Movements of bats (Mammalia, Chiroptera) in Atlantic Forest remnants in southern Brazil

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ABSTRACT. We used mark and recapture techniques to evaluate movements of bats within and between three brazilian forest remnants. We captured bats with mist-nets in four 1 ha plots representing different degrees of isolation of riparian (two plots) and submontane (two plots) forests between July 2002 and June 2003. Using numbered aluminium tags, we marked 635 bats of seven species and 54 individuals of six species were recaptured. Overall, we recaptured *Carollia perspicillata* (Linnaeus, 1758) (short-tailed fruit bat) most frequently, especially in plots where they were banded in the riparian forest plots. These results suggest that this bat has restricted feeding areas, which are probably determined by the abundance of *Piper* Linnaeus (Piperaceae), its preferred food item. In contrast, species of the genus *Artibeus* Leach, 1821 exhibited few recaptures, suggesting high mobility and larger feeding areas. In fact *Artibeus* seems to use more of the forest remnants in their search for food, especially *Ficus* Linnaeus (Moraceae), the preferred food of this bat. Our results suggest that even small forest isolates are valuable for the maintenance of some bat species because they offer many of the resources they need or because they are spatially distributed in a pattern that allows use of the entire landscape.
KEY WORDS. *Artibeus*; *Carollia perspicillata*; foraging behavior; forest fragmentation; mark/recapture.

RESUMO. **Deslocamentos de morcegos (Mammalia, Chiroptera) em remanescentes de Floresta Atlântica no sul do Brasil.** Nós utilizamos a técnica de marcação-recaptura para avaliar os deslocamentos de morcegos dentro e entre três fragmentos florestais do sul do Brasil. Entre julho de 2002 e junho de 2003, os animais foram capturados com redes-de-neblina instaladas em quatro parcelas de 1 ha, que representavam diferentes graus de isolamento das subformações florestais, aluvial (duas parcelas) e submontana (duas parcelas). Utilizando anilhas metálicas numeradas, nós marcamos 635 morcegos de sete espécies e recapturamos 54 indivíduos de seis espécies. A maior freqüência de recaptura foi obtida para *Carollia perspicillata* (Linnaeus, 1758), especialmente nas parcelas de origem representadas pela floresta aluvial. Os resultados sugerem que este frugívoro apresenta uma área restrita de forrageio, determinada provavelmente pela abundância de *Piper* L. (Piperaceae), planta reconhecida como seu alimento preferencial. Em contraste, espécies do gênero *Artibeus* Leach, 1821 exibiram uma baixa freqüência de recaptura, sugerindo alta mobilidade e grande área de forrageio, provavelmente relacionada à exploração conjunta dos fragmentos da região na busca por recursos, em especial *Ficus* L. (Moraceae), seu alimento preferencial. Nossos resultados sugerem que mesmo pequenos fragmentos florestais são valiosos para a manutenção de algumas espécies de morcegos, seja por oferecerem muitos dos recursos que eles necessitam ou por estarem espacialmente dispostos de forma a facilitar a utilização conjunta da paisagem.
PALAVRAS-CHAVE. *Artibeus*; *Carollia perspicillata*; comportamento alimentar; fragmentação florestal; marcação e recaptura.

Fragmentation and isolation of natural habitats are the main threats to regional and global biodiversity (Noss & Csuti 1997) because they result in several consequences to the fauna, including alteration at the community level and local to regional extinctions (Lovejoy *et al.* 1984, Andrén 1994, Robinson & Robinson 1999, Stratford & Stouffer 1999). In this context, the mobility of a particular species has major implications for its survival (Kozakiewicz & Szacki 1995, Yabe & Marques 2001), besides being ecologically relevant because seed and pollen dispersers can influence the spatial distribution and genetic structure of plants (Fenton *et al.* 1992, Garcia *et al.* 2000, Slauson 2000). Some patterns of movements represent ecological and evolutionary responses that are excellent tools for the development of biological models (Heithaus & Fleming 1978, August 1981, Merriam 1995, Andrade & Marini 2001, Estrada & Coates-Estrada 2002). These patterns, which are determined by the structure of the habitat as well as by behavioral patterns of each species (Graham 2001), are particularly noteworthy in some mammalian groups. As an example, bats are the only mammals that fly, which enables them to explore the habitat in a complex way (Fenton 1992), resulting in regular local (short distance) and seasonal (long distance) movements (Trajano 1996).

Some authors suggest that bat movements are closely related to the availability of habitat resources, especially food and roosts (Heithaus & Fleming 1978, Fleming & Heithaus 1986, Fleming 1991). Since forest fragmentation and isolation tend to reduce the abundance and to modify the spatial distribution of these resources in the landscape, foraging patterns and habitat use by bat species are modified by these processes (Estrada & Coates-Estrada 2002, Evelyn & Stiles 2003, Quesada *et al.* 2004).

Although in the last decades a number of papers on the movements of small mammals have been published (*v.* Kozakiewicz & Szacki 1995), such information is unknown for most bat species (Marques 2003). In fact, even where studies on the mobility patterns of Chiroptera have been in progress for many years (Costa Rica – Heithaus *et al.* 1975, LaVal & Fitch 1977, Heithaus & Fleming 1978, Fleming & Heithaus 1986, Fleming 1988, 1991; Mexico – Morrison 1978, Estrada *et al.* 1993, Estrada & Coates-Estrada 2002; Panama – Bonaccorso 1979, Handley *et al.* 1991), there is still the need for further information in order to improve conservation efforts locally.

A significant part of the available literature regarding foraging movements, habitat use, migration, and home range refers to Old World bats (Jong 1994, Racey 1998, Winkelmann *et al.* 2000, Hoyle *et al.* 2001). In the New World, these studies are concentrated in North America (Clark *et al.* 1993, Brigham *et al.* 1997, Betts 1998, Estrada & Coates-Estrada 2002) and Central America (LaVal & Fitch 1977, Heithaus & Fleming 1978, Handley *et al.* 1991), while in South America they hardly have been done (but see Lemke 1984, Ruiz *et al.* 1997, Cosson *et al.* 1999). In countries like Brazil, which lacks basic information on the natural history of its bats (Marinho-Filho & Sazima 1998), available information on bat movements is even less extensive. A few notable exceptions include Trajano (1996), who studied bat movements among caves of southeastern Brazil and Bernard & Fenton (2003), who investigated bat movements among natural forest fragments in Central Amazonia. Additionally, there are isolated records of the distances travelled by species in Rio de Janeiro State (Esbérard 2003).

Considering the lack of information on the movements of bats among non-Amazonian forest fragments and the need of information on local assemblages due to the differencial response of species depending on particular characteristics of each region, we designed the present study. Herein, we present the first results of a long-term to be bat banding study that is being conducted in Atlantic Forest remnants of Parana State, southern Brazil, in order to investigate habitat use and movement patterns of species that live in highly fragmented forest habitats.

MATERIAL AND METHODS

Study area

The forest fragments we studied are located near the town of Fênix, Paraná State, southern Brazil (Fig. 1). The climate of the region is classified as mid-latitude humid subtropical or C*fa* (Köppen). Average annual temperature varies between 16 and 25ºC (Mikich & Oliveira 2003) and average annual rainfall ranges from 1 400 to 1 500 mm. The wet season occurs between December and March and there is no clearly defined dry season (Maack 1981). The study region is covered by the Atlantic Forest, more specifically by Semideciduous Seasonal Forest (*sensu* Veloso *et al.* 1992), that can be divided into two types or habitats according to the distance and influence of large rivers. The alluvial or riparian forest (RF) is associated with the rivers and is seasonally or occasionally flooded, and the submontane forest (SF) occupies large areas away (> 300 m) from the main rivers and is not directly influenced by them.

At present, the study region, which was once covered by continuous forest, holds few forest isolates up to 800 ha surrounded by huge areas of agriculture (especially corn and soybean) and largely destroyed riparian forests. The limits of the forest fragments with the cultivated areas that surround them are very abrupt, with no buffer zone, and the fields themselves have no bushes or trees. A detailed description of the general vegetation of the study area, as well as species composition and phenological data, can be found in Mikich & Silva (2001). However, here it is important to emphasize that some characteristics, as plant species composition and phenology, type and intensity of past forest exploration, past and present use of soil between the fragments (matrix), are all similar among the studied fragments (Mikich & Silva 2001, Mikich & Oliveira 2003).

Sampling plots

Four sampling plots of 1 ha (100 x 100 m) were established inside three forest remnants: two in the Parque Estadual Vila Rica do Espírito Santo (F1 and F2), one in Fazenda Cagibi (FC) and one in Fazenda Guajuvira (FG) (Fig. 1). The nearest plots were F1 and F2, which were 1.2 km apart, and the most distant plots were F1 and FC, which were 4.9 km apart.

Parque Estadual Vila Rica do Espírito Santo (23º55'S, 51º57'W) is a nature reserve surrounded by cultivated areas and by the Ivaí and Corumbataí rivers (Fig. 1). Most of its 354 ha are covered by one of the oldest (more than 370 years) secondary forests in Paraná State (C.V. Roderjan, pers. comm.) and is similar in species composition and structure to slightly disturbed primary forests located in the same region (Mikich &

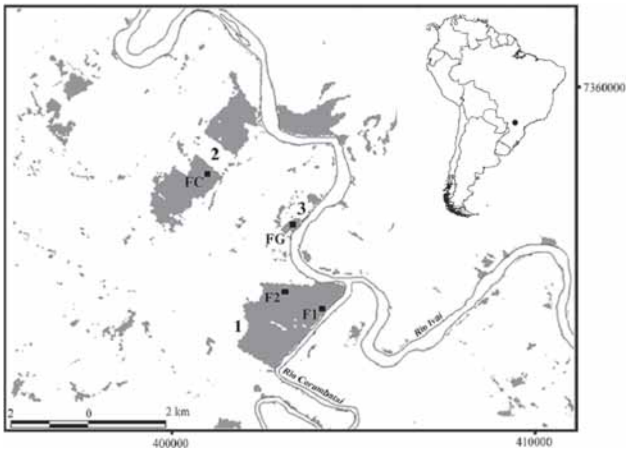

Figure 1. Location of the study plots set inside three Atlantic Forest remnants at Fênix, Parana State, southern Brazil. Legend: 1. Parque Estadual Vila Rica do Espírito Santo (F1 and F2 plots), 2. Fazenda Cagibi (FC), and 3. Fazenda Guajuvira (FG).

SILVA 2001). Since this reserve is bordered by two large rivers, it has extensive areas of RF, in addition to the SF. These two forest habitats have a contact zone approximately 3 km long. The RF, where F1 plot is set, is approximately 100 ha and extends inland for almost 300 m from the Ivaí and the Corumbataí rivers. This plot has soil with deficient drainage in some places and is open (30% coverage), with a 12 m high tree canopy. The medium (5-6 m) and the lower forest strata (1.2-2 m) also are not dense (40 and 30% coverage, respectively). The second plot (F2), set in SF, has a denser (40%) and higher (16-18 m) canopy with some individuals reaching 25 m, the sub-canopy level is also not dense, with treelets up to 6 m high.

Fazenda Cagibi (23º55'S, 51º57'W) contains 325 ha of forest divided into two blocks of different shapes and sizes (Fig. 1). It is surrounded by cultivated and pasture lands, and adjacent to the Ivaí River which runs along a small part of one forest block. There are some signs of human disturbances, mainly due to past timber exploration (MIKICH & SILVA 2001). The sampling plot (FC) was set in the forest block (184 ha) covered exclusively by SF. This plot has a denser canopy (13-14 m, up to 50% coverage) than the other ones, with several trees up to 20 m high, the medium strata is approximately 8 m high with 50% coverage, the lower strata, which is composed of bushes and herbs, ranges from 0.7 to 1.3 m high.

Fazenda Guajuvira (23º53'S, 51º57'W) is located between the other two study sites and is covered almost exclusively by secondary or disturbed primary RF. It has 24 ha divided into two portions of similar shapes and sizes and is bordered by cultivated land, pastures, and the Ivaí River (Fig. 1). The forest portion where the fourth plot (FG) was set is 14 ha, and like the RF in the Parque Vila Rica, it also extends for approximately 300 m from the Ivaí River. This plot is relatively open (30-40% coverage), 12-14 m high and has an extensive number of lianas and vines over the canopy trees. The understory has 60% coverage and is 2 m high.

Capture and banding

From July 2002 to June 2003 we netted each plot for two nights per month. The bats were captured using 10 mist-nets (12 x 2.5 m), set in the same position, end to end, in the middle of each plot along a single trail opened for this work. Nets were opened at sunset and checked every 20 minutes for six hours. Capture effort did not change among plots, with 43 200 m^2.h / plot (totalling 172 800 m^2.h), calculated according to STRAUBE & BIANCONI (2002), i.e. multiplying the area of each net by the time they remain exposed in the field by the number of repetitions by the number of nets. Following capture, all bats were identified, their forearms marked with numbered aluminum rings (Etiquetal®), and finally, released at the capture site. We calculated the "minimum" flight distances for each species based on recaptures in different plots and the linear distances between them.

Species identification followed GOODWIN & GREENHALL (1961), VIZOTTO & TADDEI (1973), BARQUEZ *et al.* (1993), and SIMMONS & VOSS (1998), and the taxonomic arrangement followed SIMMONS (2005). Specimens that could not be identified in the field were collected, preserved in alcohol (PETERSON 1965) and deposited in the Museu de História Natural Capão da Imbuia in Curitiba, Paraná State, Brazil.

RESULTS

Banding and recapture

We captured and banded 635 individuals of seven bat species of which 54 individuals (8.5% of all banded bats) of six species were recaptured. Most banded individuals belonged to two species: *Artibeus lituratus* (Olfers, 1818) (great fruit-eating bat) (387 marked) and *Carollia perspicillata* (Linnaeus, 1758) (short-tailed fruit bat) (114), the others included *A. fimbriatus* Gray, 1842 (fringed fruit-eating bat), *A. jamaicensis* Leach, 1821 (jamaican fruit-eating bat), *Sturnira lilium* (E. Geoffroy, 1810) (little yellow-shouldered bat), *Chrotopterus auritus* (Peters, 1856) (woolly false vampire bat) and *Desmodus rotundus* (E. Geoffroy, 1810) (common vampire bat) (Tab. I).

Table I. Banded and recaptured bat species between July 2002 and June 2003 in four 1 ha Atlantic Forest plots located near the small town of Fênix, Paraná State, Brazil. (Al) *Artibeus lituratus*, (Af) *Artibeus fimbriatus*, (Aj) *Artibeus jamaicensis*, (Sl) *Sturnira lilium*, (Cp) *Carollia perspicillata*, (Dr) *Desmodus rotundus*, (Ca) *Chrotopterus auritus*.

	Al	Cp	Af	Aj	Sl	Dr	Ca
Banded individuals	387	114	52	40	38	2	2
Recaptured individuals	11	30	5	3	3	2	0
Percentage of recapture (%)	2.8	26.3	9.6	7.5	7.9	100	0

The highest recapture rates were obtained for *D. rotundus* (100%, n = 2) and *C. perspicillata* (26.3%, n = 30). For the other species, except *C. auritus* (which was not recaptured), values ranged from 2.8% for *A. lituratus* to 9.6% for *A. fimbriatus* (Tab. I). There were only two double recaptures, both for *C. perspicillata* and in the same banding plot (FG and F1).

Recaptures per plot

Carollia perspicillata exhibited the highest percentage of individuals recaptured in the same plot where banding took place (18.7%), especially in plots located in the RF (F1 and FG) (Tab. II). Other species exhibited lower recapture rates for the plots in which individuals were first captured.

Movements among plots

Seventeen movements among plots were recorded for five species: *A. lituratus* (n = 5), *A. fimbriatus* (n = 2), *A. jamaicensis* (n = 1), *C. perspicillata* (n = 7) and *D. rotundus* (n = 2). Four of these movements occurred between the two plots located inside the Parque Vila Rica (F1 and F2, *A. fimbriatus, A. jamaicensis, C. perspicillata, D. rotundus*) and 13 among the different forest fragments, except between the Fazenda Cagibi and the Fazenda Guajuvira (all species except *D. rotundus*). Based on the linear distances between plots, we obtained the distances travelled by the five recaptured species. *Artibeus lituratus* showed the highest value (4.9 km), followed by *C. perspicillata* and *A. fimbriatus* (3.7 km), *D. rotundus* (1.6 km) and *A. jamaicensis* (1.2 km).

DISCUSSION

We observed elevated recapture rates within and between our sample areas for a few species during one year of sampling. According to FLEMING (1988), elevated recapture rates suggest limited feeding areas and high site fidelity. Two species, *D. rotundus* and *C. perspicillata*, had high recapture rates in the forest fragments we studied. Even though *D. rotundus* had the highest rate, we did not use it in our comparisons because of the low number of banded individuals (n = 2). *Carollia perspicillata* had the highest recapture rate, especially in the banding plots of the riparian forest, suggesting the highest fidelity to the sample area of all other recaptured species. Given that it was the second most common species (114 individuals marked), and the one recaptured most (30 recaptures), *C. perspicillata* seems to be able to use relatively small and narrow forest fragments, like the sampled portion (14 ha) of the Fazenda Guajuvira.

Carollia perspicillata feeds mainly in the mid level of the forest ("understory frugivores", *sensu* BONACCORSO 1979) (FLEMING 1988, COSSON *et al.* 1999, STOCKWELL 2001) where fruit-bearing shrubs such as the genus *Piper* L. (Piperaceae), its prefered food item (BONACCORSO 1979, FLEMING 1988, PALMEIRIM *et al.* 1989, MELLO *et al.* 2004) are usually common. In fact, at least nine *Piper* species occur in the study sites, and six of them are common or abundant in the understory. Furthermore, different species of *Piper* in our study area bear fruit sequentially so that this resource is available all year round (MIKICH & SILVA 2001). Based on this information, we speculate that this bat species in our study area does not need to move far to find food, and therefore has small feeding areas.

This strong association between the feeding behavior of *C. perspicillata* and the distribution of food has been examined in previous studies in Costa Rica (HEITHAUS & FLEMING 1978, FLEMING & HEITHAUS 1986, FLEMING 1991). These authors suggested that fruit availability is the main factor influencing the foraging behavior of this bat species based on high frequencies of recapture at the same places. Because the diet of *C. perspicillata* includes several fruit species, especially those of the genus *Piper*, there is a continuous replacement of availability and abundance of fruit species locally (HEITHAUS & FLEMING 1978).

Even though we know that the forest fragments have nine *Piper* species commonly distributed along inner roads and trails, as well as along forest edges (MIKICH & SILVA 2001), we do not yet know whether the RF plots had a higher density of these food resource compared to SF plots. Consequently, we cannot confirm that the supposed preference and higher fidelity to the RF by *C. perspicillata* is due to higher densities of *Piper*. Future studies must include both qualitative and quantitative inventories of potential food species in each forest type, as well as the collection of additional biological information on *C. perspicillata* in order to check this hypothesis.

For frugivores, if elevated recapture rates suggest fidelity to local areas (FLEMING 1988, PEDRO & TADDEI 1997), the opposite should be true when low rates are recorded. Compared to *C. perspicillata*, all other recaptured frugivore species had lower recaptures suggesting a possible higher mobility and a larger feeding area. *Artibeus lituratus*, for example, had the largest number of banded individuals (n = 387), but the lowest recapture rate (2.8%), especially in the banding plots (1.6%). Congeneric species, *A. fimbriatus* and *A. jamaicensis*, also exhibited low recapture rates in plots in which individuals were first captured (Tab. II).

Species of the genus *Artibeus* Leach, 1821 are considered feeding specialists at large fruiting trees ("canopy frugivores", *sensu* BONACCORSO 1979), especially the genus *Ficus* L. (Moraceae) (PALMEIRIM *et al.* 1989, HANDLEY *et al.* 1991, GALETTI & MORELLATO 1994). In fact, according to MIKICH (2002), these fruits are largely consumed by *Artibeus* spp., which seems to visit isolated *Ficus* trees with abundant fruit in the study area. The studied fragments have six species of *Ficus*, most rare or intermediate, i.e. represented by one or few individuals according to MIKICH & SILVA (2001). So, if we consider that *Ficus* are usually low density trees with low inter-tree synchrony in the production of large, short-lived fruit crops (MORRISON 1978, FLEMING & HEITHAUS 1981, BONACCORSO & GUSH 1987, COSSON *et al.* 1999), it is likely that the observed movements of *Artibeus* spp. are directly related to food locations in different forest fragments. In our study site these bats probably include different forest fragments or habitats in their daily feeding areas, in relation to the pattern of density and distribution of fruits, as observed in other studies (ESTRADA *et*

Table II. Percentage (and number) of individuals/species recaptured in the same plot of banding between July 2002 and June 2003 in Atlantic Forest fragments located near the small town of Fênix, Paraná State, Brazil. (Al) *Artibeus lituratus*, (Af) *Artibeus fimbriatus*, (Aj) *Artibeus jamaicensis*, (Sl) *Sturnira lilium*, (Cp) *Carollia perspicillata*.

Recapture plot (habitat type)	Bat species				
	Al	Af	Aj	Sl	Cp
F1 (Riparian forest)	1.1 (n = 1)	6.2 (n = 1)	10.0 (n = 1)	0 (n = 0)	24.2 (n = 8)
F2 (Submontane forest)	0.9 (n = 1)	7.1 (n = 1)	9.1 (n = 1)	0 (n = 0)	10.3 (n = 3)
FC (Submontane forest)	1.7 (n = 2)	7.1 (n = 1)	0 (n = 0)	14.3 (n = 2)	11.8 (n = 2)
FG (Riparian forest)	2.6 (n = 2)	0 (n = 0)	0 (n = 0)	25.0 (n = 1)	28.6 (n = 10)
Mean	1.6	5.1	4.8	9.8	18.7

al. 1993, Schulze *et al.* 2000, Estrada & Coates-Estrada 2002, Bernard & Fenton 2003). Morrison (1978) reported an increase in the distances travelled by *A. jamaicensis* on Barro Colorado Island whenever the availability of mature *Ficus* fruits was low.

Although *S. lilium* had the second highest recapture rate at the banding plot, suggesting a possible fidelity to the FG plot (which was covered by RF, Tab. II), the small number of recaptures does not allow us to confirm this hypothesis. As discussed for *C. perspicillata,* the continuation of this study could provide further information on this supposed movement pattern and/or habitat preference.

Regarding the "minimum" recapture distances reported here, we emphasize that such values do not represent daily movement patterns (which can only be obtained by radiotelemetry) or the maximum distance a single bat can fly, but they do contribute to the knowledge of the biology of these bats into this and other fragmented regions, as well as emphasize their behavioral flexibility in fragmented landscapes (other regions: Estrada *et al.* 1993, Wilson *et al.* 1996, Estrada & Coates-Estrada 2002, our region: Bianconi *et al.* 2004). Examining available data on the linear distances flown by different bat species (Heithaus & Fleming 1978, Trajano 1996, Cosson *et al.* 1999, Esbérard 2003) as well as telemetry data (Bernard & Fenton 2003), we found a wide range in published distancies, which is probably related to differential habitat use, including spatial and temporal distribution of resources (Bernard & Fenton 2003). As an example, we can mention the values obtained in Brazil by some authors, such as Esbérard (2003) for Rio de Janeiro State: *A. lituratus*-21 km, *A. fimbriatus*-25 km, *D. rotundus*-4.5 km and *S. lilium*-1.5 km, Bernard & Fenton (2003) for natural forest fragments of Central Amazonia: *C. perspicillata*-1.6 to 2.5 km, and Trajano (1996) for São Paulo State: *D. rotundus*-2.0 to 3.0 km. This information reinforces the dynamic nature of the exploratory behavior of bats, which is the product of different ecological and evolutionary pressures.

In disturbed landscapes forest fragments can be used by bats as shelters, as food sources or even as stepping stones to reach new habitats (Estrada & Coates-Estrada 2002). In our study area, although biologically impoverished if compared to intact forests, the results suggest that even small forest fragments, such as the Fazenda Guajuvira, with 24 ha, are valuable for the maintenance of some bat species. These fragments may offer many of the resources the bats need or because they are spatially distributed in a pattern that allows the use of the entire landscape, they may contribute to the maintenance of local and regional biological diversity.

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