

# Effects of Habitat Structure and Fragmentation on Diversity and Abundance of Primates in Tropical Deciduous Forests in Bolivia

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**Abstract** Habitat structure and anthropogenic disturbance are known to affect primate diversity and abundance. However, researchers have focused on lowland rain forests, whereas endangered deciduous forests have been neglected. We aimed to investigate the relationships between primate diversity and abundance and habitat parameters in 10 deciduous forest fragments southeast of Santa Cruz, Bolivia. We obtained primate data via line-transect surveys and visual and acoustic observations. In addition, we assessed the vegetation structure (canopy height, understory density), size, isolation time, and surrounding forest area of the fragments. We interpreted our results in the context of the historical distribution data for primates in the area before fragmentation and interviews with local people. We detected 5 of the 8 historically observed primate species: *Alouatta caraya*, *Aotus azarae boliviensis*, *Callithrix melanura*, *Callicebus donacophilus*, and *Cebus libidinosus juruanus*. Total species number and detection rates decreased with understory density. Detection rates also negatively correlated with forest areas in the surroundings of a fragment, which may be due to variables

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not assessed, i.e., fragment shape, distance to nearest town. Observations for *Alouatta* and *Aotus* were too few to conduct further statistics. *Cebus* and *Callicebus* were present in 90% and 70% of the sites, respectively, and their density did not correlate with any of the habitat variables assessed, signaling high ecological plasticity and adaptability to anthropogenic impact in these species. Detections of *Callithrix* were higher in areas with low forest strata. Our study provides baseline data for future fragmentation studies in Neotropical dry deciduous forests and sets a base for specific conservation measures.

**Keywords** Bolivia · Fragmentation · Habitat structure · Primates · Tropical deciduous forests

## Introduction

Two main effects determine primate diversity and abundance in a forest site: 1) structural variables of the habitat or habitat quality and 2) indirect and direct anthropogenic impacts (Brown *et al.* 1985; Chapman and Peres 2001; Rylands 1987). At a regional scale, the diversity and density of primates in natural forests, both in the Neotropics and elsewhere, are known to depend on primary forest productivity, precipitation, and climatic seasonality (Peres 1997; Pinto *et al.* 2009). More locally, different monkey species typically occupy different forest microhabitats, preferring different forest strata or forest types of different structure, e.g., liana thickets (Bobadilla and Ferrari 2000; Mittermeier and van Roosmalen 1981; Wallace *et al.* 1998).

In terms of anthropogenic impacts, habitat fragmentation and directly related problems such as timber extraction and hunting for food, pets, and artifacts are the main threats for primates (Chapman *et al.* 2003; Laurance *et al.* 2000; Mittermeier *et al.* 2005; Robinson and Redford 1991). This may lead to directional shifts in community composition, crowding tendencies, and altered sex ratios (Baranga 2004; Chiarello and De Melo 2001; Martins 2005; Peres 2001; Rode *et al.* 2006). Generally speaking, primate richness decreased with fragment size (Harcourt and Doherty 2005), but in some isolated relatively small forest patches (<50 km<sup>2</sup>) primate densities have been found to increase, possibly owing to the absence of main predators such as large cats and birds of prey (González-Solís *et al.* 2001), the density compensation phenomenon (Peres and Dolman 2000), and the ecological plasticity of some primate species (González-Solís *et al.* 2001). Understanding the habitat preferences of a species is essential to predict its reaction to habitat disturbance and to put conservation measures in place. However, it is often difficult to disentangle the 2 effects regarding the distribution pattern of a species owing to naturally occurring hot- and coldspots for single species on a small scale (Brown *et al.* 1985), a lack of prefragmentation data from the same site (Chapman and Peres 2001), or synergistic interactions between environmental and anthropogenic factors (Pinto *et al.* 2009).

The aforementioned trends are mostly based on studies conducted in evergreen rainforests (Albernaz and Magnusson 1999; Mittermeier and van Roosmalen 1981; Rylands 1987). The Brazilian Atlantic forest and the Amazon Basin have

been particular foci of research (Chiarello 2003; Laurance and Bierregaard 1997; Phillips *et al.* 2004; Schwarzkopf and Rylands 1989). However, 40–50% of all tropical forests was originally deciduous forest (Gentry 1995; Janzen 1988; Murphy and Lugo 1995), which are also home to a large number of often endangered and little known primate species (Mittermeier *et al.* 2005; Nowak 1999). Further, this forest type is among the most endangered lowland tropical forest ecosystems (Janzen 1988) owing to a relatively high soil fertility when compared to other tropical biomes and, consequently, a high human colonization with intensive agricultural activity (Steininger *et al.* 2001; Williams 1989). Today, only few large areas of intact deciduous tropical forest remain in the tropics and subtropics (Maas 1995), and a number of researchers have pointed out a serious neglect of studies and conservation programs in these ecosystems (Sánchez-Azofeifa *et al.* 2005; Wallace *et al.* 1998).

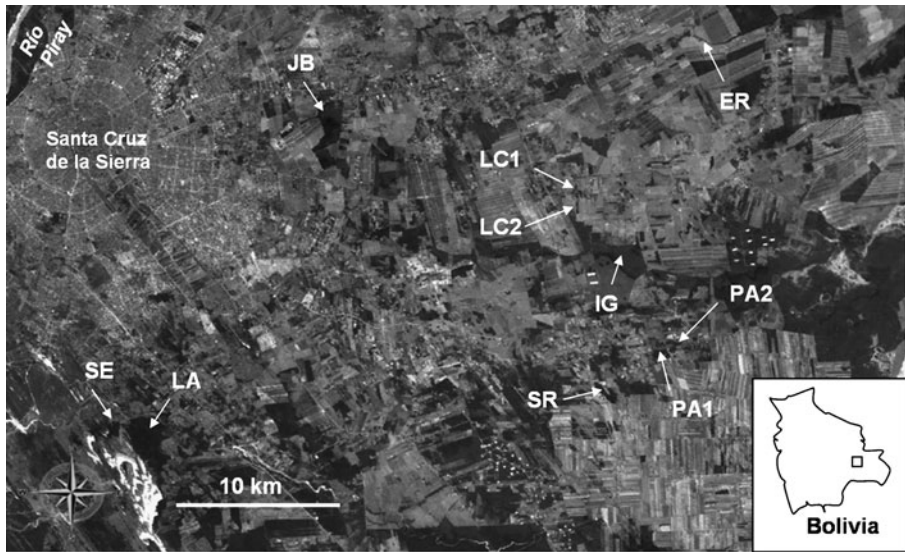
To begin to remedy these deficiencies, we collected data on primate diversity and abundance in the Chiquitano dry forest ecoregion in lowland Bolivia. This ecoregion has a size of *ca.* 102,000 km<sup>2</sup> (Ibisch *et al.* 2003) and contains the largest until recently unfragmented area of deciduous tropical forest in the world (Gentry 1993). However, over the last decades, the area has undergone profound changes through deforestation and fragmentation (Camacho *et al.* 2001; Steininger *et al.* 2001). Our aim was to identify natural (vegetation structure) and anthropogenic (fragmentation, isolation) factors influencing primate diversity and abundance in the endangered deciduous forests. To tease apart the effects of habitat structure and anthropogenic disturbance despite the restrictions of our small scale, short-term (December 2005–March 2006) study, we sampled fragments that differed systematically in their natural vegetation parameters and human impact factors and controlled for correlations between the habitat variables. In addition, we collected data on primate distribution and abundance before fragmentation from the literature and interviews with local landowners. We discuss our findings with regard to taxon-specific habitat preferences and aim to identify species that are immediately endangered by fragmentation in the study area.

## Materials and Methods

### Study Area

We collected data in 10 forest fragments  $\leq 30$  km south and east of the Bolivian city of Santa Cruz de la Sierra (17°44′–17°55′S; 62°53′–63°10′W; Fig. 1). We chose 19 fragments according to their size and accessibility after overflying the area in a Cessna airplane. Subsequently, we visited the fragments and visually assessed their average tree height and shrub density as well as the percentage of forested area in the surroundings of the remnants. We then chose 2 or 3 fragments of approximately the same size in 4 different size ranges (1–3 ha, 3–5 ha, 10–70 ha, and >150 ha) that differed in vegetation structure and surrounding landscape matrix.

Forest fragments ranged in size from 1.1 to 303 ha (Table I). Most were situated on private farmland (LC1, LC2, IG, PA1, PA2, SR, and ER). Three other study sites



**Fig. 1** Detail of the study area east of Santa Cruz de la Sierra in the Departamento de Santa Cruz, Bolivia, with locations of the study sites. Black and dark gray areas in the satellite image indicate forest areas. Study site abbreviations: ER = El Rodeo, IG = Ignacio, JB = Jardín Botánico, LC1 = Los Cupesis 1, LC2 = Los Cupesis 2, LA = Lomas de Arena, P1 = Paurito 1, P2 = Paurito 2, SE = Sendéro Ecológico, SR = Santa Rita. (Satellite image modified from NASA World Wind 1.3.5.).

included the Botanical Garden (JB) of Santa Cruz and 2 forest fragments in the small reserve Parque Regional Lomas de Arena 20 km south of the city center (SE, LA). We used an annotated species list for the local primate fauna of Lomas de Arena (LA) from previous surveys by Guillén Villarroel *et al.* (2004).

All forest fragments had similar topographic, edaphic, and climatic conditions, as well as the same altitude of *ca.* 430 m. The entire study area lies in the alluvial plain of the Río Grande, characterized by a flat topography and Andean-derived alluvial sediments deposited by the river (Krüger 2006; Steininger *et al.* 2001). The climate is tropical and seasonally wet, with a mean temperature of 27°C and a mean annual precipitation of 1,500 mm with a standard deviation of 283 mm (Krüger 2006). About 70% of the annual precipitation falls in the rainy season from October to March (Krüger 2006). The study area is situated in a biogeographic transition zone between the mesophytic, semideciduous Cerrado forests of the Chiquitano dry forest ecoregion and the meso- to xerophytic and lower-stature woodlands of the Gran Chaco (Ibisch *et al.* 2003). The typical Cerrado forest, which was present in most of the study sites, shows 2 tree strata, sporadically overtopped by emergents like *Schinopsis brasiliensis*. The superior stratum consists of a 15–30 m tall, partially closed canopy with (semi-)deciduous tree species like *Anadenanthera colubrina*, *Acosmium cardenasii*, *Caesalpinia floribunda*, *Aspidosperma cylindrocarpon*, *Chorisia speciosa*, and *Tabebuia impetiginosa*. The lower stratum (3–15 m tall) consists mostly of evergreen trees, shrubs, and liana (Killeen *et al.* 1998; Navarro and Maldonado 2002). Further east and south of Santa Cruz de la Sierra, the xerophytic woodlands of the Chaco begin. These semideciduous forests are low (4–10 m, emergents  $\leq$ 20 m tall) with open canopies, and partially feature a thick,  $\leq$ 6 m

**Table 1** Habitat characteristics and sampling effort of the ten forest fragments included in the study, ordered by fragment size

Study site	Fragment size (ha)	Isolation time (a)	Surrounding forest area (%) <sup>a</sup>	No. of line-transect surveys	Length of line-transect (km)	No. of recording/vegetation structure stations	Study period (d)
Lomas de Arena (LA)	303	25	1/5/6/13	7	1.3/2.3/1.5/1.3/1.3/1.3/1.5	10	11
Ignacio (IG)	259	33	3/8/15/14	2	5.7/1.5	7	8
Jardín Botánico e(IB)	170	17.5	3/9/10/13	4	3.8/2/1/1	10	12
Sendéro Ecológico (SE)	66	30	2/3/8/14	3	2.5/2.5/2.5	6	5
Santa Rita	20.3	4	0/6/8/29	3	2.2/0.75/0.75	4	4
Paurito 2 (PA2)	10.4	8	21/22/31/32	Whole area survey	Whole area survey	4	5
Paurito 1 (PA1)	4	8	13/27/36/32	Whole area survey	Whole area survey	2	5
Los Cupepis 2 (LC2)	3.8	3.8	0/17/29/30	Whole area survey	Whole area survey	1	4
Los Cupepis 1 (LC1)	3	3	4/5/9/14	Whole area survey	Whole area survey	2	4
El Rodeo (ER)	1.1	30	0/13/21/24	Whole area survey	Whole area survey	1	5

<sup>a</sup> Categories: In 100/200/500/1,000 m range around the study site

tall thorn scrub. Dominant tree species include *Aspidosperma quebracho-blanco*, *Schinopsis cornuta*, *Schinopsis lorentzii*, and the tree-cactus species *Browningia caineana* (Navarro and Maldonado 2002). The landscape matrix in which the study sites are immersed is composed predominantly of pasturelands and agricultural fields, interspersed by other small forest fragments.

## Data Collection

We collected data from December 2005 to March 2006 during the austral summer, which is characterized by frequent rainfalls (180 mm/mo) and constantly high temperatures of 30°C on average (Navarro and Maldonado 2002). We restricted data collection to these months to guarantee similar climate and vegetation conditions over the entire study period and avoid seasonal bias in the probability of detecting species. Time of data acquisition per site was 4–12 days, depending on fragment size (Table 1). We interrupted data collection during heavy rainfalls. However, rainfalls were usually short, so we continued data collection after 30 min or so. For each forest fragment we determined its size, isolation time, percentage of forest cover in the surrounding matrix area, and data on vegetation structure (Table 1). We determined fragment size using a handheld Garmin E-Trex GPS navigation device, and, for the two largest study sites (LA and IG), by measuring size on a satellite image from NASA World Wind 1.3.5 after enlarging the image via Photoshop 7.0 (Adobe Systems Inc. 2002; resolution: 40×40 m, Fig. 1). We obtained data on isolation time of the forest fragments through interviews with landowners when we requested permission to work on their property. For the analysis of the surrounding forest area we assessed the percentage of forested area in different ranges around the study sites. We drew a line tracing the fragment shape at 100 m, 200 m, 500 m, and 1,000 m of the fragment border on the enlarged NASA satellite image in Photoshop using the measure tool. Then we counted all pixels in the space between the fragment border and the drawn line. We identified picture elements representing forest area by their dark green color and matched borders of the fragments and surrounding forest blocks in the satellite image with GPS coordinates taken in the field.

We obtained data on vegetation structure at a number of points varying according to fragment size (Table 1), each covering a 7.5 m radius circle. Data included mean canopy height, number of lying and standing dead logs with a diameter at breast height (DBH) >16 cm, number of shrubs (woody plants 0.5–3 m tall), and number of trees (woody plants >3 m tall) in 4 DBH classes: <16 cm, 16–30 cm, 31–60 cm, >60 cm. For each vegetation structure variable we calculated the mean for each fragment. We also calculated the mean basal wood area (m<sup>2</sup>/ha) for each study site using the total number of trees. Because we did not measure the DBH values of trees in the smallest class (<16 cm) individually, we assumed a mean DBH of 11 cm for each tree for the calculations.

Before fieldwork, we took references for the primate species reported for the study area and their distributional ranges from Anderson (1997), Emmons and Feer (1997), Eisenberg and Redford (1999), Salazar-Bravo *et al.* (2003), and Guillén Villarroel *et al.* (2004) and asked local landowners which species they have seen in the study site in the past. The taxonomy we use follows Groves (2001), except for *Callicebus donacophilus*, which van Roosmalen *et al.* (2002)

considered as a full species. We acquired primatological data (number of species, detections of different individuals/groups per study day) in the field by standardized, opportunistic visual surveys using a pair of Zeiss 10×40 binoculars and guide books (Eisenberg and Redford 1999; Emmons and Feer 1997; Appendix 1). In addition, we collected acoustic data using standardized point count sound recordings at the vegetation structure stations via a Sony TCM 5000-EV portable cassette recorder and a Sennheiser ME 80 directional microphone (Table I). We set acoustic data collection points 250 m apart. Thereby, we were able to separate clearly primate vocalizations between 2 neighboring points in the recordings and avoid multiple counts of the same individuals. We conducted the recordings following Haselmayer and Quinn (2000). Recording time was  $\geq 8$  min per point. During the recordings, we stood silently on the point of data collection and changed the orientation of the microphone every minute for the first 8 min of the recording time in a fixed manner (east, south, west, north, repeated once). If primates vocalized, we directed the microphone freely in the direction of the vocalizations for another 7 min to collect additional recordings to facilitate identification of species. We sampled  $\geq 3$  recordings per sound recording station, regardless of primate vocalizations heard. Each morning, we conducted  $\leq 6$  recordings beginning between 05:00 and 06:00 h for *ca.* 3 h, depending on weather conditions. We changed the order in which recording stations were visited in a given fragment daily. In total, we obtained 244 point count recordings. In addition, we conducted 1 or 2 short recordings (5–10 min) in each fragment after sunset (19:50–20:50 h) to detect crepuscular and nocturnal species like *Aotus azarae boliviensis*. We identified primate vocalizations heard or recorded using Emmons *et al.* (1997). We considered vocalizations recorded from different directions as independent. Because it was not possible to assess the exact number of callers in most recordings, we rated each vocalization as detection of 1 individual in the further analyses. In forest fragments  $< 20$  ha, we surveyed the whole area (Schwarzkopf and Rylands 1989); in larger fragments we performed standardized line-transect surveys (Buckland *et al.* 1993; Peres 1999; Table I) to assess primate diversity and detection rates.

## Data Analyses

To reduce the number of habitat parameters, we performed principal component analyses (PCA), followed by bivariate correlation analyses (Pearson correlation, 2-tailed test of significance) to test for mutual dependence between the habitat parameters. We tested the impact of the PCs on primate diversity and abundance using multiple regression analyses. Variables tested were total species number and mean number of primate detections per study day (in total and by species; visual and acoustic detections combined). We took mean numbers of detections per study day as a proxy for population densities in this study, because we were not able to perform a large number of standardized line-transects in every study site due to constraints caused by a parallel ornithological data collection. Nevertheless, we consider our results as robust because we were able to assess the entire primate community in small fragments  $< 20$  ha, and, therefore, could avoid double counting of the same individuals. In larger fragments, the combination of different methods

(acoustic recordings, transect walks and opportunistic observations by 3 researchers) should have provided a realistic image of the different species and groups living in the particular fragment. To avoid multiple counts of the same individuals, we compared observations of the same species from different researchers regarding time and locality each day. We counted observations separately only if they were made at approximately the same time but  $\geq 250$  m apart from each other. Significance level is  $p \leq 0.05$ .

## Results

### Habitat Parameters

Fragment size and isolation time correlated poorly with all other habitat variables, so we excluded them from the PCA data set and used them as single variables in further analyses. PCA of the 11 remaining variables revealed 3 components with eigenvalues  $>1$ , cumulatively accounting for 82.3% of the total variance (Table II). The first component showed heavy factor loadings for all variables concerning the percentage of forest area in different sized ranges around the fragments, so we labeled it “surrounding forest area.” The second component showed heavy factor loadings for canopy height, number of trees of the largest category, basal tree area, and number of dead logs, and was labeled “forest maturity.” We labeled the third component “understory density” due to heavy

**Table II** Eigenvalues and proportions of variance of the 3 components extracted in the principal component analysis (PCA) and rotated component matrix

		Component		
		Surrounding forest area	Forest maturity	Understory density
Total		4.168	3.159	1.732
Initial eigenvalues	% of variance	37.889	28.714	15.745
	Cumulative %	37.889	66.603	82.348
Variables	Canopy height	-0.027	<b>0.822</b>	-0.200
	Number of shrubs	0.150	0.034	<b>0.959</b>
	Small trees	0.048	-0.445	<b>0.840</b>
	Middle-sized trees	-0.359	-0.206	<b>0.814</b>
	Large trees	0.033	<b>0.877</b>	-0.343
	Basal wood area	0.483	<b>0.674</b>	-0.237
	Dead wood	-0.064	<b>0.835</b>	0.104
	% forest in 100 m radius	<b>0.725</b>	-0.242	-0.158
	% forest in 200 m radius	<b>0.974</b>	-0.010	-0.033
	% forest in 500 m radius	<b>0.956</b>	0.123	-0.050
% forest in 1000 m radius	<b>0.889</b>	0.172	0.074	

Heavy loadings for each component are displayed in bold



factor loadings for the number of shrubs and the number of small and mid-sized trees (16–60 cm DBH).

### Primate Data

We detected the presence of *Alouatta caraya*, *Aotus azarae boliviensis*, *Callithrix melanura*, *Callicebus donacophilus*, and *Cebus libidinosus juruanus*. Species observed in the greatest number of sites were *Cebus libidinosus juruanus* (9 sites), *Callicebus donacophilus* (7 sites), and *Callithrix melanura* (6 sites). We detected *Aotus azarae boliviensis* and *Alouatta caraya* in only 2 and 1 forest fragment, respectively (Appendix 1). We had only acoustic evidence for howlers in the JB. However, recent visual observations confirmed that the species is *Alouatta caraya* (*pers. comm.* by Rebecca Rimbach to Lennart Pyritz, January 2010), an unmistakable species due to sexual dichromatism. Total species number and mean primate detections per day decreased significantly with understory density; surrounding forest area also had a significant negative impact on mean primate detections per day. Fragment size did not have a significant impact on mean primate detections per day (Table III).

We conducted single-species analyses only for *Callithrix melanura*, *Cebus libidinosus juruanus*, and *Callicebus donacophilus*, because observation numbers were too low for *Alouatta caraya* and *Aotus boliviensis*. Multiple regression models were significant for *Callithrix melanura* and *Callicebus donacophilus* (Table IV), but not for *Cebus libidinosus juruanus*. Forest maturity, understory density, and surrounding forest area correlated negatively with mean detections of *Callithrix melanura* per day. For *Callicebus donacophilus*, the regression model was significant, but no single predictor variable had any significant impact on mean daily detections.

### Discussion

Of the 8 primate species that have been reported historically in the vicinity of Santa Cruz (Anderson 1997), we observed only 5 in the present study. This could be due to

**Table III** Multiple regression models including habitat parameters, total primate species number, and mean number of detections per day

Dependent variable	Adjusted $R^2$	$p$ -value for model	Predictor variables	Standardized beta coefficients	$p$ -values for single predictor variables
Total species no.	0.79	0.00*	Understory density	-0.84	0.00*
			Fragment size	0.23	0.19
Mean no. of detections per day	0.81	0.01*	Understory density	-0.80	0.00*
			Surrounding forest area	-0.47	0.02*

Significance is indicated by a \*

**Table IV** Multiple regression models including habitat parameters and mean number of detections per day for *Callithrix melanura* and *Callicebus donacophilus*, respectively

Dependent variable	Adjusted $R^2$	$p$ -value for model	Predictor variables	Standardized beta coefficients	$p$ -values for single predictor variables
Mean no. of detections of <i>Callithrix melanura</i> per day	0.82	0.03*	Forest maturity	-0.87	0.01*
			Understorey density	-0.64	0.02*
			Surrounding forest area	-0.57	0.05*
			Fragment size	-0.53	0.06
			Isolation time	-0.33	0.27
Mean no. of detections of <i>Callicebus donacophilus</i> per day	0.56	0.05*	Isolation time	0.64	0.11
			Understorey density	-0.61	0.07
			Fragment size	0.33	0.31
			Forest maturity	0.30	0.29

Significance is indicated by a \*

sampling restraints; however, primate species' numbers observed in the present study match numbers reported in interviews with local people and from other recent surveys conducted in the same area and thus seem reliable. In JB, where 4 primate species were reported (*pers. comm.* by the director of JB Dario Melgar to Lennart Pyritz) we recorded a total of 5 species including *Alouatta caraya* that had not been mentioned by Melgar. In LA, we observed 3 species during the study period, only 1 (*Aotus azarae boliviensis*) less than in a reference mammal species list for the reserve (Guillén Villarroel *et al.* 2004).

Anderson (1997) reported sightings for *Alouatta sara* and *Ateles chamek* in our study area, 2 species we did not find. However, historical evidence is extremely sparse. *Ateles chamek*, e.g., is known only from 2 sightings in 1941 and 1976. The 2 species are among the largest Neotropical primate species and have likely become locally extinct during the last decades owing to heavy hunting pressure (Peres 2001). Correspondingly, we recorded the largest species, *Alouatta caraya*, only in the botanical garden of Santa Cruz, which has been protected for *ca.* 20 yr. We did not observe the third historically sighted species—*Saimiri boliviensis boliviensis*—which is usually rated a robust species present in forest fragments as small as 0.8–2 ha (Baldwin and Baldwin 1976; Mittermeier and Coimbra-Filho 1977), and there are 13 sightings documented (Anderson 1997). However, none of the local people we interviewed, not even old Mennonite farmers who were among the first settlers in the area (Steininger *et al.* 2001), could ever remember having seen *Saimiri boliviensis boliviensis*. It may be that a large proportion was captured and kept as pets or sold long ago, as *Saimiri* seems to be of high value in the black market for exotic pets (Duarte-Quiroga and Estrada 2003). The rest may have disappeared as a result of genetic depletion, stochastic events, or social dysfunction (Lande and Barrowclough 1987). Otherwise, historical sightings reflect well the overall patterns of our observations (23 for *Cebus libidinosus juruanus*, 14 for *Callicebus donacophilus*, 8 for *Aotus azarae boliviensis*). However, Anderson (1997) quotes only 3 sightings for *Callithrix melanura*, a species we observed in more than half of our study sites. In general, historical observations from the area should be interpreted cautiously owing to often imprecise information.

In contrast to the findings of many other studies (Chiarello and De Melo 2001; Martins 2005), the impact of fragment size on total species number was not significant (Table III). Further, none of the habitat variables correlated significantly with presence or detection rates of *Cebus libidinosus juruanus* and *Callicebus donacophilus* (Table IV). This might be explained by a general high ecological plasticity and adaptability of the local species (González-Solís *et al.* 2001), which has also been reported for Brazilian Atlantic forest primates (Chiarello 1999). In fact, a number of species/genera present in our study sites have been rated as highly robust to different habitat structures (*Cebus apella*: Wallace *et al.* 1998; *Cebus libidinosus juruanus*: Chiarello 2003; *Callithrix melanura*: Ferrari *et al.* 2003).

The high adaptability of capuchins (*Cebus* spp.) is due to several factors. They are flexible in their diet (Galetti and Pedroni 1994), occupy a variety of different habitats including small remnants (Chiarello 2003), and recolonize fragments even if the surrounding second growth is only 2 m in height (Mittermeier and Coimbra-Filho 1977). They even adapt to urban habitats (Fragaszy *et al.* 2004) and the vicinity of industrialized cities (Pinto *et al.* 2009). Titi monkeys (*Callicebus* spp.) also seem to adapt to a small home range size. We observed *Callicebus donacophilus* in 7 out of 10 fragments, with some of them even displaying considerable proportions of low Chaco-forest (IG, LC1), and in remnants as small as 3 ha (LC1). Similar results on home range size were revealed by Mason (1971) for *Callicebus*, Kinzey *et al.* (1977) for *Callicebus torquatus torquatus*, and Chiarello (2003) for *Callicebus personatus*. A high tolerance toward habitat fragmentation and a high ecological adaptability were also reported for *Callicebus coimbrai* in the Atlantic forest, where a number of groups lived in fragments of only 3–20 ha in size (Jerusalinsky *et al.* 2006).

In general, except for SE and LA, where we observed a puma (*Puma concolor*) once and found puma footprints, respectively, we did not record any evidence, e.g., dung, vocalizations, of large predators in the study area. This also might facilitate primate persistence in small fragments (González-Solís *et al.* 2001).

Understorey density showed a strong negative impact on total species number and primate detections per day (Table III) and detection rates of *Callithrix melanura* (Table IV). Probably, naturally occurring thick thorn scrub (Chaco forest type; Navarro and Maldonado 2002) that was present in some fragments south of the city center, e.g., IG, SR, was responsible for high scores in understorey density. This thorn scrub is virtually impermeable and presumably too low (3–4 m) to provide an appropriate habitat for any Neotropical primate species (Coimbra-Filho and Mittermeier 1981). This probably accounts also for the absence of *Callithrix melanura*, although it often occurs in disturbed, human-made habitats (Albernaz and Magnusson 1999; Ferrari *et al.* 2003; Sussman 2000). Reduced visibility of species in fragments with high understorey density may also play a role. However, we used different survey methods including acoustic recordings, which should have compensated for potential visual restraints.

Although *Callithrix melanura* has been observed in intermediate and high canopy forest (Stallings and Mittermeier 1989), forest maturity had a negative impact on the species, too (Table IV). This is in accordance with Hershkovitz (1977) and Wallace *et al.* (1998), who found that *Callithrix* generally prefers lower forest strata. Sites with intermediate scores in forest maturity may thus represent adequate habitat for

the species providing lower forest strata, but no impermeable thorn scrub. In general, observed patterns could also be caused by the patchy distribution of *Callithrix melanura* even under undisturbed conditions in continuous forest, resulting in inhomogeneous patterns already before fragmentation (Ferrari *et al.* 2003; Veracini 1997).

The PCA component surrounding forest area (percentage of forest area in different sized ranges around the fragments) had a negative effect on primate detections per day (Table III) and numbers of *Callithrix melanura* (Table IV), which is surprising. Parameters not controlled for in this study, such as irregularities in fragment shape or the distance to the nearest farm/village, may account for this pattern (Arroyo-Rodríguez *et al.* 2008). In general, the number of variables tested in this study was restricted owing to time restraints, and the observed patterns may be caused by parameters that we did not evaluate. Pinto *et al.* (2009), e.g., stressed the importance of incorporating the landscape matrix, e.g., crops, gardens, swamp, fields, surrounding the fragments, because they found densities of *Callicebus* to correlate positively with agriculture, while the picture was reversed for *Alouatta*. Future studies in the area should therefore incorporate details on land use. Finally, some of our sites may represent natural “coldspots” of primate diversity irrespective of habitat quality (Pinto *et al.* 2009), which could have outweighed the effects of variables assessed in this study.

## Conclusions

This was a short-term study, and future studies should also incorporate data on fragment shape; land use; distance to nearest town; and social parameters, e.g., income of the local people to estimate hunting pressure, in the study area, as these might explain distribution patterns better for single species than the variables we assessed. Nevertheless, our study provides a valuable basis for future studies of fragmentation in the threatened Neotropical dry forests. If the fragments studied by us are surveyed throughout the next years or decades, long-term effects, e.g., time-delayed extinctions, of species might be monitored and the impacts of habitat parameters and anthropogenic disturbance could be untangled more clearly, enabling specific conservation measures for endangered species.

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## Appendix 1

Table V Primatological data collected through observations and recordings in 9 of 10 study sites (in order of visits)

Family	Species	Individuals recorded during line-transect surveys	Individuals observed opportunistically	Group sizes observed	Mean group size (s.d.)	Vocalizations heard/recorded	Mean no. of detections per day (s.d.)
<b>Study site: JB</b>							
Callitrichidae	<i>Callithrix melanura</i>	1	4	1/4	2.5 (2.1)	0	0.4 (1.2)
Cebidae	<i>Cebus libidinosus juruamus</i>	3	18	1/2/3/3/3/4	2.6 (0.9)	4	2.1 (1.5)
	<i>Aotus azarae boliviensis</i>	4 (3 adults, 1 infant)	0	4	4 (0)	0	0.3 (1.2)
	<i>Callicebus donacophilus</i>	1	1	1/1	1 (0)	9	0.9 (0.8)
	<i>Alouatta caraya</i>	0	0	0	0	2	0.2 (0.6)
<b>Study site: SE</b>							
Callitrichidae	<i>Callithrix melanura</i>	0	3	1/4	1/2	0	0.6 (0.9)
Cebidae	<i>Cebus libidinosus juruamus</i>	0	0	1/2/2/3/3/3/4	0	2	0.4 (0.5)
	<i>Callicebus donacophilus</i>	0	0	1/1	0	9	1.8 (1.1)
<b>Study site: LA</b>							
Callitrichidae	<i>Callithrix melanura</i>	0	3	3	3 (0)	0	0.3 (0.9)
Cebidae	<i>Cebus libidinosus juruamus</i>	0	0	0	0	1	0.1 (0.3)
	<i>Callicebus donacophilus</i>	2	10	1/2/3/6	3 (2.1)	13	2.4 (2.1)
<b>Study site: LCI</b>							
Cebidae	<i>Callicebus donacophilus</i>	Whole area survey	2	2	2 (0)	1	0.8 (1)
<b>Study site: LC2</b>							
Cebidae	<i>Cebus libidinosus juruamus</i>	Whole area survey	5	2/3	2.5 (0.7)	0	1.3 (1.5)
	<i>Aotus azarae boliviensis</i>	Whole area survey	2	2	2 (0)	0	0.5 (1)
	<i>Callicebus donacophilus</i>	Whole area survey	2	2	2 (0)	0	0.5 (1)

Table V (continued)

Family	Species	Individuals recorded during line-transect surveys	Individuals observed opportunistically	Group sizes observed	Mean group size (s.d.)	Vocalizations heard/recorded	Mean no. of detections per day (s.d.)
<b>Study site: P1</b>							
Callitrichidae	<i>Callithrix melanura</i>	Whole area survey	2	2	2 (0)	0	0.4 (0.9)
Cebidae	<i>Cebus libidinosus juruamus</i>	Whole area survey	0	0	0	1	0.2 (0.4)
<b>Study site: P2</b>							
Callitrichidae	<i>Callithrix melanura</i>	Whole area survey	1	1	1 (1)	0	0.2 (0.4)
Cebidae	<i>Cebus libidinosus juruamus</i>	Whole area survey	0	0	0	1	0.2 (0.4)
	<i>Callicebus donacophilus</i>	Whole area survey	0	0	0	3	0.6 (0.9)
<b>Study site: IG</b>							
Cebidae	<i>Cebus libidinosus juruamus</i>	0	0	0	0	2	0.3
	<i>Callicebus donacophilus</i>	0	0	0	0	6	0.8
<b>Study site: SR</b>							
Cebidae	<i>Callithrix melanura</i>	0	2	2	2 (0)	0	0.5 (1)
	<i>Cebus libidinosus juruamus</i>	0	6	6	6 (0)	0	1.5 (3)

No primates were observed in study site El Rodeo (ER). s.d. = standard deviation

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