Shelter availability and use by mammals and birds in an Atlantic forest area

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Abstract

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This paper describes the types of ground-level shelters, their availability and use by mammals and birds at Parque Estadual Carlos Botelho (PECB), an Atlantic forest area at southeastern Brazil. Eight types of shelters were found: shelters without tunnels under living trees, shelters with tunnels under living trees, shelters under mounds formed by adventitious roots, shelters under fallen trees, burrows not supported by trees or roots, riverbank shelters, stream tunnels and rock shelters. Mammal species that used shelters more frequently were *Agouti paca*, *Philander frenata*, *Lontra longicaudis*, *Metachirus nudicaudatus* and *Trinomys iheringi*. Utilization of shelter types and shelter topographic locations by these six species was roughly similar to the proportions in which shelters of different types and locations were monitored, with the exception of otters, which are semi-aquatic mammals and used mainly riverbank shelters.

Contrary to expectations, animals did not choose shelters with entrances fitted to their sizes. Shelters were used either by a single species or by different species. I hypothesize that at the PECB other factors such as microclimate inside shelters must be more important in determining shelter use than shelter external characteristics or topographic location. Some species, as coatis *Nasua nasua* and probably small didelphids and birds, enter shelters to search for invertebrates and small vertebrates.

Key words: Shelter site, Atlantic forest, resource availability, Mammalia, Aves

Resumo

Beisiegel, B.M. **Disponibilidade de abrigos e seu uso por mamíferos e aves em uma área de Mata Atlântica**. *Biota Neotrop.* Jan/Abr 2006, vol. 6, no. 1, http://www.biotaneotropica.org.br/v6n1/pt/abstract?article+bn00206012006. ISSN 1676-0611.

Este artigo descreve os tipos de abrigos encontrados no solo, sua disponibilidade e uso por mamíferos e aves no Parque Estadual Carlos Botelho (PECB), uma área de Mata Atlântica no sudeste do Brasil. Foram encontrados oito tipos de abrigos: abrigos sem túneis sob árvores vivas, abrigos com túneis sob árvores vivas, abrigos sob raízes adventícias, abrigos sob árvores caídas, escavações não sustentadas por raízes ou árvores, abrigos em barrancos de rios, túneis formados por riachos e abrigos entre rochas. Os mamíferos que mais usaram os abrigos foram *Agouti paca, Philander frenata, Lontra longicaudis, Metachirus nudicaudatus* e *Trinomys iheringi*. A utilização dos tipos de abrigos e das localizações dos mesmos por estas seis espécies foi, de forma geral, proporcional à quantidade de abrigos monitorados para cada tipo e cada topografia, com a exceção das lontras, que sendo mamíferos semi-aquáticos utilizaram principalmente abrigos nos barrancos de rios.

Ao contrário do esperado, os animais não escolheram abrigos cujas entradas correspondessem a seus tamanhos corporais. Os abrigos foram usados tanto por uma só espécie quanto por várias espécies. Sugiro que no PECB fatores como microclima no interior dos abrigos usados pelas espécies devem ser mais importantes na seleção dos abrigos do que as características externas e localização dos mesmos quanto à topografia. Algumas espécies, como quatis *Nasua nasua* e provavelmente pequenos didelfídeos e aves, entram nos abrigos em busca de invertebrados e pequenos vertebrados.

Palavras-chave: Abrigo, Mata Atlântica, disponibilidade de recursos, Mammalia, Aves

Introduction

Shelter is an essential resource to many species of animals (McComb & Noble 1981, Ruggiero et al. 1998) and shelter availability may be a limiting factor in home range use for some species, as northern raccoons, *Procyon lotor* (Endres & Smith 1993), badgers, *Meles meles* (Doncaster & Woodrofe 1993) and red foxes, *Vulpes vulpes* (Lucherini et al. 1995) although not for others as fox squirrels, *Sciurus niger* (Robb *et al.* 1996) and otters, *Lontra longicaudis* (Pardini 1996, Pardini & Trajano 1999).

Shelter can afford protection against predators and from weather (Berner & Gysel 1967). Compared to external environment, shelter temperatures are more stable, with lower maximum and higher minimum temperatures (Berner & Gysel 1967). Shelter use by mammals and birds at Atlantic Forest areas has been subject of only a few investigations (e.g. Miles et al. 1981, Monteiro-Filho & Marcondes-Machado 1996, Pardini & Trajano 1999, Briani et al. 2001).

In the present paper I report on the types of shelters found in an Atlantic forest area, the Parque Estadual Carlos Botelho (PECB), and their use by mammals and birds. I described the animals that used the shelters, verified whether, in a short-term, each shelter was used by a single species or more than one and discussed the hypothesis that mammal species display preferences for shelter types or shelter topographic location.

Material and Methods

Study area

The PECB is located in the state of São Paulo, southeastern Brazil, at 24°00' - 24°15' S and 47°45' - 48°10' W, and its total area is 37,793.63 ha. Three other reserves, the Parque Estadual Intervales, the Parque Estadual Turístico do Alto Ribeira and the Estação Ecológica de Xitué are contiguous to the PECB, and together they have an area of 116,836.99 ha, being one of the major Atlantic Forest remnant areas.

This study was conducted in the São Miguel Arcanjo Base of the PECB. This area is located in the Guapiara Highlands, in the Atlantic Plateau. The topography is characterized by low, parallel hills (Pfeifer et al. 1986). The altitude ranges from 700 to 839 m. A river, five big streams and hundreds of small streams form a dense drainage that belongs to the Paranapanema River drainage. The climate is type Cfb of Koeppen, described as mesothermic humid without a dry winter. There is marked seasonality in rainfall, however, with a wetter season from October to March and a drier season from April to September. Annual precipitation is 1.475 to 2.582 mm and the average precipitation in the drier month is 49 mm (Pfeifer et al. 1986, Negreiros et al. 1995). Average temperatures are 18°C to 20°C, with a minimum of 3°C and maximum of 29°C (Domingues & Silva 1988). Vegetation is classified as Latifoliate Pluvial Tropical Forest (Domingues & Silva 1988). The study area comprised mainly primary forest, although logging occurred in many places in the past, and there are some patches of secondary forest.

The Park has a diverse and abundant fauna with at least 267 species of birds in 42 families (Figueiredo & Custódio-Filho 2003), including the jacu, *Penelope obscura*, the jacutinga, *Pipile jacutinga* and other endangered species, plus 23 species endemic to the Atlantic forest (Sick 1986). The rich mammalian fauna of the Park includes the two large South American felids, *Panthera onca* and *Puma concolor*, the two peccaries, *Tayassu tajacu* and *T. pecari*, deer (*Mazama sp.*), paca (*Agouti paca*), agouti (*Dasyprocta azarae*), bush dog (*Speothos venaticus*), crab-eating fox (*Cerdocyon thous*) and many other species of medium and large mammals (Beisiegel 1999, Beisiegel & Ades 2002, 2004).

Data collection and analysis

Most of this work was conducted from February 1997 to August 1999. The shelters were found in the course of a study on the bush dog, Speothos venaticus. Thus, the shelters marked had the characteristics expected for a canid shelter such as the presence of tunnels and multiple entrances (Egoscue 1962, Kilgore Jr 1969, Johnsingh 1982, Aquino & Puertas 1997). This limited the work to (1) ground level shelters; (2) shelters that had at least one entrance that was large enough to allow the passage of a bush dog (roughly 15 cm diameter). I did not attempt to identify individually the animals using the shelters, nor did I attempt to explore the shelters with devices such as periscopes or fiber-optic systems, which would allow a thorough inspection of the interior of the shelters (Moriarty & McComb 1982). Since the bush dog is a semi-aquatic species and may have a very large home range (Beisiegel 1999, Beisiegel & Ades 2004), almost all the streams that were accessible in up to half a day walking from the internal road of the park were searched, comprising an area of roughly 4,000 ha. In addition to stream vicinities, which included hillsides, hilltops were also searched because of the high shelter densities found in these areas.

Two methods were used to identify the animals that used the shelters, consisting of placing at the entrances of the shelters (1) sand plots to register tracks and (2) passive infra-red camera traps (Trail Master 500[®] and Trail Master camera kit[®], Goodson and Associates, Inc.). Sand plots were used in 339 shelters and camera traps were used in 62 shelters. In 38 of these both methods were used, totaling 363 shelters for which I attempted identification of users.

The minimum time lapse between consecutive pictures was 2 min and for each picture the camera registered the date and time. For sand plots, I registered the dates of

placement and checking of plots and the tracks found. Tracks of mammals were identified using the guide by Becker & Dalponte (1991). Whenever possible the animals were identified to species or genus, but in many instances it was just possible to identify the Family (e.g. Didelphidae) or even just Class (e.g., Mammalia, Aves) or size of the animal.

Sampling periods for sand plots (number of days from placement to last checking) ranged from one to 446 days (average = 71 days, s.d. = 62 days). During the sampling period, each sand plot was checked from one to 14 times (average = 2.5 times, s.d. = 1.9). Sampling periods for camera traps varied from one to 22 days (average = 6.7 days, s.d. = 4.7 days). However, these are just indices of the real sampling effort, since many factors affected data collection for both methods. Rain was the main problem for the use of sand plots, but sometimes the large number of tracks accumulated in a plot also prevented the identification of the user. Camera traps sometimes ran out of film or batteries, but the most frequent trouble was the false triggering of the sensors by the heath or by the raising of water levels.

The shelters were classified in types according to external and internal features and maximum height of entrances and topography were described for 91 of the shelters which users had been identified. To evaluate availability of shelters in different topographic features, strip counts of shelters were conducted along 9,362 linear meters, comprising 2,139 m of hilltops, 1,733 m of hillsides, 2,075 m of small streams (which comprised slopes and narrow valleys), 1,589 m of river plains along large streams (only large valleys), 574 m of river plains with undifferentiated alluvial deposits (which had shelter types and availability different from river plains, see below) and 1,252 m inside large streams (counting only riverbank shelters). In trails with a good visibility of the ground, all shelters in a 5-meter wide strip were counted, and in trails with dense herbaceous vegetation all shelters were counted in a 3-meter wide strip. This was due to the fact that, in sites with dense vegetation cover, a shelter would only be seen if it was very near the trail. Trails were either marked each 50 m or measured with a GPS (E-Trex, Garmin). The density of river bank shelters were estimated as the number found per km of margin and for the remaining shelters, as the number per area, calculated multiplying the length of the trails by the width of the searched strips (3 or 5 meters).

The work was performed in many steps. I began to mark the shelters that could be used by *Speothos venaticus* in February 1997, without recognizing different shelter types or topographies; sand plots were placed on shelter entrances from September 1997 and camera traps were used from June 1998 to the end of the study. Shelter types and topographic locations began to be noted on May 1998. Many shelters were monitored with sand plots before May 1998 and I did not return to many of them to note topographic location or shelter type after the monitoring period. Therefore, shelter characteristics were not noted for all shelters marked or monitored. A total of 742 shelters were marked, from which 504 could be assigned to one of the eight shelter types described below. Also from these 742 shelters, 343 were monitored with sand plots and /or camera traps, but shelter type and location were not noted for all of the monitored shelters. Of the 343 monitored shelters, type was noted for 253 shelters and topographic location was noted for 294. Both type and topography were noted for 232 of them.

Transect counts of shelters were conducted during 2001-2002. Due to the large number of marked shelters, great extension of the study area and small number of camera traps (three cameras), the shelters that were selected to be monitored were those that appeared most likely to be used by a group of *Speothos venaticus*. These shelters were the larger ones, or had most evidences of frequent use, such as entrances with clean paths leading to them, or were located near the sites where most bush dog tracks were found (Beisiegel & Ades 2004). Therefore, there was no systematic or random selection of the shelters that were monitored and the results described below can be only qualitatively interpreted.

Results

Shelter site types

Eight types of shelter sites were found (Figures 1 and 2). Most shelters (n=504) could readily be assigned to one of these eight types, based on internal characteristics, such as the presence and the size of chambers (defined as cavities with an inner diameter larger than entrance width) and of tunnels (defined as a cavity with a diameter much smaller than its observable length) and on the location of the shelter, such as under living tree, under adventitious roots of one or many trees, under fallen log, under rocks, or not under any of these, on riverbanks, and on tunnels formed by small streams. In a few cases, shelters presented characteristics of two or more types.

Shelters without tunnels under living trees (WT)

These shelters are located under or among the roots of a living tree or inside the hollow basis of a tree, and they do not form tunnels, being composed mainly by a cavity. The largest width of the shelter is observed at the entrance or a chamber with a smaller entrance. Few shelters of this type were marked because I considered them unlikely to be used by bush dogs. One shelter fitted with a camera trap had a strong animal smell and was regularly used by a didelphid (*Marmosops* sp.) and a bird (*Grallaria varia*, Passeriformes: Formicariidae). Two shelters had felid feces inside them, suggesting that they could be used as territorial marks. Many shelters of this type were located on or near hilltops and from inside them an animal could have a good view of the surroundings. I also observed a whitelipped peccary, *Tayassu pecari*, entering a shelter of this type and staying there for some minutes, during daytime. From the 504 shelters for which the type was described, 34 were WT shelters. In the strip counts one shelter of this type was found on a hilltop and three on hillsides.

Shelters with tunnels under living trees (TULT)

These were different from the WT type described above because they always were composed of at least one tunnel, which could just connect two entrances or connect different entrances and chambers, not all of which were visible from outside. They could be (a) the cavity inside the basis of a living tree, with the trunk or roots delimiting the entrances of the shelter; (b) a tunnel dug under the tree roots. Didelphids (Philander frenata and Metachirus nudicaudatus), pacas, one armadillo (Dasypus novemcinctus), one otter (Lontra longicaudis), unidentified birds, unidentified small rodents, coatis and unidentified large animals used these shelters. Of the 504 shelters, 174 were of this type. In the strip counts, eight TULT shelters were found on hilltops, seven on hillsides, six on river plains and four on small streams. These were the most frequent shelters found at hillsides and riparian habitats (Table 1).

Shelters under mounds formed by adventitious roots (UMAR)

These shelters were mainly found on two types of sites: hilltops and some river plains. These sites probably had soils less compacted when compared to the rest of the study area. This is due, in the hilltops, probably to declivity, and, in some river plains, to undifferentiated alluvial deposits (Domingues & Silva 1988) with high sand and water content. Due to this soil "softness" these sites have many trees with adventitious roots (also called prop or stilt roots), which increase the stability of the trees (Waisel, Eshel & Kafkafi 1996). These adventitious roots are normally covered by leaf-litter, which in turn harbor other trees, thus forming large mounds, with large chambers and, probably due to soil softness, large tunnels (frequently more than 50 cm diameter) inside them. These shelters can be connected by tunnels, and thus comprise an area of several square meters. They may have small (Figure 1) or very large entrances (Figure 2a). At hilltops and river plains with undifferentiated alluvial deposits they were found in a higher density than the other types of shelters (Table 1). Although these shelters were larger than the other types (Figure 1), mainly small mammals and birds used them. Of the 504 shelters, 138 were of this type. On the strip counts they were found on hilltops (61 shelters) and river plains with undifferentiated alluvial deposits (22 shelters).

These were dug normally under the basis of a fallen tree. Entrances might be dug among or below roots or below the trunk. Often the fallen trunk itself had a cavity inside it, which was used as a tunnel with sometimes many entrances to it. The roots of the fallen tree could also form a shelter, similar to a WT shelter but having tunnels exiting from the inner part of the shelter. Pacas, didelphids, birds and small rodents used these shelters. Of the 504 shelters, 79 were of this type. In the systematic strip counts, one FT shelter was found on a hilltop, three on hillsides, three on river plains and four on small streams.

Burrows not located under fallen trees, tree roots or rocks (BU)

These shelters consisted in a tunnel or chamber that were dug at a slope or at the plain ground, with no supports such as roots, rocks or fallen trees. Their entrances were frequently found in groups of three close (ca. 1-2 m) to one another, sometimes clearly differing in age. Frequently, they were used only once or a few times. Two of these shelters were used many times: one of them was used by a pair of juruvas, Baryphtengus ruficapillus (Figure 2b) when it was marked in 1997 and it was still used by juruvas and also by a rodent (Trinomys iheringi) when a camera trap was used to monitor it one year later. These were the only animals that used this shelter. Other similar shelter was repeatedly used by a pair of juruvas, and no other animals were observed to use it. This was the only shelter type found at the internal roads and firebreaks of the park. Of the 504 shelters, 22 were of this type. In the strip counts they were found on hilltops (one shelter), hillsides (one shelter) and small streams (one shelter).

Riverbank shelters (RB)

These consisted of tunnels dug at the banks along rivers. They could have either (a) many entrances at different heights from the water level, which were used by otters, pacas and small rodents; (b) just one obvious entrance at the water level, from which often a small stream exited (Figure 2c), making it difficult to see the interior of these shelters, which were used by otters; and (c) one entrance at the water level in which the water entered, with a dry platform inside it, which were used by pacas and likely by otters, since some of them had otter tracks and feces on nearby beaches. In one shelter fitted with a camera trap, pictures of a Chironectes minimus and of a rodent were obtained, both of which were swimming and thus could be just passing in front of the shelter. Entrances of these three types could also belong to the same shelter. Of 504 shelters, 45 were of this type. In the systematic strips counts, nine RB shelters were found.

Shelters under fallen trees (FT)

Stream tunnels (ST)

These shelters were formed by a partly subterraneous small streams, which opened large tunnels. Animal tracks could be found entering the tunnel in the mud of the stream (Figure 2d). The animals could use these tunnels in the dry season or use side tunnels exiting from the stream tunnels. Of the 504 shelters, eight were of this type, and two of these were used by pacas. In the systematic strip counts no shelter of this type was found.

Rock shelters (RO)

These shelters were cavities among rocks, presenting evidences of use by animals. They could have one or more entrances. This type was very rare at the PECB, although it is one of the most frequently mentioned in the literature, being reportedly used by many species (e. g. *Speothos venaticus*, Linares 1967; *Metachirus nudicaudatus*, Miles et al. 1981; *Procyon lotor*, Endres & Smith 1993; *Martes americana*, Ruggiero et al. 1998; *Lontra longicaudis*, Pardini & Trajano 1999). Of the 504 shelters, only four rock shelters with some evidence of use were found; one of them was used by a paca and the users of the others were not identified. In the systematic strip counts no shelter of this type was found.

Monitored shelters

I identified at least the size of the animals using 133 of the 363 monitored shelters. The disparity between the number of monitored shelters and the number of shelters which had their users identified is due to the problems described above, such as rain and false triggering of camera traps. Sand plots alone identified the animals using 72 shelters and camera traps alone identified the animals using (or passing in front or above) 31 shelters. Animals using eight shelters were identified by both methods and at four shelters I either saw the animal exiting from it or found signs (tracks, feces or feathers) that allowed the identification of the animals. Overall success of camera traps in identifying the users of shelters was higher than the success of the sand plot method (76% vs. 28%). Table 2 presents the number of shelters of each type and in each topographic location monitored. Most monitored shelters were of TULT (n = 103, or 40.6% of monitored shelters), UMAR (n= 64, or 25.2% of monitored shelters) and FT (n = 49, or 19.3% of monitored shelters) types, but it is not possible to determine whether this was due to these shelters being the most common types (see item 3.7 below) or to they having more characteristics of a shelter which could be used by bush dogs. There was less disparity among the amount of monitored shelters in the main topographic features, hilltops (n = 63, 21.3% of monitored shelters), hillsides (n = 49, 16.7% of monitored shelters), river plains (n = 68, 23.1% of monitored shelters) and small streams (n = 91, 31% of monitored shelters). Less

shelters were monitored in riverbanks (n = 16, 5.4% of monitored shelters) and river plains with undifferentiated alluvial deposits (n = 7, 2.4% of monitored shelters), due to the small proportion of the study area occupied by these topographies.

Shelter use in relation to shelter type

Animals in pictures obtained by camera traps could be entering or exiting, be inside the shelters, just be in front of them or be on the tree above them (Table 3). In some of these pictures, it was not possible to know whether the animals entered the shelters after the pictures were taken, because the minimum time lapse between consecutive pictures was of two minutes. Because of this, results were divided in two types: all records and records of animals inside shelters. Both types are presented in Table 3 and on item 3.4, but the other Tables and analysis considered only the animals that entered the shelters.

Two species of birds were pictured inside the shelters and tracks registered the use of 31 different shelters by unidentified birds. Eight mammal species were identified by tracks, pictures, feces or sightings and two mammals were identified to genus level by pictures.

For animals identified to species level, Agouti paca, Philander frenata, Nasua nasua, Trinomys iheringi, Metachirus nudicaudatus and Lontra longicaudis were the species that used more shelters (Table 3). A. paca was the species with the highest number of used shelters and also the species which used the highest number of shelter types, using all types except WT and BU (Table 3). The percent of TULT shelters used by pacas (43% of the shelters used by the species for which the type has been recorded) was similar to the percent of TULT shelters in relation to the total number of shelters monitored (40.6%). The percents of RB (7%), ST (4%) and RO (2%) shelters used by this species were also similar to the percent of monitored shelters of these types. The percent of UMAR shelters used by pacas (9%) was much lower than the percent of monitored shelters of these type and the percent of FT shelters used by pacas (35%) was higher than that of monitored shelters of these type.

All other identified species used one to three types of shelters (Table 3). *P. frenata*, despite being the species which used the second highest number of shelters, used shelters of only two types (TULT and UMAR). *T. iheringi* may have used more shelters than the six listed in Table 3, because in some pictures appeared small rodents that resembled *T. iheringi* but could not be identified with certainty. *L. longicaudis* used three RB and one TULT shelters. *N. nasua* entered five shelters of TULT and UMAR types and was registered in front of three more shelters, being one TULT, one UMAR and one ST. Table 1. Shelter availability at the Parque Estadual Carlos Botelho, in number of shelters / hectare, divided by shelter types and location. For river banks, availability is given as number of shelters / linear km of stream.

			Shelter	location		
Shelter type	Hilltop	Hillside	River banks	River plain	River plain	Small stream
					with	
					undifferentiated	
					alluvial deposit	
WT	0.9	3.5	0	0	0	0
TULT	7.5	8.1	0	11.3	0	3.9
UMAR	57.0	0	0	0	168.4	0
FT	0.9	3.5	0	5.7	0	3.9
BU	0.9	1.2	0	0	0	1
RB	0	0	7.2	0	0	3.9
Total	67.3	16.2	7.2	17.0	168.4	12.5

Table 2. Number of monitored shelters for which either type, topographic location, or both, were recorded, at the Parque Estadual Carlos Botelho.

					topograph	у			
		ht	hs	rb	rp	rpuad	SS	not recorded	total
	wt	1	3		2		3	2	11
	tult	9	16		31		41	6	103
	umar	45	4			7		8	64
0	ft	2	9		20		14	4	49
ype	bu	1	1		1		1	2	6
-	rb			15					15
	st		1		2		2		5
	rd						1		1
	not recorded	5	15	1	12		29		62
	total	63	49	16	68	7	91	22	

Family	Species					Shelt	er type			
		ΤW	TULT	UMAR	FT	BU	RB	ST	RO	Not d
Momotidae	Baryphtengus ruficapillus					(2)				
Formicariidae	Grallaria varia	(1)								
	Batara cinerea			1						
ė	Unidentified bird		(16)	(1)	(6)		(1)	(1)		(3)
Didelphidae	Marmosops sp.	(1)	-							
	Philander frenata		(1)	(9)						
	Metachirus nudicaudatus		(1)	(2)	(1)					(1)
	Monodelphis cf . americana		-							
	Monodelphis cf. scalops			-						
	Chironectes minimus						-			
·	Unidentified didelphid		1	(1)	(1)					
Agoutidae	Agouti paca		(20)	(4)	(16)		(3)	(2)	(1)	(9)
Echimyidae	Trinomys iheringi		(3)	(1)		(1)				(1)
Echimyidae?	Unidentified very large rodent		(1)							
Sciuridae	Sciurus ingrami		2 (1)	1						
Muridae	Oryzomys sp.		1							
i	Unidentified small rodent		(8)	(1)	(9)		2 (1)			(3)
Dasypodidae	Dasypus novemcinctus		(1)							
Mustelidae	Lontra longicaudis		(1)				(3)			
Procyonidae	Nasua nasua		4 (3)	3 (2)						
Tayassuidae	Tayassu pecari	(1)								
i	Unidentified small animal (track		(6)	(4)	(2)		(1)			(2)
	size up to two cm)									
i	Unidentified large animal		(11)	(4)	(2)		(2)			(9)

Among the types of shelters, TULT type was the one that presented the highest number of shelters used, as well as the one that was used by the highest number of species (Table 3). The only species that did not use this type of shelter were those that used only one or two shelters (*B. ruficapillus*, *G. varia*, *Marmosops* sp. and *T. pecari*). UMAR shelters, which were the larger ones, were proportionally more used by the small *Philander frenata*, small rodents and small unidentified animals. RB shelters were mainly used by pacas and otters.

Multiple and repeated users

Sixty-five shelters were used by more than one species or were used by the same species on more than one day or night. Nineteen of these were used only by one species: one (TULT) by an unidentified small bird; two (RB) by otters; ten by pacas (3 TULT, 5 FT, 1 RB, 1 of unidentified type); two (UMAR) by *P. frenata*; one (TULT) by coatis and three (1 TULT, 1 UMAR, 1 of unidentified type) by *T. iheringi*.

Thirteen shelters were used by the same species (or the same individual) on more than one night or day and were also used by other species. Six of these were used only by a pair of species (both species used the shelter more than once and no other animal used it): one WT shelter was used twice by Marmosops sp. and four times by Grallaria varia; one BU shelter was used by a pair of juruvas (Baryphtengus ruficapillus) and by Trinomys iheringi; one TULT shelter was used twice by otters and twice by Metachirus nudicaudatus; M. nudicaudatus also used one FT shelter on two of four nights in which the camera trap was used, and this shelter was also repeatedly used by A. paca (three nights); one UMAR shelter was used by Philander frenata and a small unidentified rodent and a TULT shelter was used many times by Agouti paca and a squirrel was pictured inside it two times. One TULT shelter was used many times by Trinomys iheringi and Philander frenata and coatis also entered it. Two TULT shelters were used repeatedly by three species and other species used them once: one of these was repeatedly used by Philander frenata, one unidentified mouse and one unidentified rodent, and Agouti paca and Metachirus nudicaudatus also used it. The other one was used many times by pacas, Trinomys iheringi and Philander frenata, and M. nudicaudatus used it once (Figure 3). This shelter was also entered by coatis and one young didelphid was pictured over its entrance. The four remaining shelters were used more than once by one species and once by another species: two TULT shelters were used repeatedly by pacas, one of them also by a bird and one of them also by a bird and a rodent; one TULT shelter was used on four nights by Philander frenata and once by a rodent; and one UMAR shelter was used twice by P. frenata and once by M. nudicaudatus.

Five shelters were used by one species more than once, but it was not possible to determinate the species (unidentified birds, rodents, didelphids and small animals). In these shelters, identical unidentified tracks were found repeatedly. On one ST shelter monitored by camera trap *Nasua nasua*, *Monodelphis americana* and one unidentified rodent were pictured on at least two different days each species, but none of them inside the shelter.

Fourteen shelters were used by two species, once by each one of them. Seven shelters were used by three species, once by each one of them. For the remaining six of the 65 shelters it was not possible to determine how many species entered the shelter due to differences in the definition of the tracks on the many monitoring days; on one of them, for instance, the tracks found on one day allowed only to determinate that a large animal had entered the shelter and on other day tracks of paca were found on the shelter; so it was not possible to determinate whether the large animal which tracks were found before was also a paca or not.

Shelter use in relation to topographic location

Pacas used shelters in all types of location (Table 4), including three shelters at hilltops. Percents of topographic locations of shelters used by pacas were similar to percents of shelters monitored in each topography, except for shelters in river plains, which percent were almost twice the percent of monitored shelters, and shelters in hilltops, which percent was much smaller than that of monitored shelters. Philander frenata, Metachirus nudicaudatus and Trinomys iheringi used shelters at hilltops, hillsides and small streams, which were among the topographies where more shelters were monitored, but did not use shelters at river plains, which also had a high number of monitored shelters. Coatis used shelters on four locations, but they were probably only foraging inside the shelters. Most shelters used by otters were on riverbanks, but this species also used one shelter in a small stream. Other species used shelters in only one location type, but they used a small number of identified shelters.

Shelter use in relation to entrance height

Contrary to expectation, animals rarely chose a shelter with entrances fitting their own size (Table 4). This was clearly evident in most pictures (Figure 4; see also Figure 2 b). As a measure of the relationship between shelter entrance size and body size of the users, I compared shoulder height (SH) of the users with maximum height of shelter entrances, for the few species for which I found the SH value. Pacas have shoulder heights of 27-32 cm (Emmons & Feer 1990), and the average entrance height of the shelters used by them was 41.5 cm. *Metachirus nudicaudatus* has a shoulder height of 11-17.5 cm (Richard-Hansen et al. 1999)

			Location	of shelters			Max	cimum height	of entrances	(cm)	SH (cm)
1	HT	HS	RB	RP	RPUAD	SS	Z	range	average	s.d.	
B. ruficapillus		2 (100%)					1		30		
G. varia		1 (100%)									
Marmosops sp.		1 (100%)									
P. frenata	6 (46%)	3 (23%)				4 (31%)	10	20-200	63.9	53.9	12-24.5
M. nudicaudatus	1 (20%)	3 (60%)				1 (20%)	ŝ	20-60	40	20	11-17.5
A. paca	3 (6%)	10 (20%)	3 (6%)	20 (40%)	2 (4%)	12 (24%)	30	16-100	41.5	19.5	27-32
T. iheringi	1 (17%)	3 (50%)				2 (33%)	3	20-200	83.3	101.2	
S. ingrami		1 (100%)					1		24		
Oryzomys sp.		1 (100%)									
D. novemcinctus		1 (100%)					1		48		17-27.5
L. longicaudis			3 (75%)			1 (25%)	4	20-60	35	15.1	
N. nasua	1 (20%)	1 (20%)			1 (20%)	2 (40%)	4	20-200	83.5	79.6	

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and maximum heights of entrances of three shelters used by the species were 20, 40 and 60 cm. The only shelter used by an armadillo *Dasypus novemcinctus* (SH 17-27.5 cm, Richard-Hansen et al. 1999) had a maximum entrance height of 48 cm; SH of *Philander frenata* was not found but the values for the similar *P. opossum* are 12 to 24.5 cm (Richard-Hansen et al. 1999), while the average entrance height of its dens was 83.5 cm.

Shelter availability in relation to shelter type and topographic location

Topography was varied across the study area. Parts of the area had extended river plains, while others had streams surrounded by high, steep hillsides. The trails used to estimate shelter availability in this study were selected in order to cover the six topographies of the area but not to determine the proportion of the total study area covered by each topographic location. Therefore, the estimative of number of shelters of each type by hectare can only be applied to each topographic location, and not to the total area.

Shelter availability was similar (12.5 - 17 shelters / ha) at hillsides, river plains and small streams (Table 1). At hilltops and river plains with undifferentiated alluvial deposits, however, shelter availability was higher (*ca.* four to ten times higher). The shelters found in these sites were mostly of UMAR type. River plains with undifferentiated alluvial deposits had a very high density of shelters of this type, but this topography represented a small proportion of the study area. Therefore, the overall availability of UMAR shelters across the study area must not be much increased by this high density.

TULT was the most common shelter type in all topographies except hilltops and river plains with undifferentiated alluvial deposits. So, despite the absence of a comparative estimative of number of shelters / hectare for the entire study area, this was probably the most common shelter type. FT shelters were the second most common type found in most topographies, and BU and WT shelters were less found in all topographies. ST and RO shelters were not found in the systematic searches, thus being probably the less frequent shelter types in the study area. The availability of RB type was estimated as number of shelters / linear km of margin and is not comparable to the estimates of the other shelter types.

Discussion

This study represents a basic description of the types of shelter found, of their use by mammals and birds and of their availability in Atlantic Forest sites, providing an initial step for future studies of shelter use in this biome. Since there was no attempt to verify what kind of use by the animals was involved, animals which used shelters identified in this study could use them as nocturnal or diurnal sleeping sites, natal dens, scent-marking sites, temporary resting sites (Prestrud 1992, Larivière & Messier 1998) or food caches (Post et al. 1993), or they could be entering the shelters to forage.

Of the animals which entered the shelters, B. ruficapillus, A. paca, L. longicaudis, M. nudicudatus, P. frenata and D. novemcinctus are reported to use groundlevel shelters as sleeping or resting sites (Miles et al. 1981, Carter & Encarnação 1983, Sick 1986, Beck-King & Helversen 1999, Pardini & Trajano 1999, Moraes Jr. 2004). All these species were observed to use repeatedly the same shelters in this study, except D. novemcintus. This species is reported to use a shelter for some time, but it can have up to five entrances (Carter & Encarnação 1983), so if the armadillo photographed entering the shelter used it more than once as a sleeping site, it could have used other entrances during the three days in which a camera trap was used in this shelter. At the Amazonian forest much more nests of Metachirus nudicaudatus were found on the ground level than nests of Philander opossum, which nested mainly 8-10 m above the ground (Miles et al. 1981). The opposite result found in this study may reflect either a population density much greater for P. frenata than for M. nudicaudatus at the PECB, a real difference in the degree of arboreality between P. frenata and M. nudicaudatus, or the preferential use of less conspicuous shelters by M. nudicaudatus (Miles et al. 1981, Moraes Jr. 2004). Actually, Miles et al. (1981) stated that shelters of *M. nudicaudatus* were found only due to the use of spool-and-line devices, for they were perfectly concealed among leaf mounds. Other data obtained in this study may also suggest interesting subjects for future ecological studies of some species. Philander frenata was the main user of the very large UMAR shelters found on hilltops. These shelters had deeply caved paths entering them, suggesting long - term use; it would be valuable to follow the use of these shelters in a long-term study in order to verify whether they are used always by the same individuals or some of their progeny as it happens with other species as European badgers Meles meles (Doncaster & Woodrofe 1993).

Animals that appeared in pictures but were not entering, exiting or inside the shelters could be just passing in front of them, investigating them or using them as a resource. It was already mentioned that felids could use WT shelters as deposition sites for scent marks. Coatis (*Nasua nasua*) probably entered shelters to search for invertebrates and little vertebrates inside them (Beisiegel 2001), since I never observed coatis resting inside shelters in the course of a long-term study (Beisiegel & Mantovani 2006). I observed a white-lipped peccary (*Tayassu pecari*) enter a WT shelter and stay there for some minutes. The animal could either be foraging there or leaving a scent mark, although the latter is improbable since these animals scent–mark other

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members of the herd rather than objects of the environment (Hernandez et al. 1995). Squirrels (Sciurus ingrami) were sometimes photographed at shelter entrances and a squirrel was pictured twice at a shelter used by an Agouti paca, entering the shelter and exiting it with a big seed in its mouth (Figure 5). As both Agouti paca and squirrels are frugivore /granivore (Robinson & Redford 1986, Emmons & Feer 1990, Jannini 2000) the squirrel probably entered the shelter searching for seeds left by the paca. The other pictures of squirrels could be due to the same behavior or squirrels could be only passing in front of the sensor. Although S. ingrami use tree cavities to shelter (Monteiro-Filho & Marcondes-Machado 1996) it is likely that they use only nests located well above the ground. One small didelphid and one Marmosops sp. pictured outside shelters were looking to the interior of the shelter when photographed, probably searching for invertebrates. The formicariid Grallaria varia used the interior of a shelter on many days, but Sick (1986) states that they use perches as sleeping sites, making it unlikely that the bird used the shelter to sleep. Still, this species is frequently observed at the PECB and the constancy of use of a single shelter by (possibly) a single individual is interesting. On the other hand, the position of Monodelphis spp. in all the pictures suggested that their presence was not related to shelter use.

Species that used many times the same shelter seldom used it on consecutive nights. This could be misleading because most shelters had more than one entrance, but the animals might be using many shelters. In a Costa Rican forest site, two *Agouti paca* used an average of 3.5 burrows at a time (Beck-King et al. 1999). The raccoons (*Procyon lotor*) studied by Endres & Smith (1993) used an average of 27.2 to 41 shelters / year, and one female *Metachirus nudicaudatus* used four different sleeping sites on three nights (Moraes Jr. 2004). Alternation in shelter use may be a strategy of predator avoidance and of parasite control.

Simultaneous use of the same shelter by many species observed in this study is not uncommon in other regions. Northern raccoons (*Procyon lotor*), opossums (*Didelphis marsupialis*) and striped skunks (*Mephitis mephitis*) sometimes shared the same shelters in Kansas (Shirer & Fitch 1970). In general the skunks excavated the shelters and the other two species benefited from their burrows, which were also used by six other mammal species and nine species of reptiles.

Utilization of shelter types and shelter topographic locations by the six species for which more shelters were identified was roughly similar to the proportions in which shelters of these types and locations were monitored, with the one obvious exception of otters, which are aquatic mammals and used mainly riverbank shelters.

However, other interesting exceptions occurred. Philander frenata did not use FT shelters and Nasua nasua did not enter FT shelters, nor was photographed near them, although both species used the TULT and UMAR shelters and the number of FT shelters monitored was similar to the number of UMAR shelters monitored. FT shelters occurred on the same topographic locations of TULT shelters, so it would be interesting to investigate whether these species really do not enter FT shelters (and why) or this is due to a small number of identified shelters. The proportionally low use of UMAR shelters by pacas is not surprising, because most monitored shelters of this type were located at hilltops. Pacas prefer areas near water, since they are good swimmers which, when pursued, flee to the water (Pérez 1992). Due to this preference, it is surprising that pacas used three shelters at hilltops. If the choice of shelter site location by pacas is determined by availability of streams as sources of drinking water or preferred sites to forage, this data could be attributed to the large amount of streams that exist in the study area; anywhere there is one watercourse that can be quickly reached by mobile animals, such as mammals and birds. On the other hand, if the choice of shelter is determined by the possibility of using water as an escape route during an attempted predation, the use of this three hilltop shelters is difficult to understand. Also surprising was the utilization of a TULT shelter near a small stream by otters. This stream was less than one meter in width and too shallow to allow an otter to swim in most of its extension. At the study area, most streams are small and otter presence is mainly restricted to the larger ones (pers. obs.), where the animals can swim. Pardini (1996) verified that during the dry season otters increase the numbers of feces deposited at conspicuous sites at the Betari river, SP, and suggested that one explanation for this increase could be that the feces are used as scent marks and the enhancement of competition for food in the dry season causes the increase of deposition of scent marks. At the PECB, otters also increase the frequency of scent mark deposition at the drier season, including the use of some scent marking sites on very small streams on which they are not able to swim (pers. obs.). This may be due to lower food availability at the drier season, which may force the animals to expand the area where they search for food. The enhanced use of small streams on the drier season can explain one of the occasions in which otter tracks were found in this small stream shelter, in June 1998, but otter tracks were also found in it once in the wetter season (February 1998).

Other intriguing result was the absence of use of shelters on river plains by three of the species with most identified shelters: *T. iheringi*, *P. frenata* and *M. nudicaudatus*. This result is still more interesting because *T. iheringi* was frequently photographed by camera traps on river margins and *P. frenata* also uses river plains (pers. obs.). Again, it is impossible to attribute this result to an avoidance of shelters in river plains by these species or to insufficient data. If shelter site availability was a limiting resource to mammals and birds at the PECB, it would be expected that more shelters would be used at the hilltops and river plains with undifferentiated alluvial deposits, where there is a high density of shelters. Instead, it appears that other factors determinate shelter choice.

The lack of correspondence between the body size of the animals and the size of shelters' entrances agrees with the hypothesis that other factors are more important in shelter site choice than shelter site characteristics and location. However, shelter site entrances would have to be measured to a greater depth to confirm this hypothesis. The use of shelters with the minimum entrance size possible would have the advantages of increased heat retention and exclusion of a larger variety of predatory mammals (Robb et al. 1996), and it is still possible that the animals using shelters with large entrance dimensions would work their way inside the shelter into smaller and deeper cavities than those apparent from my visual search (Shirer & Fitch 1970). Similar shelter sites may also have different internal characteristics not covered in this work, such as temperature stability and humidity (Berner & Gysel 1967).

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Figure 1. Schematic representations of the external view and longitudinal (defined as a section which is parallel to plane defined by the greatest length of the structure) or frontal (defined as a section perpendicular to the longitudinal one) sections of the different types of shelters found in the Parque Estadual Carlos Botelho, an Atlantic Forest area in Southeastern Brazil. The vertical broken lines indicate the position of sections. Abbreviations are: T = tree, e = entrance, ch = chamber, tu = tunnel, ar = adventitious roots, ch/tu = chamber or tunnel; WT = shelter without tunnels under living tree; UMAR = shelter under mound formed by adventitious roots; FT = shelters under fallen trees; BU = burrows not supported by trees or roots; RB = riverbank shelters; ST = stream tunnels and RO = rock shelters.

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Figure 2. Pictures of different types of shelters found in the Parque Estadual Carlos Botelho (PECB), an Atlantic Forest area in Southeastern Brazil. (a) A very large entrance of a Shelter under mound formed by adventitious roots (UMAR) (emphasized in black), with a camera trap on the right, with a sensor located at a height of 12 cm; (b) Baryphtengus ruficapillus in the entrance of a Burrow (BU) shelter; (c) Entrance of a River bank (RB) shelter, used by an otter, from which a small stream exits; (d) Entrance of a River bank (RB) shelter with a dry platform inside it, and a rodent swimming on the right; (e) Stream tunnel (ST) shelter.





Figure 3. Philander frenata (a) and Agouti paca (b) using the same Shelter with tunnel under a living tree (TULT).



Figure 4. Metachirus nudicaudatus exiting a Shelter under mound formed by adventitious roots (UMAR). The entrance of the shelter, larger than the animal's body size, is emphasized by a red line.





Figure 5. Sciurus ingrami exiting a Shelter with tunnel under a living tree (TULT), used by a paca, with a big seed in its mouth, probably left in the shelter by the paca.