



Original Investigation

Positional behaviour and tail use by the bare-tailed woolly opossum *Caluromys philander* (Didelphimorphia, Didelphidae)Matheus Fernandes Dalloz^{a,b,*}, Diogo Loretto^{a,b}, Bernardo Papi^a, Priscilla Cobra^a, Marcus Vinícius Vieira^a^a Laboratório de Vertebrados, Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil^b Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

ARTICLE INFO

Article history:

Received 9 September 2011

Accepted 5 March 2012

Keywords:

Artificial nests
Atlantic forest
Camera trap
Grasping ability
Tail use

ABSTRACT

We present the first quantitative description of postural behaviour of a free ranging metatherian, the bare-tailed woolly opossum, *Caluromys philander*. Postural behaviour was observed using 10 camera traps set in front of artificial nests, located in the understory of an Atlantic forest site in Rio de Janeiro, Brazil. Seven locomotory and positional modes were identified, with a predominance of diagonal couplets. Individuals used three types of grasp as observed in captivity, but the frequency of digital grasping was higher in the wild. The tail was used as an additional grasping limb, preventing falls and freeing hands to other activities, but the tail was also used to carry leaves for nest building. The use of camera traps may represent a breakthrough in the study of positional behaviours in the wild.

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Introduction

Arboreal animals present many adaptations to safely use the vertical strata of the forest, such as elongation of the limbs, opposable hallux and pollex, prehensile tails, and specific locomotory modes, such as diagonal couplets (Dublin 1903; Lemelin 1999; Stevens 2008; Wallace and Demes 2008). Establishing the relationship between behaviour traits and morphological specializations, and determining converging adaptations, contribute to the comprehension of how natural selection operates in arboreal species. However, due to the difficulty in observing arboreal small mammals moving in the wild, such as didelphids, there is a lack of field studies for these groups, and most positional behaviour observations are made in captivity (Antunes 2003; Delciellos and Vieira 2006, 2007, 2009; Youlatos 2008, 2010).

An interesting species for positional behavioural studies in didelphids is the bare-tailed woolly opossum, *Caluromys philander* (Linnaeus, 1758) (Didelphimorphia, Didelphidae). Remarkably arboreal, it inhabits neotropical rainforests from the Atlantic Forest in southeastern Brazil up to the Amazonia forest in French Guiana and Venezuela (Nowak 1999; Reis et al. 2011). *Caluromys philander* converges with primates in many aspects, including highly arboreal skills (Charles-Dominique et al. 1981; Rasmussen 1990;

Julien-Laferrrière 1995; Leite et al. 1996; Grelle 2003) and large and forward-oriented eyes, distinctly from other didelphid marsupials (Eisenberg and Wilson 1981; Ravosa and Savakova 2004). *Caluromys philander* has also relatively long digits and an opposable nail-bearing hallux (Szalay 1994; Lemelin 1999; Argot 2002), used to grab small diameter supports. It features an agile and diverse locomotor and postural behaviour (Rasmussen 1990; Lemelin 1999; Delciellos 2005), walking mainly in a diagonal sequence gait (Schmitt and Lemelin 2002; Lemelin et al. 2003; Delciellos 2005). Therefore, the species is considered an extant analog of early primate ancestors, a good model for studying primate evolution and evolutionary convergences among arboreal mammals (Rasmussen 1990; Argot 2002, 2003; Schmitt and Lemelin 2002; Youlatos 2008).

Caluromys philander forages mainly on the canopy, as reported by Charles-Dominique (1983), Leite et al. (1996), and Grelle (2003). The species has a prehensile tail like other small arboreal didelphids (Cartmill 1985; Youlatos 2003). Acting as a fifth limb, it allows the animal to grasp and prop supports of small diameter as the animal moves, hence helping arboreal locomotion (Cunha and Vieira 2002; Delciellos and Vieira 2009). The tail is also used to hold and carry objects. This habit was described for some didelphids (Hunsaker & Shupe, 1977 *apud* Unger 1982) and some Australian marsupials (Hartman, 1952 *apud* Unger 1982), mostly in captivity. However, records of didelphids using its prehensile tail to carry material in the wild are only anecdotal. Likewise, the objects carried are virtually unknown.

Here, we present an analysis of the positional and locomotory modes performed by *C. philander* in the wild, applying a classification adapted from Youlatos (2008). Furthermore, we determined

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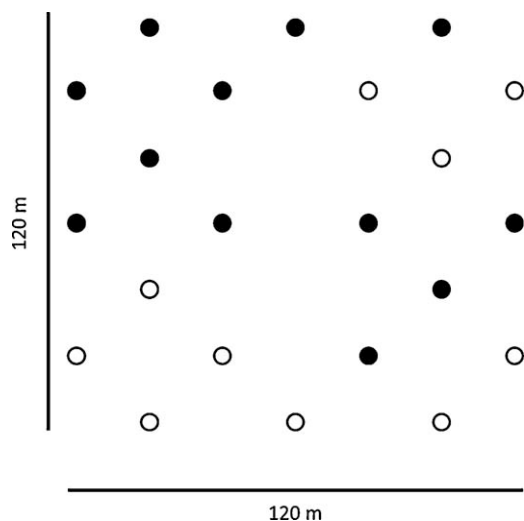


Fig. 1. Spatial design of nests and camera traps. Each circle represents a tree with nests and the white circles are the ones that received cameras. The trees with nests are uniformly distributed starting from a randomly point.

the use of three different types of grasping, classified as digital, hallucal, and zygodactylous. Lastly, we describe the use of the prehensile tail by *C. philander*, including how the species carries leaves to build its nest. This is the first quantitative description of postural behaviour of a free ranging metatherian, and also the first using camera traps.

Material and methods

We conducted the study in the Serra dos Órgãos National Park, in a locality known as Garrafão (22°28'28"S; 42°59'86"W), 100 km from Rio de Janeiro city, in the municipality of Guapimirim, Rio de Janeiro State, Brazil. The climate is mild humid-mesothermic (Nimer 1989) and the vegetation is classified as dense evergreen montane forest (IBGE, 1992), with a dense canopy and understory cover (Macedo et al. 2007). The canopy reaches up to 20 m and the understory up to 9 m, representing an intermediate stratum.

This study was part of a population ecology programme started in 2003, carried by the Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro (see Loretto 2005, 2006; Loretto and Vieira 2011, for details). We monitored small mammal populations monthly using 252 artificial nests (AN), made of painted bamboo, *Bambusa vulgaris* var. *vittata* Schrad., placed at ground level, 2.5, 5 and 7.5 m high in 63 trees. The trees were equally spaced in a 1.44 ha square grid (Fig. 1), starting from a random initial place. The artificial nests do not attract species using bait, but are used as shelters, permanently opened to entry and leave of individuals, hence less intrusive (Tubelis 2000; Prevedello et al. 2008). We installed wood ladders fixed on tree trunks to set and access the nests (see Prevedello et al. 2008, for details).

Additionally to the artificial nests, we installed 10 analogical camera traps, nine at 5 m high and one at 2.5 m, facing the most visited artificial nests in order to increase the chances of photographing an individual during its normal activity period (Fig. 2). Potential augmented frequencies of any postural behaviour due to the use of artificial nests are of least concern as our objective was not to report total frequency of postural and locomotory modes.

The camera traps consisted of a conventional photographic camera with passive infrared sensors and flash light (Tigrinus®, model 4.0D—www.tigrinus.com.br). We used climbing slings with girth hitch knots to ascend tree trunks and set the cameras. This is an adaption of the scaling ladders technique (Stubsgaard 1997) where the ladder was actually the trunk and the slings acted as steps.



Fig. 2. View of the camera trap facing the artificial nest.

Using other two slings, one set above the other, attached to the researcher's harness, the trunk can be easily climbed by altering the height of each step. The cameras were distributed at least 30 m from each other, covering a variety of understory structures (Fig. 1) and were maintained in the field from April 2008 to April 2009. Cameras were programmed to function continuously, 24 h per day, with a time system set for a 4-min shot delay to avoid capturing images of the same individuals doing repeated movements, or in the same postural mode.

In each picture we analysed the postural or locomotory mode performed applying the positional behaviour classification used by Youlatos (2008) in a study using captive *C. philander* (Table 1). We only used pictures that had a complete and clear image of the body and limbs, so we could correctly distinguish the modes performed. To define the type of grasp used by hands and feet (Table 1) we only considered pictures where all fingers or toes were visible in at least one hand or foot. The number of pictures with clearly visible fingers or toes differed between hands and feet. We analysed also the way the animal was using the tail, using only pictures in which the whole tail was visible. We observed whether the tail was actively used in the locomotion, *i.e.* curling or effectively holding branches, and if not, what its position in relation to the body.

Results

We obtained 90 pictures of *C. philander* using the understory for its regular activities, and 128 pictures of nine other mammal species, *Didelphis aurita* (Wied-Neuwied, 1826), *Gracilinanus microtarsus* (Wagner, 1842), *Guerlinguetus ingrami* (Thomas, 1901), *Marmosa paraguayana* (Thomas, 1905), *Marmosops incanus* (Lund, 1840), *Sphiggurus villosus* (F. Cuvier, 1823) and three other rodent species we could not identify. Based on our previous trapping data (Macedo et al. 2007) and morphological traits visible in the pictures, we suspect that one of these rodents is *Rhipidomys itoan* Costa et al., 2011, and the other two belong to the genera *Juliomys* González, 2000, and *Phyllomys* Lund, 1839. In 77 pictures of *C. philander* we were able to analyse the positional and locomotory modes performed by the individuals. In the remaining 13 pictures bodies or limbs were not entirely visible. The predominant locomotory mode was diagonal couplets (42%), followed by clamber (30%), climb (26%), and bridge (2%). There was no record of suspensory or leap modes. In relation to the positional modes, the most frequently recorded was stand (71%), followed by bipedal (23%) and tail-hang (6%). There was no record of foot-hang, cantilever and sit (Table 2; Figs. 3 and 4).

Table 1
Definitions of positional and locomotory modes.

Positional modes	Bipedal	Above-branch bipedal posture with semi-extended or extended feet allowing rotatory movements of the body
	Foot-hang	Below-branch suspensory posture with the feet supporting the body; the tail may or may not be used
	Sit	Above-branch crouched bipedal posture with only the feet touching the branch
	Stand	Above-branch quadrupedal posture with semi-extended or crouched limbs
Locomotory modes	Tail-hang	Below-branch suspensory posture with the tail supporting the body
	Bridge	Crossing short gaps whilst keeping at least three limbs anchored
	Clamber (up, horizontal, down)	Body displacement in various directions using multiple branches
	Climb (up, down)	Upward or downward body displacement along single steep or vertical branches
	Diagonal couplets	Hind limb ahead is in the opposite side of forelimb ahead
Grasping types	Lateral couplets	Hind limb ahead is in the same side of forelimb ahead
	Leap	Horizontal body displacement that incorporates a significant brief or long airborne phase
	Suspensory	Below-branch quadrupedal locomotion
	Digital grasping	Grasp using the claws or tips of all digits
	Hallucal grasping	Grasp where the hallux or pollex is opposed to the lateral digits that fully or partly embrace the branch
	Zygodactylous grasping	Grasp between digits II and III

Table 2
Observed frequency of locomotory and positional modes.

Locomotory modes	No. of pictures	Percentage (%)	Positional modes	No. of pictures	Percentage (%)
Diagonal couplets	25	42	Stand	12	71
Clamber	18	30	Bipedal	4	23
Climb	16	26	Tail-hang	1	6
Bridge	1	2			
Total	60			17	

We analysed 43 and 45 pictures of hand and feet grasps, respectively. Zygodactylous was the most frequent hand grasp mode, but digital grasp was also common (61% and 30%, respectively). Hallucal grasp was rarely used with hands (9%). For feet grasping, the opposite pattern was observed: hallucal grasp was used more frequently (73%) than digital grasp (27%). There was no record of feet holding using a zygodactylous grasp (Table 3).

The type of grasp used varied with the positional mode. Hands held with zygodactylous grasp in all pictures where individuals performed diagonal couplets and in most of the pictures in clamber mode. Conversely, in bipedal position the hands held more with hallucal grasp. Zygodactylous and digital grasps were equally used when climbing. Feet held with hallucal grasp in all diagonal couplets records, and digital grasp was predominant only when climbing. For clamber and bipedal modes both types of grasp were equally used. Grasp modes were also recognizable in a few bridge, stand and tail hang positional modes (Table 4).

Tail use was extensively recorded by camera traps as well. One of them, installed at 5 m high, recorded the nest building behaviour of an individual. The record encompasses 10 pictures of a *C. philander* female climbing up and down carrying leaves to build its nest. The animal carried the leaves curling the tail, making a loop to hold them (Fig. 5a). The process of carrying leaves was repeated at least 10 times, during approximately 80 min, from 01:21 to 02:42 a.m. – first and last record, respectively. The individual did not use the AN to which the camera trap was facing, but 13 days later we

recorded a *Caluromys* nest in the AN placed 2.5 m above the camera trap (personal observation, see details about nest identification in Loretto 2006). We could not determine from which tree and height the leaves were collected.

The other 63 pictures registered different tail positions. In most pictures, the tail remained slightly curved, almost stretched, and aligned with the same longitudinal plane of the body, regardless of the positional mode (Table 5; Fig. 3). However, in five pictures the individuals were using the tail as a hook, loosely curled around a branch, but not holding it (Fig. 5b). Finally, in only one record the tail was used to effectively hold the branch while the hands were free, in a tail-hang mode.

Discussion

Camera traps recorded a great diversity of positional behaviours performed by *C. philander* in the wild. In captivity, using video recordings, Youlatos (2008) observed 12 distinct postural and locomotory modes, seven of those also recorded by us using camera traps to study free-ranging individuals. Video recording in captivity allows detailed descriptions of movement traits, and supports variety and environment configuration can also be manipulated to increase the chances of recording several positional and postural modes. However, data on positional behaviour collected in the wild remains essential as a link between natural history, morphology, and behaviour ecology. It can provide the information needed to support and define homologies, perform functional-adaptive analyses, and guide the design of ecological morphology studies in captivity (Dickinson et al. 2000; Stafford et al. 2003). Our results are the first to fill the lack of field data for an arboreal metatherian.

Installing cameras in the canopy could enrich the results as both understory and canopy have complex but different arboreal structures (Parker 1995), and *C. philander* is known to move in both strata (Charles-Dominique et al. 1981; Julien-laferrière 1997). Therefore, future studies in the field should also consider exploring

Table 3
Number of pictures with each grasp type used by hands and feet.

Type	Hands	Feet
Zygodactylous	26 (61%)	0
Digital	13 (30%)	12 (27%)
Hallucal	4 (9%)	33 (73%)
Total	43	45

Table 4
Number of pictures with each grasp type used by hands and feet in each locomotory and positional mode.

Mode	Hallucal	Zygodactylous	Digital	Hallucal	Digital
	Hands – postural modes			Feet – postural modes	
Bipedal	3 (75%)	1 (25%)	0	2 (50%)	2 (50%)
Bridge	0	1 (100%)	0	1 (100%)	0
Stand	0	2 (100%)	0	2 (100%)	0
Tail-hang				1	0
	Hands – locomotory modes			Feet – locomotory modes	
Clamber	1 (20%)	3 (60%)	1 (20%)	2 (50%)	2 (50%)
Climb	0	5 (56%)	4 (44%)	1 (11%)	8 (89%)
Diagonal	0	16 (100%)	0	18 (100%)	0

Table 5
Positions of the tail recorded by each positional and locomotory mode. Stretched means a tail displacement stretched, or slightly curve, but not curled.

Postures	Tail position		Locomotion	Tail position	
	Stretched	Curled		Stretched	Curled
Bipedal	4 (100%)	0	Diagonal Couplets	11 (85%)	2 (15%)
Ridge	1 (100%)	0	Clamber	11 (85%)	2 (15%)
Stand	7 (87.5%)	1 (12.5%)	Climb	12 (75%)	4 (25%)

the canopy. Likewise, the influence of sex and age on positional behaviour is to be revealed, especially for non-primate groups. We could not determine sex from pictures, and age class can only be determined by teeth eruption (see Macedo et al. 2006; Astúa de Moraes and Leiner 2008). These sample limitations could be solved by previously marking individuals in the study area with coloured collars that could be distinguished in pictures. Marking individuals also would allow information on the number of individuals registered, hence verifying the frequency of repeated individuals in the pictures.

The predominance of diagonal couplets and the frequency of other locomotory modes on arboreal supports are in accordance with observations of animals in captivity (Youlatos 2008). Therefore, diagonal couplets play a major role in the locomotion of *C. philander* in arboreal environments, when the species walks on fine and terminal branches. Diagonal couplets provide stability in thin terminal branches, and use of diagonal couplets seems to be a common specialization among arboreal animals (Hildebrand 1985; Tardieu 1992; Stevens 2008; Wallace and Demes 2008).

The frequent use of zygodactylous grasp by animals in the wild is also in agreement with observations of animals in captivity (Youlatos 2010), but only in the wild the digital grasp was also frequently observed. The zygodactylous grasp offers security and

equilibrium for above-ground movements on supports that can be at least partially embraced by hands (Youlatos 2010). The digital grasp was especially frequent in clamber and climbing modes, used mostly when climbing vertical branches, when a full grasp may be not possible and the individual had to spike its claws to move. The use of claws would be particularly important if the support surface were excessively slick or during rainy periods, when supports are wet. These conditions would be more likely observed in the wild than in captivity, hence the more frequent use of digital grasp. The digital grasp can also be related to the climbing of tree trunks in the understory, which would be necessary to reach the canopy. These hypotheses can be further tested in experiments in captivity.

The tail had at least three different uses: as an additional grasping limb preventing falls, helping balance during locomotion on branches, and helping to carry leaves for nest building. In the former, the tail was used curled around thin arboreal supports as a hook, enabling a quick hold if necessary. This hook-tail position was described previously for individuals in an artificial setting (Antunes 2003), but it was not common in the field data – only five pictures showed it, and it could not be associated to a specific postural or locomotion mode. The hook-tail position can be related to movements in unsafe branches or otherwise difficult to move, or it can just be a reflexive motion induced by the contact with the support. Even so, using the tail as an additional grasping limb would minimize risks of falls, an advantage for an arboreal animal. The tail was not always curled around the support, and frequently it was aligned with the body, just slightly curved, suggesting a more effective position for a swift displacement. Moreover, keeping the tail in this position, with slightly lateral movements, might help to acquire a correct balance in locomotion, maintaining the equilibrium.

The pictures showing the female carrying leaves with its tail are an interesting record as building nests using leaves is a common habit of many small mammals (Ceballos 1990; Nowak 1999), and it is still anecdotal or briefly described how these animals manage to build their nests (Layne 1951, Hartman 1952 and Hunsaker & Shupe 1977 *apud* Unger 1982). Rodents and marsupials are known to build nests in trees cavities, palms, fallen logs, and even directly on the ground (Ceballos 1990; Loretto et al. 2005; Moraes and Chiarello 2005; Nowak 1999). The tail seems to play a crucial role in nest building, which certainly is an advantageous behaviour to improve body temperature control, to secure, bear and raise young (Fadem et al. 1986; Lynch and Possidente 1978). Carrying objects using the tail free the hands and feet to walk and



Fig. 3. Individual in diagonal couplets, showing a slightly curve and stretched tail, which was the predominant position, and also holding with hallucal grasp of the feet and zygodactylous grasp of hands (shown by arrows). The artificial nest is shown behind him, with the entrance facing the camera.



Fig. 4. Postures recorded by the camera traps. (a) Individual climbing down a vertical and wet trunk, using a digital grasp. (b) In clamber mode with hands and feet in different directions, grabbing different supports. The arrows point to the feet, one grabbing the entrance and the other the middle of the nest, whereas the hand was grabbing the trunk. (c) Bridge mode. (d) An individual standing on the top of an artificial nest. (e) An individual in bipedal position looking at the entrance of an artificial nest. (f) Tail-hang position.

collect food, without compromising walking stability in arboreal environments.

This is the first use of camera traps to record locomotory modes of small arboreal mammals in detail. Camera traps have become popular as a sampling technique, but few studies used such traps in arboreal environments (Kierulff et al. 2004). Field biologists have been using camera traps to study population density, activity periods, sampling communities, animal behaviour, and also to investigate nest predation through the combined use with artificial nests (Bridges and Noss 2011). Previously locomotion studies were mostly limited to captivity conditions, particularly concerning cryptic, arboreal and nocturnal species. This study opens a new window for locomotory and positional behaviour studies, allowing experimental designs to be performed efficiently also in natural conditions. This may be especially promising using modern digital camera traps with video-recording devices.

Although cameras have been recognized as a non-invasive method, they can be invasive especially for nocturnal species as reported by Schipper (2007), who recorded an avoidance behaviour to camera traps by another canopy specialist, the

kinkajou *Potos flavus* Schreber, 1774 (Carnivora, Procyonidae). The reason kinkajous avoided camera traps is unknown, but the author suggests that the flash light may cause discomfort to their light-sensitive eyes. *C. philander* has some similarities with *P. flavus* (see Charles-Dominique et al. 1981; Julien-Laferrière 1999), including light-sensitive eyes, but the *C. philander* female who was photographed carrying leaves to build its nest did not exhibit any avoidance behaviour to our camera traps, which also use flash lights.

The pictures presented here, of a free-living *C. philander* carrying leaves with its tail, provides new evidence on this particular behaviour that may represent a common habit for most didelphids and other arboreal small mammals with a prehensile tail (Hartman, 1952 *apud* Unger 1982), but poorly documented so far. The visual records also provided data on tail use and positional behaviour in the wild by a non-primate mammal, which is scarce in the literature and can contribute with further inferences about evolutionary convergences among arboreal mammals. This is probably the first study using camera traps to reveal positional behaviour of a species in the wild, adding another valuable use for this method.

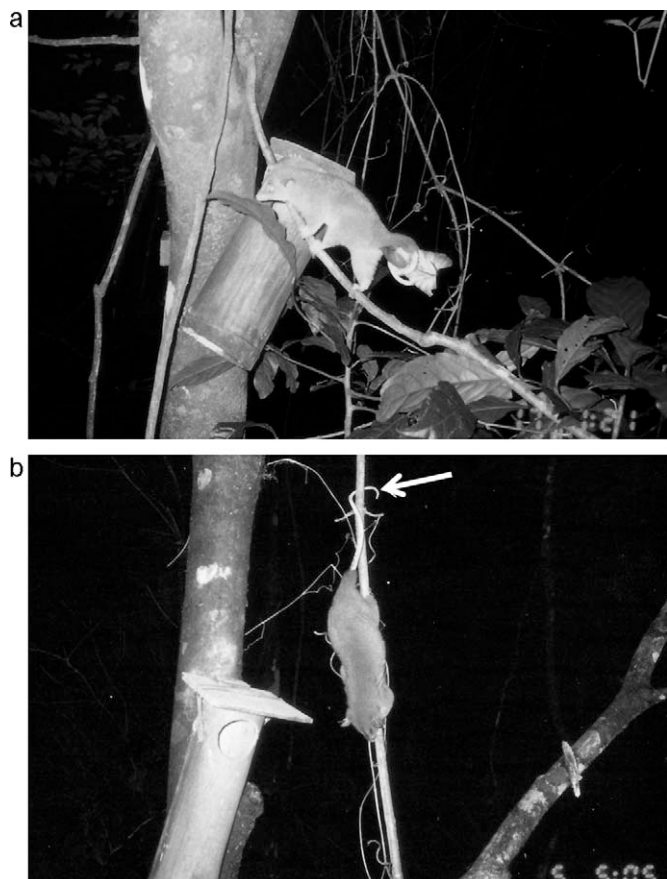


Fig. 5. (a) Female of *C. philander* carrying material with its tail. (b) An individual descending a vertical branch using the tail as a hook (shown by the arrow).

Acknowledgements

We are thankful to the technicians Angela Maria Marcondes, Nélio P. Barros and Rosana Juazeiro for the support in the laboratory. Students of the Laboratório de Vertebrados provided valuable help in the field work. Special thanks to Ernesto B. V. Castro, Cecilia Cronemberguer de Faria and all the Serra dos Órgãos National Park team for their logistic support. Ana Claudia Delciellos, Vanina Zini Antunes, Jayme Prevedello and three anonymous reviewers gave valuable comments on early versions of this manuscript. This study was approved by the ICMBIO/IBAMA (Proc. 16704-1), and fomented by CNPq, CAPES, PIBIC/CNPq, and FAPERJ.

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