connected by movement at each distance threshold, irrespective of cost but limited by movement barriers (urban areas, rivers, and high elevation).

Assessment of functional connectivity

To assess functional connectivity, we used a graph theoretical approach (Urban and Keitt 2001) in the program Conefor Sensinode ver2.2 (Saura and Torne 2009). Input files for Conefor Sensinode were a patch identification file from Circuitscape and a file containing the distance between pairs of habitat patches. Depending on the scenario, either the resistance distance matrices or Euclidean distance matrices created in Circuitscape were used as the ‘distances’ between pairs of habitat patches.

We determined eight metrics of landscape connectivity within Conefor Sensinode: number of links among patches, number of components, area of the largest component, average area of all components, number/percentage of patches in the largest component,

Table 1 Metrics used to measure range-wide functional landscape connectivity (divided by regions north and south of the Rio Pardo) for GHLTs in Bahia, Brazil

Metric	Value if no connectivity		Value if total connectivity		Pattern with increasing connectivity
	North	South	North	South	
Number of links	0	0	∞	∞	Increases
Number of components	540	229	1	1	Decreases
Size of largest component (ha)	654,256	44,204	812,816	116,988	Increases
Average component size (ha)	235	87	812,816	116,988	Increases
Number (percentage) of patches in largest component	1 (0.1%)	1 (0.4%)	540 (100%)	229 (100%)	Increases
Number (percentage) of isolated patches	540 (100%)	229 (100%)	0 (0%)	0 (0%)	Decreases
IIC	0	0	1	1	Increases

number/percentage of isolated patches, and the integral index of connectivity (IIC; Table 1). IIC (Pascual-Hortal and Saura 2006) was calculated as:

$$IIC = \frac{\left(\sum_{i=1}^n \sum_{j=1}^n (a_i * a_j) / (1 + nl_{ij}) \right)}{A_L^2}$$

where n is the total number of patches in the landscape, a_i and a_j are the areas of patch i and patch j respectively, nl_{ij} is the number of links in the shortest path between patches i and j , and A_L is the total size of the landscape. This metric is based on the habitat availability concept where the patch itself is a space within which connectivity occurs, integrating both inter- and intra-patch connectivity in the measure of total landscape connectivity.

Connectivity modeling scenarios

We modeled functional landscape connectivity under three scenarios that represent examples of how conspecific/heterospecific attraction could theoretically influence functional connectivity:

Scenario one: general functional landscape connectivity

Functional landscape connectivity was based only on landscape features, and conspecific/heterospecific attraction was not considered. Dispersal could occur between any pair of patches falling within given resistance distance and Euclidean distance thresholds. It is unknown how costly is too costly when it comes to dispersal decisions across matrix for GHLTs, and some dispersers may be more willing to cross hostile matrix than others. Such dispersers may travel farther across open pasture, allowing connections between patches with high resistance distance values. Other dispersers may only travel between patches where forested stepping stones reduce movement costs, allowing connections only between patches with low resistance distance values. There is also uncertainty surrounding how far GHLTs will disperse across open matrix between habitat patches. Thus, we examined connectivity patterns at multiple resistance distance and Euclidean distance thresholds to

explore the consequences of varying opportunities for dispersal between patches and expected connectivity to increase with increasing thresholds.

Scenario two: dispersers increase resistance distance threshold in response to attraction

We assumed that a disperser, responding to conspecific/heterospecific attraction, would risk higher movement costs to reach an occupied patch. Thus, the resistance distance threshold would increase. We modeled this scenario by first setting the baseline resistance distance threshold of one (i.e. any pair of patches, irrespective of occupancy, was considered connected if it was separated by a resistance distance value of one or less). Second, we assumed that occupied patches would draw dispersers across higher resistance distance thresholds. For example, in the simulation where the threshold for occupied patches was increased to five, a pair of patches could be considered connected if it met one of two criteria: (1) the pair was separated by a resistance distance value of one or less or (2) the pair was separated by a resistance distance value of five or less and one of those patches was occupied. Simulations were repeated such that the resistance distance threshold for occupied patches was increased to 10, 20, 30, and 40.

Scenario three: dispersers only move between occupied patches

We assumed that dispersers would only move to occupied patches in response to conspecific/heterospecific attraction. Thus, connectivity could only occur for pairs of patches that fell within the maximum resistance distance threshold and where one of those patches was occupied.

Scenarios two and three explored examples of possible ways in which conspecific/heterospecific attraction could theoretically impact connectivity measures, and patch occupancy by GHLTs and/or Weid's marmosets was important for these two scenarios. Patches were considered occupied by GHLTs and/or Wied's marmosets based on positive survey results between 2005 and 2008 by Neves (2008) and Raboy et al. (2010) (Fig. 2). We did not differentiate between patch occupancy by GHLTs versus Wied's marmosets because the relative strength of conspecific versus heterospecific attraction is unknown and because the overall known level of occupancy throughout the landscape is low. Because our analysis employs a graph theoretical framework and is not a simulation of metapopulation dynamics, occupancy does not change through time to reflect colonization and local extinction of patches.

Results

Scenario one: general functional landscape connectivity

Functional landscape connectivity for GHLTs was extremely low according to the IIC metric (all distance thresholds) and at small resistance distance and Euclidean distance thresholds for all other metrics (Fig. 3) in both the regions north (Table 2) and south (Table 3) of the Rio Pardo. The number of components and the number/percentage of isolated patches decreased while the number of links, average component size, largest component size, and number/percentage of patches connected to the largest component increased dramatically with increasing resistance and Euclidean distance thresholds (Tables 2, 3; Fig. 3). According to

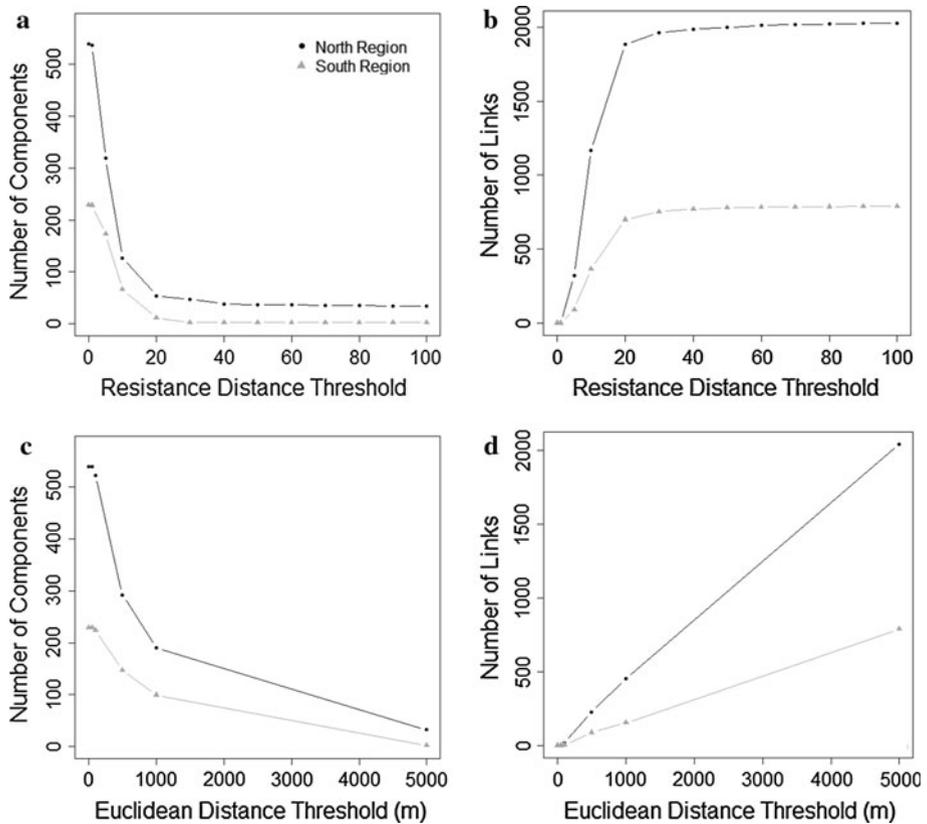


Fig. 3 Range-wide functional connectivity, as measured by **a, c** the number of components and **b, d** the number of links among habitat patches for GHLTs in the regions north (*circles*) and south (*triangles*) of the Rio Pardo at varying **a, b** resistance distance and **c, d** Euclidean distance thresholds

IIC, connectivity also increased with increasing resistance distance and Euclidean distance thresholds, although less substantially (Tables 2, 3). Critical distances, where connectivity did not increase appreciably with further increases in distance, were at a resistance distance of 30 and at a Euclidean distance above 5 km (Fig. 3).

Scenario two: dispersers increase resistance distance threshold in response to attraction

Functional connectivity increased for both the regions north and south of the Rio Pardo as resistance distance threshold was increased for occupied patches (Fig. 4). In this scenario where dispersers crossed more hostile matrix to reach an occupied patch in response to conspecific/heterospecific attraction, connectivity measurements were substantially higher compared to measurements not including attraction.

Scenario three: dispersers only move to occupied patches

Connectivity decreased for both the regions north and south of the Rio Pardo as dispersal was limited to occupied patches (as compared to connectivity when dispersal could occur

Table 2 Metrics describing functional habitat connectivity for GHLTs in the region north of the Rio Pardo in Bahia, Brazil at varying resistance distance and Euclidean distance thresholds

Distance	IIC	Size of largest component (ha)	Average component size (ha)		Median component size (ha)	Patches in largest component		Isolated patches (no links)	
			With largest component	Without largest component ^a		Number	%	Number	%
Resistance distance (unitless)									
0	0.131	654,256	540	249	80	1	<1	540	100
1	0.135	674,812	1,468	212	80	1	<1	536	99
5	0.138	694,336	2,471	295	88	118	22	270	50
10	0.142	731,016	6,206	454	100	328	61	95	18
20	0.145	772,364	14,596	299	70	470	87	48	9
30	0.145	772,912	16,771	333	80	475	88	41	8
40	0.145	776,388	20,743	320	76	486	90	33	6
50	0.145	776,760	21,895	327	68	491	91	33	6
60	0.145	776,760	21,895	327	68	491	91	33	6
70	0.145	776,824	22,521	335	72	492	91	32	6
80	0.145	776,824	22,521	335	72	492	91	32	6
90	0.145	776,888	23,183	343	76	493	91	31	6
100	0.145	776,888	23,183	343	76	493	91	31	6
200	0.145	776,980	23,885	351	72	494	91	30	6
300	0.145	777,044	24,632	361	76	495	92	29	5
Euclidean distance (m)									
0	0.131	654,256	1,462	249	80	1	<1	540	100
50	0.131	654,256	1,462	249	80	1	<1	538	99.6
100	0.131	654,860	1,507	255	80	6	1	511	95
500	0.137	688,420	2,699	243	100	102	19	225	42
1,000	0.138	695,416	4,147	490	140	144	27	124	23
5,000	0.145	772,240	24,632	515	70	495	92	29	5

^a Because the area of the largest component was so much larger than the next largest component (due to the substantial area of the largest patch compared to others in the landscape), we calculated the average component area with and without the area of the largest component

between any pair of patches within the resistance distance threshold; Fig. 5). In this extreme example, where dispersers limited dispersal decisions in response to conspecific/heterospecific attraction, connectivity measurements were dramatically lower than expected as compared to measurements not including attraction.

Discussion

General functional landscape connectivity

Realistic distance thresholds for GHLTs are most likely between 1 and 5 (resistance distance) and between 100 m and 1 km (Euclidean distance). At these thresholds,

Table 3 Metrics describing functional habitat connectivity for GHLTs in the region south of the Rio Pardo in Bahia, Brazil at varying resistance distance and Euclidean distance thresholds

Distance	IIC	Size of largest component (ha)	Average component size (ha)		Median component size (ha)	Patches in largest component		Isolated patches (no links)		
			With largest component	Without largest component ^b		Number	%	Number	%	
Resistance distance (unitless)										
0	0.008	44,204	469	277	88	1	<1	229	100	
1	0.009	50,944	471	248	88	1	<1	227	99	
5	0.014	80,648	620	154	88	43	19	159	69	
10	0.014	83,832	1,626	361	100	77	34	43	19	
20	0.016	105,608	9,754	168	72	212	93	7	3	
30 ^a	0.016	107,248	53,646	44	53,646	228	99.6	1	<1	
Euclidean distance (m)										
0	0.008	44,204	469	277	88	1	<1	229	100	
50	0.008	44,204	469	277	88	1	<1	229	100	
100	0.008	44,848	479	280	92	3	1	220	96	
500	0.013	78,252	730	199	120	41	18	115	50	
1,000	0.014	81,132	1,084	267	140	51	22	61	27	
5,000	0.016	107,248	53,646	44	53,646	228	99.6	1	<1	

^a Results same for all resistance distances between 30 and 300

^b Because the area of the largest component was so much larger than the next largest component (due to the substantial area of the largest patch compared to others in the landscape), we calculated the average component area with and without the largest component

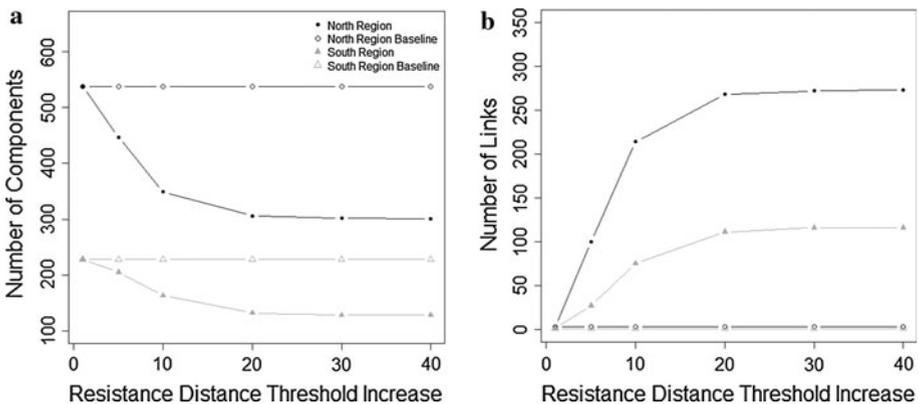


Fig. 4 Range-wide functional connectivity, as measured by **a** the number of components and **b** the number of links among habitat patches for GHLTs in the regions north (*circles*) and south (*triangles*) regions of the Rio Pardo. Connectivity models assumed that dispersers are willing to move across more costly matrix to reach occupied patches in response to conspecific/heterospecific attraction (scenario two; *closed symbols*) as compared to the baseline scenario of random dispersal at a constant cost threshold of one (*open symbols*)

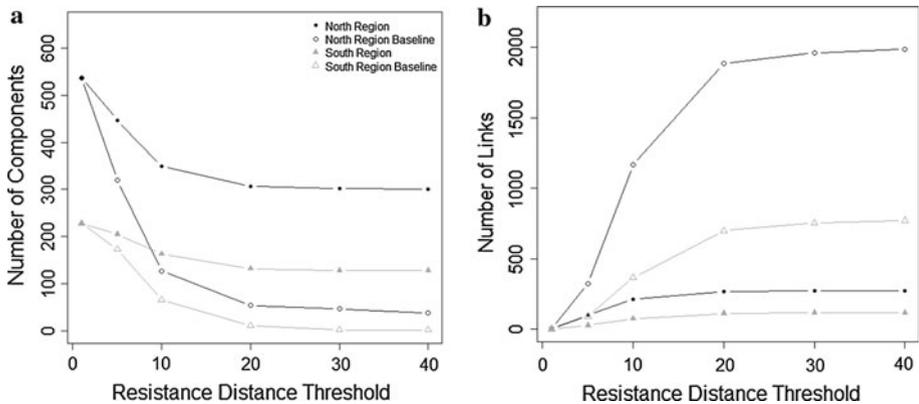


Fig. 5 Range-wide functional connectivity, as measured by **a** the number of components and **b** the number of links among habitat patches for GHLTs in the regions north (*circles*) and south (*triangles*) regions of the Rio Pardo, for GHLTs. Connectivity models assumed that dispersers would only move to occupied patches in response to conspecific/heterospecific attraction (scenario three; *closed symbols*) as compared to the baseline scenario of random dispersal at equivalent distance thresholds (*open symbols*)

range-wide functional landscape connectivity for GHLTs is low. Low levels of connectivity are consistent with the Brazilian Atlantic Forest as a whole (Ribeiro et al. 2009).

This low level of connectivity, and associated low level of consistent inter-patch movement, may have important implications for the survival of the GHLT metapopulation by not allowing access to multiple habitats and resources (Dunning et al. 1992; Kozakiewicz 1995), the rescue of declining populations through immigration and increased genetic heterozygosity (Brown and Kodric-Brown 1977; Richards 2000), and recolonization of extirpated patches (Henderson et al. 1985). Local extinctions are expected to occur, ultimately resulting in a range contraction as populations along the edge of the geographic range are lost without recolonization (Channell and Lomolino 2000a, b; Lomolino and Channell 1995). Connectivity was particularly low in the region south of the Rio Pardo. A contraction at the southwestern portion of the species' range, within this region south of the Rio Pardo, was observed in recent years (Raboy et al. 2010; Raboy unpublished data), and loss of connectivity may be responsible for this pattern. Studies that examine how connectivity has changed in that area of range reduction represent possible future directions for research.

In addition, Zeigler et al. (2010) found that only a small percentage of forest patches (22 out of 15,713; 0.14%) in the GHLT range are large enough to support a viable population that is not reliant on the influx of new immigrants. Viable populations that are also capable of maintaining genetic diversity required larger forest patches, and an even smaller percentage of such forest patches (2 out of 15,713; 0.01%) exist. Even at a Euclidean distance threshold of 1 km, an optimistic distance for how far a GHLT will travel through non-forest matrix, the average component size (excluding the largest component) is 490 and 267 ha north and south of the Rio Pardo, respectively. Thus, even allowing for resource acquisition by movement between patches, the combined component area available for most populations of GHLTs is likely much lower than the 1,045 ha required to support a viable population of GHLTs (Zeigler et al. 2010). Relatively isolated populations restricted to small patches or components of patches, without the influx of new immigrants or additional space to allow for population expansion, will quickly become vulnerable to extinction through demographic and environmental stochasticity, genetic drift, inbreeding depression, and Alleé effects (Ellstrand and Elam 1993; Oostermeijer et al. 2003). Because

little opportunity may exist for consistent inter-patch movement over areas large enough to support a viable population, large habitat patches are of critical importance for the conservation of the species (Zeigler et al. 2010).

Social behavior in measures of connectivity

Predicted connectivity patterns changed as we incorporated conspecific/heterospecific attraction into our analysis. If, as in scenario two, dispersers change their behavior by traveling across more hostile matrix to reach occupied patches, functional landscape connectivity would increase relative to scenario one where social behavior was not considered. Conversely, if dispersers only move between occupied patches (scenario three), functional connectivity would be lower than expected, especially in landscapes where only a small percentage of all patches are occupied. Neighboring patches separated by short distances and mildly hostile matrix, a situation where some connectivity may be expected, may have no exchange of individuals if one of those patches is unoccupied. Over longer time frames, as individuals preferentially choose to settle in occupied habitat patches, metapopulation extinction/colonization dynamics will be strikingly different as well (Smith and Peacock 1990). For example, new individuals dispersing into already occupied patches may provide a rescue effect for those populations while vacant patches with otherwise suitable habitat remain vacant. Because dispersers would only be moving between the same neighboring group of occupied patches, individuals would quickly become aggregated in response to conspecific/heterospecific attraction (Seppänen et al. 2007) as seen in the distributional patterns that have been observed for the Columbian ground squirrel (Weddell 1991), bobolink, and savanna sparrow (Nocera et al. 2006). Ultimately, extinction rates for existing populations and colonization rates in vacant habitat patches will be lower than expected with random dispersal (Ray et al. 1991; Smith and Peacock 1990). Such changes in metapopulation dynamics and distributional patterns may have severe consequences for the extinction risk of GHLTs and other organisms where conspecific/heterospecific attraction could influence movement decisions. As fragmentation and the distance between habitat patches in the landscape increases, the distance between patches may become too large, and potential dispersers may not be able to perceive the social stimuli that indicate a neighboring patch is occupied, thereby further depressing dispersal and colonization rates (Ray et al. 1991). Over time, individuals would eventually be found in a few populations and habitat patches, increasing the probability of simultaneous extinction due to stochasticity or environmental catastrophes (Gilpin 1990).

Perceptual range

One important consideration not explicitly incorporated into our analysis of functional connectivity is the perceptual range of the species. A species' perceptual range defines the "fraction of the landscape that is both detectable and accessible via movement, and therefore defines the spatial scale at which an individual interacts with the landscape" (Olden et al. 2004). Most studies of perceptual range focus on a species' ability to visually perceive landscape elements (e.g. Mech and Zollner 2002); however, in the case of conspecific/heterospecific attraction, perceptual range would refer to a disperser's ability to see, hear, or smell other individuals in the landscape. Long-range communication among callitrichid primates occurs through vocal signals called 'long-calls'. Long-calls are used to defend territories against other groups, to maintain group cohesion, and to attract mates (reviewed in Snowdon et al. 1986). In addition, a number of studies have found that

different callitrichid species share vocal signals (Epple 1969) and respond to each other's vocalizations as often as they respond to conspecific vocalizations (e.g. Porter 2001), facilitating coordination between heterospecific groups.

In our study system, auditory stimuli would most likely influence long-distance attraction of dispersers to other GHLTs or marmosets (and occupied habitat patches). Attraction will only occur, and can only impact connectivity patterns, within the auditory perceptual range of the species. However, it is not clear how close a dispersing GHLT would need to be to an occupied habitat patch to hear other monkeys and to perceive that the patch is in fact occupied. This uncertainty limits our ability to understand the degree to which conspecific or heterospecific attraction impacts movement decisions and overall connectivity patterns in this landscape.

Perceptual range is also context-dependent (Zollner and Lima 1997). For example, the olfactory-based perceptual range of cactus bugs (*Chelinidea vittiger*) was dependent on the size of the target habitat patch, matrix structure, and direction of the habitat patch relative to prevailing winds because of how scent travels in the system (Schooley and Wiens 2003). For GHLTs, vocalizations may travel farther in open pasture than they would in dense forest canopy, and the perceptual range of the species may change depending on surrounding landcover type.

Conclusions

Traditional measurements of functional connectivity considering only patch size, location, and surrounding matrix do not capture the movement dynamics and distributional patterns seen in real systems (Winfree et al. 2005). Like Fletcher and Sieving (2010), we suggest that movement, and ultimately functional connectivity, is a function of social behavior, transfer of information regarding habitat suitability, and structural landscape features for certain species. In cases where dispersers cross more hostile matrix to reach occupied patches or travel only to occupied patches, measurements of functional connectivity would be different than expected in cases of random dispersal, as explored here with GHLTs. We recommend that conspecific/heterospecific attraction be further researched in the context of connectivity in future field studies and that attraction be explored in measurements of connectivity for social species and species that utilize public information.

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