Mammalian Biology
Zeitschrift für Säugetierkunde

www.elsevier.de/mambio

ORIGINAL INVESTIGATION

Habitat selection by large mammals in a southern Brazilian Atlantic Forest

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Received 6 December 2007; accepted 22 February 2009

Abstract

Habitat selection, which is mainly a consequence of competition and predation, allows species to coexist. The present study was conducted in two reserves in an Atlantic Forest area in Santa Catarina State, southern Brazil, and provided information on several large mammal species through photographic records. Records were related to certain environmental parameters, such as width of passages (trails and roads), vegetation density and proximity to water, in order to assess the relationship between each mammal species and its microhabitat. Thirty-two camera trap stations were placed during 17 months for 150.8 (±62.2) days on average. Terrestrial mammals tended to use different habitats: *Puma concolor* used mainly dirt roads and open areas; *Leopardus pardalis*, *Cerdocyon thous* and *Nasua nasua* used more large trails and intermediate-forested sites; and *Cuniculus paca*, *Dasypus novemcinctus*, *Leopardus tigrinus*, *Eira barbara* and *Leopardus wiedii* were recorded more often on narrow trails and in densely forested sites. Some of these forest species, such as *D. novemcinctus*, *C. paca* and *L. pardalis*, also showed relationships with watercourses. Information on habitat selection allows more effort to be addressed to the habitat associated with focal species, and indicates the significance of environmental heterogeneity, which makes it possible for species to coexist.

Keywords: Camera trap; Environmental parameters; Microhabitat; Neotropical mammal community; Species interaction

Introduction

Animal and plant species often occur in many different habitats in the same region, where they may experience different development rates, life spans, and birth and death rates (Pulliam and Danielson 1991). This habitat selection allows species to coexist (Orians and Wittenberg 1991). It is in part a consequence of competition and predation, stabilising both of them, and acting as an optimal-foraging process (Rosenzweig 1991) or resource partitioning (Schoener 1974). In some cases, experience in a natal habitat affects habitat selection after the individual leaves its natal land and begins to search for new habitats (Stamps and

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doi:10.1016/j.mambio.2009.02.006
Mamm. biol. 74 (2009) 182–190

Swaisgood 2007). Multispecies studies have emphasised the potential for differential susceptibility and optimal habitat selection to maintain community diversity (Rosenzweig 1991).

Habitat-selection theorists have drawn their inspirations primarily from mobile animals, by imagining them moving through environments pursuing and capturing prey, seeking shelter, and avoiding predators (Orians 1991). This process affects nearly all individual subsequent choices (Orians and Wittenberg 1991).

However, habitat selection can be viewed at different spatial scales. On a micro-scale, habitat selection becomes the fine-grained theory of optimal foraging, in which foragers choose prey from among various types that they encounter at random. On slightly larger scales, in which different habitat patches are incorporated, individuals may choose to search within patches or to pass through them without looking for prey, nest sites, or other resources. On macro-scales, the study of habitat selection becomes the study of emigration and immigration (Orians 1991). Scale also affects the costs of habitat selection. Small-scale variation can be handled without shifts in home ranges, whereas large-scale changes require such shifts, often over long distances (Morris 1987). The longer the distance, the less knowledge that organisms are likely to have about the environments into which they move (Orians 1991).

In the Atlantic Forest, most studies focusing on large-sized mammal communities rely on effects of forest fragmentation and hunting (e.g. Chiarello 1999; Cullen-Jr et al. 2000; Quadros and Cáceres 2001), and a few of them have treated of habitat selection on its direct meaning (Santos et al. 2004), with some comparing ecologically similar species (Vieira and Port 2007) or even analysing habitat use of a sole species (Di Bitetti et al. 2006).

Since the majority of the studies undertaking micro-scale habitat selection in the Atlantic Forest has focused on small mammals (e.g. Gentile and Fernandez 1999; Dalmagro and Vieira 2005) and due to the scarce information on large-sized mammals in the biome, our aim was to examine the relationships between relative abundance of large mammal species and different microhabitats in a dense Atlantic Forest of southern Brazil. These different microhabitats were around trails of different width and dirt roads where frequencies of movements of mammals in such ways were examined by camera traps.

Material and methods

Study site

The study was conducted in an Atlantic Forest area in Santa Catarina, southern Brazil, in two reserves: Reserva Ecológica do Caraguatá-REC (4200 ha; central coordinates 27°25′51″ S, 48°51′01″ W), and a section of the Parque Estadual da Serra do Tabuleiro-PEST (5000 ha; central coordinates 27°51′36″ S, 48°38′33″ W).

The two study areas are located in the hills of the Serra do Mar, at altitudes between 420 and 1100 m asl, and are 40 km apart (Fig. 1). The main vegetation type is the dense broadleaf evergreen Atlantic Forest with montane and high-montane patches (Veloso et al. 1991). There are few relicts of *Araucaria angustifolia* in the two areas, since they comprise bordering patches of the mixed broadleaf evergreen forest as well (Gaplan 1986). The climate is subtropical with a high annual rainfall (1800 mm). Mean annual temperature varies between 20 °C and 24 °C in January and

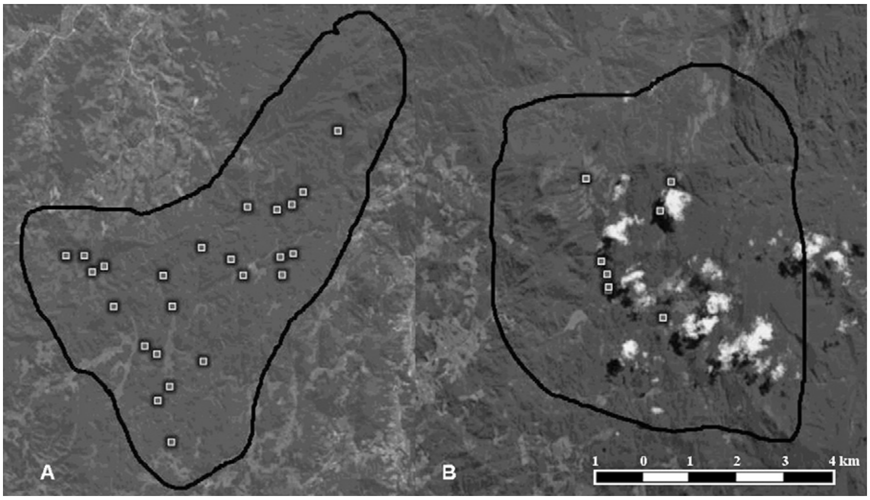

Fig. 1. The two study areas (A – Reserva Ecológica do Caraguatá – REC; B – Parque Estadual da Serra do Tabuleiro – PEST), far 40 km apart, lied in the Atlantic Forest of southern Brazil. Points in the picture are the camera-trap stations.

between 12 °C and 16 °C in July in both areas (Gaplan 1986).

Trapping procedures

Data were collected from Tigrinus® camera-traps installed throughout the two study areas. The equipment consisted of a conventional photographic camera with an infrared sensor programmed to shoot when an animal interrupts the beam. Thirty-two camera-trap stations were placed during 17 mo of study (August 2005–December 2006). The stations were installed in intervals of 1–1.5 km between the nearest sites, covering an approximate area of 30.54 km^2. The difficult of placing traps at regular distances from each other was due to the irregular, hilly relief of the study areas. The 32 camera-trap sampled the sites for 151 days on average (151 ± 62.2 SD) (Table 1). No baits were used to lure animals to the cameras. Each station was classified by considering the width of trail or road, proximity to water (stream or river) and vegetation density (open area; secondary forest, termed intermediate coverage; and dense canopy, meaning primary forest and termed dense coverage). The classification was done during the fieldwork and by analysis of a satellite image obtained from Google Earth® (Fig. 2). The trails or roads were categorised as narrow trail (0.5–1.5 m wide), wide trail (> 1.5 m wide), or dirt road (with frequent vehicular traffic and usually 4 m or more wide). Only a 50-m radius around each capture station was considered, in order to classify the proximity (presence or absence) to water, and vegetation density. All sites where capture stations (different trails/road, vegetation types and with or without water) were set were considered here as "habitat" since it was the unit of the environment currently focused in the study. In this sense, the use of a given trail type or dirt road by a given species was

Table 1. Trap-night, classification of vegetation density and trails, proximity of water and abundance index of the mammalian species recorded in each station, sampled in two Atlantic Forest reserves (REC and PEST) in southern Brazil.

Station	Area	Trap-night	Vegetation	Trail	Water	Abundance index
1	REC	151	Open area	Road	Yes	0.37
2	REC	152	Open area	Narrow	Yes	0.03
3	REC	130	Intermediate coverage	Narrow	Yes	0.04
4	REC	81	Dense coverage	Narrow	yes	0.31
5	REC	98	Intermediate coverage	Narrow	Yes	0.37
6	REC	134	Intermediate coverage	Narrow	No	0.03
7	REC	111	Intermediate coverage	Large	No	0.11
8	REC	184	Intermediate coverage	Large	No	0.02
9	REC	216	Intermediate coverage	Large	No	0.01
10	REC	82	Open area	Road	No	0.26
11	REC	196	Intermediate coverage	Narrow	No	0.02
12	REC	28	Open area	Road	No	0.08
13	REC	197	Dense coverage	Large	No	0.04
14	REC	125	Open area	Narrow	No	0.02
15	REC	130	Dense coverage	Large	Yes	0.12
16	REC	124	Intermediate coverage	Narrow	Yes	0.34
17	REC	218	Dense coverage	Narrow	Yes	0.06
18	REC	218	Open area	Large	No	0.07
19	REC	223	Intermediate coverage	Narrow	Yes	0.09
20	REC	217	Intermediate coverage	Narrow	No	0.11
21	REC	282	Dense coverage	Narrow	No	0.02
22	REC	186	Intermediate coverage	Narrow	No	0.04
23	PEST	195	Intermediate coverage	Narrow	Yes	0.1
24	PEST	192	Open area	Narrow	No	0.45
25	PEST	188	Open area	Narrow	No	0.16
26	PEST	126	Intermediate coverage	Narrow	No	0.08
27	PEST	246	Open area	Large	Yes	0.18
28	PEST	80	Intermediate coverage	Narrow	No	0.12
29	PEST	102	Intermediate coverage	Narrow	No	0.02
30	PEST	80	Intermediate coverage	Narrow	Yes	0.26
31	PEST	80	Intermediate coverage	Narrow	No	0.17
32	PEST	53	Open area	Narrow	Yes	0.08

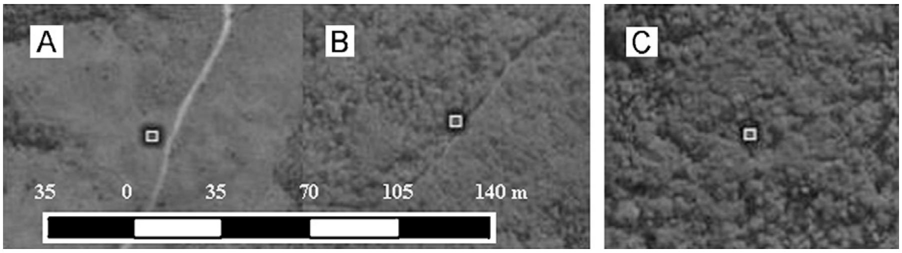

Fig. 2. Classification of vegetation density in two Atlantic Forest reserves in southern Brazil. Open area (A), intermediate coverage (B), and dense coverage (C).

understood that the animal was related to the surrounding habitats, and not purely used it to move between more distant areas.

A significant relationship between vegetation density and altitude was found ($r = 0.374$; $n = 32$; $p = 0.035$), leading us to exclude the parameter "altitude" from the analyses. We observed more densely covered areas at higher altitudes. A reasonable relationship between dense forest cover and narrow trails was observed, even though it was not significant ($r = -0.344$; $n = 32$; $p = 0.054$), so we included both of these parameters in the analyses.

Data analysis

The use of photographic rates as indices of abundance is subject to a number of assumptions, mainly when individuals are not identifiable (Jennelle et al. 2002). However, camera-trap rates should on average be correlated with animal abundance if animal movement with respect to the location of the camera traps was random. A camera trap based index of abundance is likely to be at least as reliable as other methods used to infer cryptic mammal abundance (Carbone et al. 2002).

The abundance index of each species was calculated by dividing the number of captures (photo or sequence of photos) of each species at each station (microhabitat) by the sampling effort (in days) at that site. Each species would thus have an index of relative frequency of use for each microhabitat. Photocaptures of a given species at a station, on the same day, and during a 1-h interval, were considered as a unique capture, in order to avoid replications of the same individuals. Only species with a minimum number of 10 valid records were considered for the analyses.

A Canonical Correspondence Analysis was used to assess possible relationships between the abundance index of mammal species and environmental parameters (width of passages, proximity to water, and vegetation density). The program used was Statistica® 5.0. Normality and homogeneity of variance of the data were verified prior to the analysis, and all data accorded with these premises.

Pearson correlations of the trapping successes of the species recorded were done in order to examine direct, paired relationships between them. Normality and homogeneity of variance of the data were verified prior to each analysis. Bonferroni correction was applied on this analysis since it was based on multiple hypotheses of relationships among species (Sokal and Rohlf 1995).

Results

Seventeen species were recorded during the study. For nine of them the number of captures obtained was sufficient for statistical comparisons. The main species recorded were from the orders Carnivora, Cingulata and Rodentia: *Leopardus tigrinus*, *Cerdocyon thous*, *Dasypus novemcinctus*, *Nasua nasua*, *L. pardalis*, *Puma concolor*, *Cuniculus paca*, *Eira barbara* and *L. wiedii* (Table 2).

The Canonical Correspondence Analysis (CCA) between mammal species and environmental parameters revealed significant relationships (Canonical $R = 0.84$; $\chi^2 = 44.6$; $P = 0.018$). Eigenvalues were: Root $1 = 0.70$; Root $2 = 0.36$.

Analysing the first root of CCA results indicated that *P. concolor* showed strong relationships to dirt roads and open areas, whereas *L. pardalis*, *C. thous* and *N. nasua* related more to wide trails and intermediate forest coverage. Still considering the first root, *C. paca*, *D. novemcinctus*, *L. tigrinus*, *E. barbara* and *L. wiedii* (in a decreasing order of importance) tended to use narrow trails, and were also related to dense vegetation. *Leopardus wiedii* used both wide and narrow trails, tending towards the latter (Fig. 3).

The second root indicated that proximity to water was important for *D. novemcinctus*, *L. pardalis* and *C. paca*, in a decreasing order of importance. In fact, *D. novemcinctus* and *C. paca* were the most important species relating to water courses by considering both

Table 2. Capture records in two areas of dense Atlantic Forest in southern Brazil, from August 2005 to December 2006, listing the records considered in the habitat analysis, in each area. Records of the same species at the same station made within a 1-h time interval were excluded from the analysis.

Species	Common name	Area	No. of records	Use in the analysis
Didelphidae				
Didelphis albiventris	White-eared opossum	REC	2	No
Didelphis aurita	Black-eared opossum	Both	1	No
Philander frenatus	Four-eyed opossum	Both	5	No
Dasypodidae				
Dasypus novemcinctus	Nine-banded armadillo	Both	49	Yes
Canidae				
Cerdocyon thous	Crab-eating fox	Both	50	Yes
Felidae				
Leopardus tigrinus	Oncilla	Both	62	Yes
Leopardus wiedii	Margay	Both	15	Yes
Leopardus pardalis	Ocelot	REC	21	Yes
Puma concolor	Cougar	Both	17	Yes
Mustelidae				
Eira barbara	Tayra	Both	12	Yes
Procyonidae				
Nasua nasua	Coati	Both	23	Yes
Procyon cancrivorus	Crab-eating racoon	Both	4	No
Tapiridae				
Tapirus terrestris	Tapir	PEST	3	No
Tayassuidae				
Pecary tajacu	Collared peccary	Both	7	No
Hydrochoeridae				
Hydrochoerus hydrochaeris	Capybara	REC	3	No
Cuniculidae				
Cuniculus paca	Paca	REC	12	Yes
Dasyproctidae				
Dasyprocta azarae	Agouti	Both	8	No

first and second roots at same time. The second root also informed that *L. wiedii* and *E. barbara* avoided large trails near streams (Fig. 3).

Results of Pearson correlations between pairs of species showed significant results. Relationships between *P. concolor* and *N. nasua* ($r = 0.6455$; $N = 13$; $P = 0.017$), *L. tigrinus* and *E. barbara* ($r = 0.5747$; $N = 21$; $P = 0.006$) and *L. wiedii* and *E. barbara* ($r = 0.6048$; $N = 13$; $P = 0.028$) were significant and positively correlated. However, only the pair *L. tigrinus* and *E. barbara* showed significant correlation following Bonferroni correction, when assuming a lower alpha value (0.01) (Sokal and Rohlf 1995).

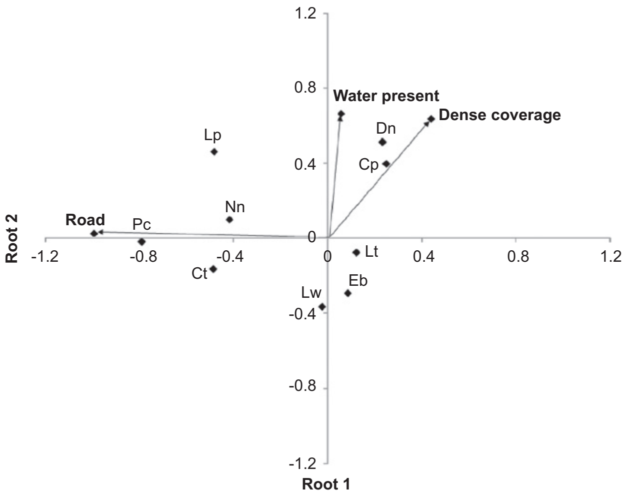

Fig. 3. Relationships between mammal species and some environmental parameters (width of trails or roads, proximity to water, and vegetation density, increasing starting from zero) in two Atlantic Forest reserves in southern Brazil (Canonical $R = 0.84$; $\chi^2 = 44.6$; $p = 0.018$; Eigenvalues: Root $1 = 0.70$; Root $2 = 0.36$). Legends: Cp: *Cuniculus paca*; Ct: *Cerdocyon thous*; Dn: *Dasypus novemcinctus*; Eb: *Eira barbara*; Lp: *Leopardus pardalis*; Lt: *Leopardus tigrinus*; Lw: *Leopardus wiedii*; Nn: *Nasua nasua*; Pc: *Puma concolor*.

Discussion

The terrestrial mammal community of the dense Atlantic Forest of southern Brazil showed trends towards the use of different habitats.

Regarding *Puma concolor* use of space, some felids normally tend to use forest trails, which are usually well-worn and dry. Such characteristics facilitate in walking quietly and easily, helping these animals to surprise their prey (Emmons et al. 1989), since they ambush or capture them by stalking followed by a short rush (Branch 1995). The use mainly of open areas and dirt roads by *P. concolor* can be explained in part by the greater ease in bringing an animal down in these sites, since they can manoeuvre within striking distance of their prey (Currier 1983). Besides hunting activities, juvenile cougars can use large trails and dirt roads to disperse easily (see Beier 1995).

Our results suggest that *L. pardalis* selected large trails. Di Bitetti et al. (2006) mentioned ocelots as having higher capture rates on old dirt roads than on trails in semideciduous forest of the Iguazú National Park, assuming that this was linked to a traditional route or a landmark in their territories. The use of intermediate-cover sites and trails in the study areas reflects the habitat-tolerance of ocelots, which is well adapted to secondary vegetation (Jacob 2002). *Leopardus pardalis* usually uses well-watered habitats such as gallery forests (Mondolfi 1986; Cáceres et al. 2007) or riparian sites (López-Gonzalez et al. 2003), suggesting that proximity to a water source is reasonably important, probably due to food sources. This may be related to its feeding habit, since ocelots can prey on fish, crabs and small mammals that are abundant in these sites (Ludlow and Sunquist 1987; Emmons 1988; Murray and Gardner 1997; Cáceres 2003).

We believe that the relationships of *C. thous* with wider trails and intermediate forest coverage is related to its generalist foraging habits (Berta 1982; Rocha et al. 2004), being rather a habitat generalist and opportunistic species (Medel and Jaksic 1988; Maffei and Taber 2003; Vieira and Port 2007). However, the relationship of the crab-eating fox with more forested habitats has been reported elsewhere (Eisenberg and Redford 1999; Santos et al. 2004) and may be primarily related to its feeding habits (Olmos 1993; Facure and Monteiro-Filho 1996) which are presumably more adapted to forest than to grassland prey.

The relationship of *N. nasua* to intermediate-coverage sites is probably related to its habit requirements, since the species is primarily a forest dweller (Gompper and Decker 1998; Cáceres et al. 2007). Its difficulty in climbing smooth, vertical trunks of large trees, commonly found in dense forests (McClearn 1992), may be related to the use of less-mature, secondary forests as we have seen in the study region. The preference for large trails may be linked with its foraging activities in small familiar groups, since it is primarily terrestrial (Gompper and Decker 1998) and forages mainly on the ground (Bisbal 1986).

Cuniculus paca was recorded more frequently in densely forested habitats here, which is in agreement with findings elsewhere (Pérez 1992; Trolle and Kéry 2005). It travels along fixed trails, but if any of these trails is altered, it immediately rejects it and uses another path (Pérez 1992). Besides hypotheses of feeding site selection and microclimatic adaptation, this microhabitat use may be related to a safe strategy, since *C. paca* is frequently smaller than its predators, hindering its movement through dense forests and narrow trails, which would also facilitate its escape from predation. Its association with watercourses (see also in Pérez 1992) corroborates escape from predation hypothesis, since watercourses could be used as escape route.

Dasypus novemcinctus showed positive relationships with forested habitats (Emmons and Feer 1997; Schaefer and Hostetler 2003) as well as narrow trails (McBee and Baker 1982; Trolle and Kéry 2005) as mentioned elsewhere. In our study, sites with dense forest cover and narrow trails were importantly correlated, indicating high potential sources of resources (like food) for the species. Higher rates of movement of the nine-banded armadillo have been observed in sites where foraging behaviour is facilitated by soil moisture (Taber 1945; Schaefer and Hostetler 2003), similar to the findings seen in densely forested sites of the study areas (F.V.B.

Goulart, pers. obs.). An anti-predator strategy may further explain the main use of these sites by *D. novemcinctus* (McBee and Baker 1982) since dense forested habitats will facilitate prey escape or camouflage (sensu Caro 2005). The relationship between *D. novemcinctus* and proximity to water may be associated with at least two factors: (1) in regard to feeding habits, the species prefers sites near watercourses because its foraging is facilitated by moist soil (Taber 1945); (2) proximity to water may imply an escape strategy from predators, since this species can swim for considerable distances (McBee and Baker 1982).

The preference of *L. tigrinus* for forested sites here was expected, because the species is known to be more associated with forested habitats elsewhere (Mondolfi 1986), besides of being considered a forest dweller in Southern Brazil (Cáceres et al. 2007). Oncillas were reported to use armadillo trails (Guix 1997), in part corroborating our results here. Besides pursuit of prey, the use of narrow trails by oncillas may be associated with a non-overlapping strategy among forest felid species, since other ground competitors or predators were recorded using wider trails (ocelots, crab-eating foxes) or roads (cougars) in this study.

Although *L. wiedii* has arboreal adaptations, it usually travels on the ground (Oliveira 1994, 1998). We recorded this species in denser forested habitats and narrower forest trails. Our records for use of trails may be partly related to facilitating movement between richer feeding sites in the forest, since they hunt mainly arboreal prey (Oliveira 1998). The use of primary forest without interference of trails was not evaluated here, and hence it was not possible to assess how intensely margays use these undisturbed primary habitats, when they are not on trails. On competition with similarly sized species, *L. wiedii* and *L. tigrinus* apparently use similar habitats in the forest, but they might differentiate in other parameters like the use of vertical space, prey type (Oliveira 1994, 1998) and time of activity (F. V. B. Goulart, unpublished data).

Our observations for *E. barbara* corroborate findings elsewhere (Quadros and Cáceres 2001), i.e. the intense use of dense forest sites and the avoidance of large trails and roads. The tayra is rarely found outside forested habitats (Cáceres et al. 2007), which may be partly related to its exploratory behaviour and food habits (Presley 2000). It consumes fruit and small vertebrates, many of which are arboreal and include rodents (Presley 2000).

Results on microhabitat selection suggest mainly a resource partitioning between local mammal species, attributed to the competition and predation effects that have occurred in the past and that are still occurring at different degrees, depending of species. Such results also suggest habitat selection by food exploitation in specific sites, adaptative acclimatisation of species to particular niches, avoidance behaviour of some habitats due to the risk of predation, and competition among ecological similar species. This last case can be exemplified by wildcat species here, since they are congeneric species (genus *Leopardus*) which facilitate the existence of competition (Krebs and Davis 1978). The observed habitat selection by mammals shows a particular structure of space use, confirming and bringing new data for Neotropical larger-sized mammals.

Information on habitat selection of Atlantic Forest mammals is of fundamental importance for their conservation and management, since one could address more effort to the habitat associated with focal species (Stamps and Swaisgood 2007). Additionally, our findings call attention to the significance of environmental heterogeneity (Orians 1991), even that originated from anthropogenic action (like forest trails and roads), which makes possible the species coexistence (Horn and MacArthur 1972), leading to the known patterns of high diversity recognised for the Atlantic Forest.

Acknowledgements

We are very grateful to Russel Wid Coffin and FATMA for allowing field research at the Reserva Ecológica do Caraguatá and Serra do Tabuleiro State Park, respectively. We also thank Conservation International/Brazil, Associação Reserva Ecológica do Caraguatá (in the person of Paulo Sérgio Schveitzer) and FUNPESQUISA/UFSC for logistical support. Appreciation is also due Júlio César, Lenoir, Wanderlei, Adílson, Aranha and Joel (Forest Rangers of Caraguatá), and to Fidêncio Rohling and his family (residents in the Serra do Tabuleiro State Park) for field support. C. H. Salvador de Oliveira, V. Piacentini, F. Souza, H. Mozerle and T. Maccarini helped us with field work in some expeditions. Janet W. Reid helped us with the English translation.

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