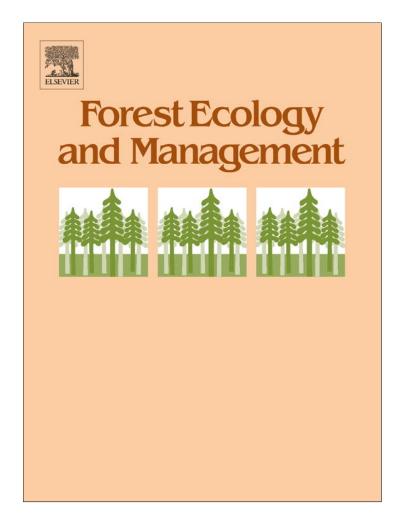
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Use of space by frugivorous bats (Chiroptera: Phyllostomidae) in a restored Atlantic forest fragment in Brazil

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ABSTRACT

We studied patterns in the use of space for foraging and roosting by two frugivorous bat species in a five-year-old restored Atlantic forest located in a fragmented landscape in southeastern Brazil. Ten individuals of *Carollia perspicillata* and eleven individuals of *Artibeus lituratus* were monitored through radio-telemetry in five sampling sessions. Each session lasted 3-8 days for each individual, with an average of 25.4 ± 10 locations for each *C. perspicillata* individual and 19 ± 4.4 for each *A. lituratus* individual. We described an average range of 124.4 ha and an average commuting distance of 1158.8 m for *A. lituratus* and an average range and commuting distance of 32 ha and 489 m, respectively, for *C. perspicillata*. We demonstrated a consistent pattern in habitat use and movements for both studied species, where they strictly used forests (restored or not) for day roosting, roosting in the foliage of trees located only in secondary forest remnants and restored areas, while restored areas were their main feeding habitat. We demonstrate that newly restored forests can be readily incorporated as foraging and roosting habitats by these species, and that *C. perspicillata* alters its roosting behavior in relation to preferred food availability. These results, when combined with data on the diet of the studied species, show consistent evidence of the potential that bats have to improve species diversity of anthropogenic plantings with their own natural seed dispersal.

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1. Introduction

The evaluation of the success of restoration projects is a strategic initiative and should be based on the monitoring of indicators of progress toward predefined goals (Holl and Aide, 2011). This practice, however, is strongly biased toward the use of only vegetational parameters as indicators of progress, and a common finding in studies of Neotropical reforestation sites is that new colonizing plant species fail to reach and become established in restored areas, especially in highly fragmented landscapes (Holl, 1999; Rodrigues et al., 2009).

Animal-mediated seed dispersal is the prevailing form of seed dissemination in tropical forests (Howe and Smallwood, 1982),

and much of the potential of these animals to visit and bring new seeds to revegetated sites depends on the availability of source areas (of plants and animals) in the landscape and the animal's efficiency in moving between these areas (Wunderle Jr., 1997). Isolation is a response to the interaction between landscape structure and dynamics (including local-scale site characteristics) with specific aspects of animal behavior (Dewalt et al., 2003; Fahrig, 2003; Fischer and Lindenmayer, 2007). Therefore, in the development of reliable indicators of the re-establishment of seed flow to non-isolated restored areas and, consequently, the successful restoration of successional dynamics, it is of paramount importance to measure the faunal contribution to this process (Lindell, 2008).

New World fruit-eating bats (Chiroptera: Phyllostomidae) are among the most abundant seed dispersers in Neotropical forests, and because they include a diverse array of early-successional plant species in their diet, they are regarded as playing an important role in the successional dynamics of these forests (Medellin and Gaona, 1999; Galindo-Gonzalez et al., 2000; Muscarella and Fleming, 2007). As highly vagile animals, some authors have argued that many species of bats may persist under conditions that are limiting to other mammals (Bernard and Fenton, 2003;

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Bianconi et al., 2006). Therefore, they may play a primary role in the re-establishment of successional dynamics by contributing to the propagule flow in recently restored areas (Muscarella and Fleming, 2007). There are few studies that empirically demonstrate this potential bats may have (see Silveira et al., 2011), particularly in the brazilian Atlantic forest, which is undergoing a recent increase in the development of new concepts and methods aimed at the recovery of this biome (Rodrigues et al., 2009). Understanding habitat use by bat species that occupy these newly restored areas may reveal important resources for its occurrence, providing a basis for understanding the role of these animals in the restoration process (Lindell, 2008; Chazdon et al., 2009).

In this study, we describe patterns in the use of space for foraging and roosting by the two most locally abundant frugivorous species, Carollia perspicillata and Artibeus lituratus, in a five-year-old restored Atlantic forest in a fragmented landscape in southeastern Brazil. A recent study conducted in the same area demonstrated that the feces of both species contained seeds of colonist plant species (i.e. allochthonous seeds from trees not planted in the original restoration project), providing evidence of the bats' contribution to the restoration of successional dynamics in the area (Silveira et al., 2011). Although these results suggest that bats are contributing to the success of restoration programs, it does not unequivocally demonstrate that forest restoration entails any advantage for the bats. Therefore, in the present study, we shift the point of view to evaluate the contribution of these restored areas to the frugivorous bats. We aimed to determine the importance of a recently restored area as a habitat for these bats in the landscape context.

We focused on elucidating the frequency of use of the restored area by these species in the context of the other habitats available in the landscape and determining whether the restored site serves only as foraging habitat or is also used for day roosting. In addition, we asked: does food availability in restored areas affect their use by bats? Despite concentrating their diet mainly on a limited set of five phylogenetically distinct plant genera, frugivorous phyllostomids are able to opportunistically forage on most of the available species within this set (Mello et al., 2011). Moreover, behavioral studies usually depict group-specific patterns influenced by the abundance and spatio-temporal distribution of available resources (Meyer et al., 2005; Thies et al., 2006; Albrecht et al., 2007). Since fruit availability is commonly believed to attract potential seed dispersers and enhance faunal recovery (Wunderle Jr., 1997; Martínez-Garza and Howe, 2003), we hypothesized that bats would select restored habitats for both foraging and roosting based on the availability of their main food resource in these habitats (Silveira et al., 2011).

2. Materials and methods

2.1. Study area

This study was conducted from July 2007 to August 2008 in the Reserve Parque São Marcelo (RPSM), Mogi-Guaçu municipality, São Paulo State, Southeast Brazil (22°22′S, 46°58′W; Fig. 1). A 987 ha private protected area, the RPSM was originally covered by typical semideciduous forest (Kronka et al., 2005) but the region has undergone a historical anthropogenic process of forest conversion to a variety of productive land uses (sugar cane, coffee and pastures). At present, it is composed of a mosaic of land cover, including semideciduous forest remnants, eucalyptus plantations, other anthropogenic land cover (cattle pastures and mixed agriculture) and heterogeneous reforested areas. These restored areas correspond to 40 patches of approximately the same size, where a high diversity (>100 species) plantation of native plant species was implemented. This 240 ha revegetation project was undertaken in 2002, replacing an area occupied by *Eucalyptus* plantations

during 7 years before restoration took place. The climate of the region is classified as *Cwa*, following Köppeńs (1948) system, with a colder and drier season from May to August and warm and wet months from September to April. For more detailed information on the restoration project, see Mandetta (2007) and Silveira et al. (2011).

2.2. Mapping and habitat classification

We created a digital map of the study area showing land covers with ArcGis 9.1 (ESRI, Inc.), starting by georeferencing aerophotographs (1:25000). We then performed a qualitative classification of the available habitats in the landscape, through photointerpretation of discrete land use information. This procedure yielded a vector layer of available habitats, which was later adjusted and validated through field visits. The availability of these habitats was assessed within a maximum sampling circle (MSC) with a radius of 3.0 km, which was positioned in the center of the study area (Fig. 1). Habitats characterized in this study were: Secondary forest remnants, Restored areas, Exotic forest plantations (Eucalyptus sp.) and Early successional forest remnants (treeless pioneer shrub vegetation). In addition, we characterized the Anthropogenic land use habitat, which encompassed all other forms of land use resulting from human activity, ranging from completely open cattle pastures to shrub plantations of annual crops. We initially considered anthropogenic shrub and anthropogenic open pasture as separate habitats during exploratory analysis. As both habitats were severely sub-utilized, we therefore chose to merge them into a single habitat type to avoid the shortcomings of having null values in the input matrices (see Data analysis section below). Moreover, although open pastures differ from shrubs in structure, both are completely distinct from the other forested anthropogenic habitat (exotic plantation) available in the landscape. This landscape classification resulted in 2,855.23 ha evaluated within the MSC, of which 19.96% corresponded to Secondary forest remnants, 9.24% to Restored areas, 18.39% to Exotic forest plantations, 8.53% to Early successional forest remnants, and 43.87% corresponded to Anthropogenic land use (Fig. 1).

2.3. Capture and handling of bats

Each sampling session involved capture, marking and monitoring of *C. perspicillata* and *A. lituratus* individuals, and lasted from 8 to 15 days. Bats were captured in the restored forest patches with mist nets, and we avoided sampling during the full moon phase or on nights of intense rain. Only non-reproductive adults were selected to be included in our radiotracking surveys for standardization purposes, avoiding specific age or reproductive-related behaviors

Captured bats were placed in individual cloth bags and taken to a field laboratory, where we performed identification and biometric procedures. A radio transmitter with a unique signaling frequency (Models BD2 and LB-2C – Holohil Inc., Canada) was affixed to the back of each bat with surgical adhesive (Skinbond®) after partial trimming of the middorsal hair between the scapulae. Radio-tagged bats were then released close to the capture site within 2 h after capture. Transmitter mass varied between 0.75 and 1.95 g depending on the body mass of each individual, resulting in the transmitter weighing <6% of the bafs weight . Radio-telemetry data were not recorded on the night of release to avoid bias resulting from the handling of individuals.

2.4. Radiotelemetry

We conducted five sampling sessions, three in the rainy season (October 2007, February and April 2008) and two in the dry season

L.C. Trevelin et al./Forest Ecology and Management 291 (2013) 136-143

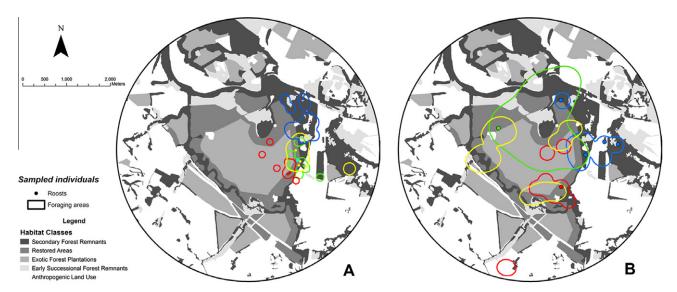


Fig. 1. Maps of the study area, highlighting Parque São Marcelo and its insertion in the surrounding landscape (MSC). We depict in the maps examples of foraging areas (contours estimated by 95% fixed kernel method) and day roosts (points) of (A) three Carollia perspicillata individuals and (B) three Artibeus lituratus individuals. Each color represents a different individual (replicate).

(July 2007 and August 2008). We marked twelve individuals of each species, and the number of sampled individuals was approximately balanced between seasons (see Table 1 for detailed information). For each monitored individual we followed a sampling protocol in order to standardize sampling regime over time: each sampling night was sub-divided into four 3-h intervals, starting at 18 h and ending at 06 h of the next day; during each interval, the entire study area was covered using a vehicle to search for marked individuals. Each individual was monitored for all four intervals and flight routes and range areas were obtained through mapping of successive locations and roost fixes. The procedure of

standardizing sampling regime over time allows inference regarding habitat use in situations where the number of location fixes differs among individuals (replicates) (Börger et al., 2006). Usually, two or three individuals were simultaneously monitored every night, and sampling always alternated among all individuals during each interval. Within the constraints imposed by the battery life-time, we were able to monitor each individual in the length of time required to sample all four intervals in a balanced way.

We performed active searches for the signal and used triangulation techniques to obtain locations (Jacob and Rudran, 2003) using a radio-receiver model *TR-5* (*Telonics Inc.*) coupled to a two-

Table 1Summary of results obtained per species. KF 95% – Fixed Kernel estimates of range use with 95% of samples; % Use – Percentage of foraging area composed by the Restored Area habitat; Commuting distance – Mean distance traveled between roosting and foraging areas. Individuals insufficiently sampled for analysis are highlighted in bold.

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Species/individuals	Sex	Season	Days sampled	Obtained locations	Day roosts	KF 95% (ha)	% Use	Commuting distance (m)
Carollia perspicillata								
1	Female	Dry	4	58	0	29.63	46.27	_
2	Male	Dry	5	31	1	16.33	29.84	722.2
3	Male	Wet	3	6	0	_	_	=
4	Male	Wet	4	23	2	15.38	23	495.9
5	Male	Wet	4	25	1	54.43	14.29	617.6
6	Female	Wet	7	21	2	17.47	38.2	198
7	Male	Wet	5	16	2	23.84	29.45	262
8	Female	Wet	6	19	1	26.85	49.61	357.7
9	Female	Wet	7	17	2	45.107	25.38	299.1
10	Female	Dry	8	27	1	40.17	28.33	958.7
11	Female	Dry	4	17	0	79.15	37.8	=
12	Female	Dry	4	25	0	28.74	34.02	=
Mean ± SD						34.2 ± 19.4	32.3 ± 10.2	488.9 ± 262.1
Artibeus lituratus								
1	Female	Dry	6	17	4	73.64	17.98	788.1
2	Female	Wet	4	18	1	30.01	45.53	2053.2
3	Female	Wet	8	16	0	154.16	41.92	_
4	Male	Wet	5	27	2	57.35	44.11	2001
5	Male	Wet	3	15	0	6.7	-	_
6	Male	Wet	5	15	1	136.03	23.26	1295.6
7	Male	Wet	6	9	0		_	_
8	Male	Wet	3	17	0	172.18	35.77	_
9	Female	Wet	5	25	1	389.72	29.06	1076.2
10	Male	Dry	6	15	1	77.94	20.63	650.9
11	Male	Dry	8	20	1	61.53	30.88	987
12	Male	Dry	4	24	2	90.1	26.45	418.2
Mean ± SD						124.3 ± 103.8	31.56 ± 9.9	1158.8 ± 598.6

element Yagi antenna. Georeferenced locations were obtained with a GPS (model *E-Trex*, *Garmim*), and bearings to the nearest degree were taken with a compass. Triangulations were made using two or more consecutive bearings, and the time between bearings did not exceed a minute and half. As bats fly at great speed, sampling was done through tracking sessions in which from 6 to 18 consecutive bearings were taken. Many of these bearings were excluded, as animals were in flight and bearings did not intersect. Therefore, our sampling scheme focused on those locations that were being effectively used for feeding and roosting by bats (Albrecht et al., 2007; Mello et al., 2008; Loayza and Loiselle, 2008).

2.5. Food resource availability

To estimate food resource availability in the restored area, populations of the main plant species comprising the diet of both bat species were monitored for reproductive activity during all telemetry sessions (fruits of Cecropia pachystachya for A. lituratus, Solanum mauritianum for both species and infructescences of Piper aduncum - hereafter referred to as fruits - for C. perspicillata; Silveira et al., 2011). Fifteen individuals of each plant species were systematically selected (first two or three individuals encountered in each plot) for monitoring in seven plots within the restored area, resulting in an availability index (percentage of fruit bearing individuals in the population; activity index of Bencke and Morellato, 2002) for each sampling session. As some species bore fruit during the course of the study (C. pachystachya and S. mauritianum), indices were arranged in two groups according to activity levels above and below 50 percent of the population and these groups were used as the treatments for hypothesis testing.

2.6. Data analysis

To determine locations obtained through triangulation, we used Maximum Likelihood Estimator and Best Biangulation Estimators, after correcting for magnetic declination in all compass bearings, using the LOAS™ (Ecological Software Solutions, Inc.) program. Location data determined for each individual were incorporated into the ArcGis database, and all subsequent spatial analyses were done using the *Home Range Tools* extension (Rodgers et al., 2007).

We estimated the "range area" of each individual in this study, following the definition proposed by Kernohan et al. (2001), as the "extent of area with a defined probability of occurrence of an animal during a specified time period". We used fixed normal density kernel estimations (FK) with 95% kernel isopleths to delineate the range areas (Worton, 1989; White and Garrott, 1990). Following the recommendations of Seaman and Powell (1996), we used least-squares cross-validation (LSCV) to estimate the smoothing parameter (H). In addition to FK 95% for the whole dataset, we generated range area estimates that excluded the diurnal roost locations of each individual. This allowed for estimates of foraging areas, which were subsequently used in hypothesis testing.

To evaluate habitat selection by both species, we used compositional analysis (Aebischer et al., 1993), which, through log-ratio transformations of composition values (the sum of the proportions of used habitats, adding to 1), enables multivariate statistical models to be fitted to the data for appropriate hypothesis testing. This analysis uses individual animals as sampling units, and assumes that all bats have equal access to all habitats, which are available constantly throughout the sampling period. To determine if habitat usage was non-random, the mean of the proportions of habitats found in the range area determined for each individual was paired and compared to the proportion of habitats available in the studied landscape using Wilks lambda test. Further pairwise comparisons between habitat use and availability were made using standard *t* tests. In cases in which data did not meet the assumptions of

parametric statistics, randomization tests were used instead (Aebischer et al., 1993).

At first, habitat availability was determined inside a pre-defined sample of the landscape (MSC), where all bats were captured and we could cover the whole area looking for their locations. Habitat analyses always requires an arbitrary measure of habitat availability (Aebischer et al., 1993), and this was fundamental to the experimental design of our study since we could standardize sampling regime to all individual sampled (Börger et al., 2006). As a second, post hoc definition of habitat availability, we generated for each species a Minimum Convex Polygon (100%MCP) encompassing the pooled locations obtained for all individuals together. This approach aimed a better approximation of the true habitat availability for each species in the landscape. We then performed compositional analysis using 100%MCPs for each species. All compositional analysis were carried out using package "adehabitat" (Calenge, 2006) for program R (R Development Core Team, 2012).

Responses in movement patterns to the availability of food resources were evaluated through the use of parameters describing the use of the area by the bats, similarly to a study of *C. perspicillata* in French Guyana by Charles-Dominique (1991). In our study, we choose two parameters that represent a standardized description of the bat's movements using the restored area as a reference: (1) % Restored Area Used, which represents the proportion of the range area of each individual corresponding to restored areas, and (2) Mean Commuting Distance, the average distance traveled by individuals between foraging areas and their day roosts. For each species, these parameters were calculated for each individual (replicate), and were then grouped accordingly to the fruit availability index described above as treatment for hypothesis test. Hypothesis testing was done using standard *t* tests, and Arc-sin transformations were applied to proportions.

3. Results

Ten individuals of A. lituratus and 11 of C. perspicillata were successfully sampled in all four intervals of the night and met all the required conditions to be included on the analysis. Sampling lasted an average of five days (5.33 ± 1.49) for each individual. We sampled a total of 503 locations, and the mean number of locations obtained per individual was 25.4 ± 10 for *C. perspicillata* and 19 ± 4.4 for A. lituratus. Initial exploratory analysis did not indicate a significant relationship between the size of estimated range areas and the number of locations obtained for either C. perspicillata $(r^2 = 0.087; p = 0.378)$ or A. lituratus $(r^2 = 0.021; p = 0.692)$. There was also no significant relationship between estimated range areas and sex for either *C. perspicillata* (t = 1.183; d.f. 9; p = 0.267) or *A.* lituratus (t = 0.817; d.f. 8; p = 0.437) and seasonality did not significantly affect the size of estimated range areas for individuals of either species (*C. perspicillata*: t = 0.456; d.f. 9; p = 0.658; A. lituratus: t = -1.447; d.f. 8; p = 0.185). Due to the small number of sampled individuals, we were unable to test the interaction between these variables. Nevertheless, the results obtained from these exploratory analyses legitimated the pooling of individuals as replicates for all subsequent analyses. Table 1 summarizes the results obtained for each individual, and Fig. 1 illustrates estimated range areas. Accumulation curves as a function of obtained locations can be found in the Supplementary material section online (Figs. SM1 and SM2).

3.1. Habitat selection

Compositional analysis revealed a significant difference in the composition of habitats comprising the range areas of both species in comparison to that available within the study area (*C. perspicillata*: Wilks λ = 0.0039; d.f. 4; p < 0.001, randomization p = 0.004; and A. lituratus: Wilks λ = 0.0587; d.f. 4; p < 0.001). The same patterns emerged when we used habitat availability based on specifics 100%MPCs in the analyses (*C. perspicillata*: Wilks λ = 0.0769; d.f. 4; p < 0.001, randomization p = 0.004; and A. lituratus: Wilks λ = 0.0805; d.f. 4; p < 0.001).

For both species, observed patterns also remained similar between analysis when comparing specific habitats through pairwise comparisons, and we ranked habitat preferences based on 100%MPCs compositional analysis. *Carollia perspicillata* showed a significant preference for *Restored areas*, also using *Secondary forest remnants* and *Exotic forest plantations* more often than expected, although use was not significantly different between the latter two habitat types. Together, these three habitats represented 84.75 % of the used habitats. *Early successional forest* and *Anthropogenic land use* were less frequently used than expected based on their availability on the landscape, accounting for only 15.25% of use (Fig. 2 and Table SM1).

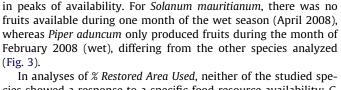
For *A. lituratus*, the *Restored areas* were also used significantly more frequently than any other habitat. There was, however, an inversion in the order of use of the following habitats, with *Exotic forest plantations* more significantly used than *Secondary forest remnants*. In fact, in this case, *Secondary forest remnants* was used in the same frequency than expected by its availability on the landscape, differing from the results obtained for *C. perspicillata* (Fig. 2). The other habitats, *Early successional forest* and *Anthropogenic land use*, were used significantly less frequently than expected based on their availability. They were also significantly less used than *Exotic forests* and *Secondary forests*. (Fig. 2 and Table SM2).

3.2. Roosting

The use of habitat for day roosting by both species was directed towards two specific habitats: Secondary forest remnants and Restored areas. In fact, we could not found roosts in any of the other habitats. Of the 11 day roosts found for eight Carollia perspicillata individuals, six were found in Secondary forest remnants, while the other five were in Restored areas. Similarly, for Artibeus lituratus, of 13 day roosts also found for eight individuals, nine were found in Secondary forest remnants, while the other four were in Restored areas. When more than one day roost was found for the same individual of either species, they were always found in the same habitat. In all the locations, bats were found roosting in the foliage of trees.

3.3. Responses to food resource availability

The overall fruit production of plant species that comprise the diets of the bats was continuous, with some species alternating



In analyses of % Restored Area Used, neither of the studied species showed a response to a specific food resource availability; *C. perspicillata* showed no significant response to the availability of *S. mauritianum* (t = 0.09; d.f. 5; p = 0.205) or *P. aduncum* (t = 1.394; d.f. 9; p = 0.098), and *A. lituratus* showed no significant response to the availability of *S. mauritianum* (t = 0.457; d.f. 8; p = 0.33) or *C. pachystachya* (t = 0.984; d.f. 8; p = 0.177). However, with Mean Commuting Distance as a proxy for movement patterns, *C. perspicillata* presented a significant reduction in response to the availability of *P. aduncum* (t = -2.293; d.f. 6; p = 0.031; Fig. 4), a pattern not observed in relation to fruit production of *S. mauritianum* (t = 4.04; d.f. 6; p = 0.997). Artibeus lituratus still showed no response to fruit production of *S. mauritianum* (t = -0.069; d.f. 6; t = 0.474) or *C. pachystachya* (t = 0.216; d.f. 6; t = 0.966).

4. Discussion

The success of restoring degraded lands depends, to a large extent, on how these habitats manage to recover faunal populations (Bowen et al., 2007). The present study provides evidence that suggests a potential recovery by populations of two frugivorous bat species in a restored area in southeastern Brazil. We found a consistent pattern toward the use of forest-structured habitats by both species, revealing the use of restored forests as main foraging and roosting habitat for individuals of *A. liturarus* and *C. perspicillata*. Although bats were not restricted to them, these habitats were more frequently used than predicted by their availability, alongside with the other forest-structured habitats available in the land-scape. The positive selection of specific habitats to forage and rest implied by our results shed light on the relative value these habitats have for the bats (Palminteri and Peres, 2012) and, consequently, to the whole recolonization process.

Both species strictly used forested habitats for day roosting, mainly using the foliage of trees located in *Secondary forest remnants* and, in some cases, in the *Restored areas*. Several studies show that roost availability is a occurrence-limiting resource in the landscape for bats (Kunz, 1982; Aguirre et al., 2003), and our findings corroborate this since both species were very specific in habitat requirements for roosting. Furthermore, our data suggest that forest remnants (mostly riparian forests) act as a source of new colonist species and individuals (Turner and Corlett, 1996; Lindenmayer et al., 2008), assisting the gradual recolonization of restored areas. A similar pattern of habitat selection was observed

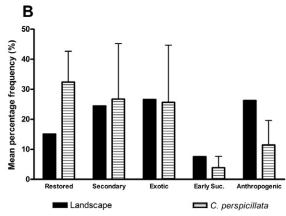


Fig. 2. Relationship between habitat use by Artibeus liturartus (A) and Carollia perspicillata (B) (as observed in the range area of both species) and habitat availability in the landscape used by each species (accessed with 100%MCP – see text for description).

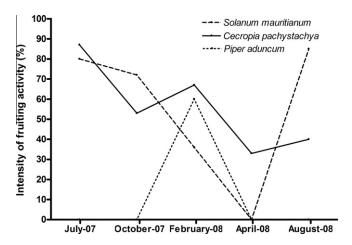


Fig. 3. Estimates of fruit availability of the three plant populations identified as major items in the diet of both bats species in the study area.

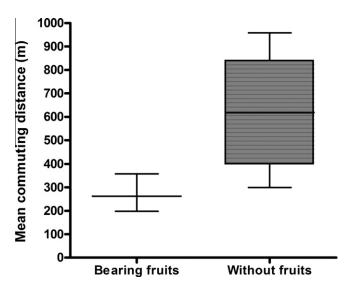


Fig. 4. Box-plot comparing mean commuting distance from roosts to foraging areas for *Carollia perspicillata* between periods with and without the presence of ripe fruits of *Piper aduncum* in the population.

in foraging movements, with *Restored areas* being the most frequently used foraging habitat for both species. Both these aspects of our data represent evidence that the restored forest habitat is contributing to the persistence of *A. lituratus* and *C. perspicillata* populations in the landscape and extending their distribution. However, determining whether these habitats act as sources or sinks, requires long-term demographic studies (Bowen et al., 2007; Lindell, 2008).

In addition, the *Exotic forests* habitat was also intensely used during movements. Primarily composed of commercial *Eucalyptus* plantations, this habitat was used in the same proportion as *Secondary forest remnants* by *Artibeus lituratus*. Some studies on Neotropical bat assemblages have shown recolonization as dependent on the nature of matrix selectivity (Cosson et al., 1999; Albrecht et al., 2007; Meyer and Kalko, 2008), and few evaluate the importance of these forest plantations and other structurally similar land covers as habitat for bats (see Faria et al., 2006; Barlow et al., 2007; and also Borkin and Parsons, 2010, 2011 for studies in New Zealand). Compared to other anthropogenic land covers, our data confirms that these forests plantations are used at least for movements by these bats, suggesting they may enhance connectivity in the landscape and facilitate recolonization of newly

restored forests, as long as associated to source habitats (Brockerhoff et al., 2008). Further studies are needed to confirm these observations.

4.1. Responses to the availability of food resources

Our roosting behavior data supports our hypothesis that the availability of fruit is determinant in the use of restored forests by *C. perspicillata*. They reduced commuting distance by roosting closer to their feeding area (restored areas) as response to the availability of *Piper aduncun*'s infructescenses in this habitat (Fig. 4). Other studies have demonstrated similar behavior and suggest that *Carollia* actively selects *Piper* species whilst foraging (Fleming and Heithaus, 1986; Thies and Kalko, 2004; Bianconi et al., 2012).

On the other hand, we failed to support other predictions related to direct responses in the use of restored areas, for roosting by A. lituratus and for foraging by both species, to the availability of each specific food item in these habitats. This non-direct relationship between the availability of specific food items and foraging movement in restored areas could indicate that they may be responding to food availability in other habitats of the landscape. While this is a valid alternative explanation, we have confirmed that Restored areas are being used as their main foraging area (this study and Silveira et al., 2011). Considering that overall availability of food resource was relatively constant (fruiting plant species alternated but maintained overall production; Fig. 3), it is feasible to assume that constant use of the restored area for foraging reflects this constancy in overall food availability. Studies in several locations have shown feeding plasticity for both species (Galetti and Morellato, 1994; Passos et al., 2003; Mello et al., 2004; Silveira et al., 2011), despite of the purported "preferences" known to phyllostomid (Mello et al., 2011). Our results may demonstrate how this plasticity reflects on foraging behavior (Fleming and Heithaus, 1986) and, consequently, on the use of the restored areas, as we initially hypothesized. In a recently restored area, where most planted species are not mature enough to bear fruits, these bat species are adapting their diets to what is available, and, consequently, using space accordingly. From the restoration viewpoint, these plant species are effective in continuously attracting and retaining these frugivores, contributing to the initial recovery of the fauna in this area (Silveira et al., 2011).

4.2. Movement patterns

There is a lack of studies directly estimating home-range or range areas for A. lituratus, but some studies report movements over large distances (Morison, 1980; Menezes Jr. et al., 2008) as well as low fidelity to local forest patches (Bianconi et al., 2006). It is suggested that large Artibeus species have large range areas (Morison, 1978; Handley et al., 1991; Costa et al., 2006) usually attributed to feeding preferences for plant species that produce abundant fruit crops over short time periods, generally occurring in low densities over large areas (particularly Moraceae of the genus Ficus - Handley et al., 1991; Galetti and Morellato, 1994; Passos et al., 2003). In the present study we confirmed the magnitude expected for range areas (Morison, 1980; Handley et al., 1991), sampled individuals were never restricted to a single patch, and only on a few occasions would they repeat the same pattern of space use during sampling days, normally alternating use between forest patches present in the landscape. On the other hand, most individuals simply flew out of the MSC, indicating that the values we presented for range area may be underestimates of the actual range area of this species.

Carollia perspicillata is a small frugivore whose feeding preferences are concentrated on plant species with low density fruit

crops every night but high spatio-temporal predictability (Marinho-Filho, 1991; Thies and Kalko, 2004). This species usually presents restricted range areas because of the constant short flight bouts in search of food that would minimize energetic costs of commuting and foraging (Fleming and Heithaus, 1986; Henry et al., 2007; Bonaccorso et al., 2007). In this study, sampled individuals were indeed highly predictable, repeating movement patterns each night, and approximately three nights were enough to reveal a great portion of their range areas, as observed in previous studies (Charles-Dominique, 1991; Bernard and Fenton, 2003). However, 32 ha estimates of average range area and a 958 m maximum commuting distance are substantially higher than those reported by Bonaccorso et al. (2007) in continuous primary forests. Maximum flight distances for C. perspicillata in fragmented landscapes (Bianconi et al., 2006; Meyer and Kalko, 2008) and a home range study by Bernard and Fenton (2003) in a naturally fragmented landscape north of Brazil also found much larger values (i.e. up to 320 ha of range area).

4.3. Implications for ecological restoration

The common strategy of attracting fauna to revegetated stands by planting species that promptly improves fruit availability and structural complexity of vegetation providing food and shelter (Wunderle Jr., 1997; Martínez-Garza and Howe, 2003; Dewalt et al., 2003; Munro et al., 2009) has been generally supported by our results. Restored patches are clearly an important habitat, used for feeding and roosting by A. lituratus and C. perspicillata only five years after the restoration effort. The movement patterns we uncovered, when combined with data on diet from Silveira et al. (2011), allowed us to understand both sides of the relationship established between restored patches and frugivorous bats. Both studies suggests that: (1) frugivorous bats readily colonize restored areas, particularly in the initial stages of restoration when other potential seed dispersers would be limited in their ability to colonize; (2) they create the possibility to augment the species diversity of the anthropogenic planting with their own natural seed dispersal (Silveira et al., 2011), promoting biological connection of plant populations between habitat patches that are otherwise physically disconnected (Pizo and dos Santos, 2011).

Our research highlights the benefits of restoration techniques that make habitats attractive to early colonists. Our data shows that the existing native forest remnants near to the restored areas were critical roosting habitats for *A. lituratus* and *C. perspicillata*, setting up the conditions for these colonization events to occur. Restoration initiatives need to be aligned with public policy that guarantees biodiversity conservation on a regional scale, ensuring the maintenance of these source habitats on the landscape. When this synergy is achieved, region-wide results can be as positive as those presented in this study. The methodology used here was satisfactory for gathering this information, and its replication is encouraged in other restored areas for data comparison.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.11. 013.

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