

Tree Hole Utilisation by the Hairy-Eared Dwarf Lemur (*Allocebus trichotis*) in Analamazaotra Special Reserve

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Key Words

Habitat use · Habitat needs · Conservation · Social system · Cheirogaleidae · Strepsirrhini · Primates · *Allocebus trichotis*

Abstract

In this study we describe tree hole characteristics and use by the hairy-eared dwarf lemur (*Allocebus trichotis*) to determine habitat needs, potential functions of tree holes and sleeping group composition. We radio-tracked 6 adult individuals between April and November 2007 in the Analamazaotra Special Reserve. Tree holes were 1–9 m high (median: 7 m), in living trees measuring 26–54 cm in diameter at breast height (median: 32 cm), and could be a limiting resource. Each individual used 4 or 5 tree holes and had high nest fidelity. Animals most often slept socially in mixed-sex groups of 2–6 individuals and occasionally shared a tree hole with white-tailed tree rats (*Brachytarsomys albicauda*). We identified two sleeping groups: one composed of 2 adult males, 2 adult females and 2 juveniles; one composed of at least 2 adult females and 2 juveniles. Although tree holes were generally group exclusive, some intergroup sleeping was observed. Tree holes could have antipredator and thermoregulatory functions. Further research into sleeping hole availability, nest use and the degree of niche separation or competition between sympatric Cheirogaleidae and other tree hole users (e.g. endemic rodents) is needed to assess better the conservation needs of these species.

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Introduction

Many nocturnal strepsirrhine primates use resting shelters as sleeping sites during the day [Kappeler, 1998; Bearder et al., 2003; Gould and Sauther, 2007; Nekaris and Bearder, 2007]. Among the nocturnal Malagasy lemurs, this is the case for sev-

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eral Cheirogaleidae and Lepilemuridae, as well as the aye-aye (*Daubentonia madagascariensis*) [Kappeler, 1998; Gould and Sauther, 2007]. Information on nest use is only available for 11 cheirogaleid species. Four species use leaf nests exclusively (*Microcebus griseorufus*, *Microcebus myoxinus*, *Mirza coquereli* and *Mirza zaza*) [Kappeler, 1998; Kappeler et al., 2005; Génin, 2008]. Tree holes are used exclusively or in combination with leaf nests by the majority of species (*Cheirogaleus major*, *Cheirogaleus medius*, *Microcebus berthae*, *Microcebus murinus*, *Microcebus ravelobensis*, *Microcebus rufus* and *Phaner pallescens*) [Martin, 1973; Wright and Martin, 1995; Radespiel, 1998; Schmid, 1998; Müller, 1999a; Schmelting, 2000; Schwab, 2000; Fietz and Dausmann, 2003; Radespiel et al., 2003; Schülke and Kappeler, 2003; Dammhahn and Kappeler, 2005; Dausmann et al., 2005; Rasoazanabary, 2006; Lahann, 2007, 2008; Deppe et al., 2008]. Although the hairy-eared dwarf lemur (*Allocebus trichotis*) has previously been observed to use tree holes and the characteristics of a few of these cavities have been reported, it is important for the survival of this enigmatic species to gather additional information on this aspect of its habitat needs [Meier and Albignac, 1991; Rakotoarison et al., 1997; Goodman and Raselimanana, 2002].

Apart from being used as diurnal resting shelters, cheirogaleids also use these sleeping sites for birthing, to raise and/or cache young and for torpor or hibernation during the dry season [Wright and Martin, 1995; Kappeler, 1998; Schmid, 1998; Fietz, 1999, 2003; Müller, 1999a, b; Fietz and Dausmann, 2003; Dausmann et al., 2005; Eberle and Kappeler, 2006; Rasoazanabary, 2006]. The advantages proposed to be driving the use of such shelters include protection against predators, energy saving through thermoregulatory advantages, less ectoparasitism and better survival of altricial young [Kappeler, 1998; Radespiel, 1998; Schmid, 1998; Radespiel et al., 2003; Dausmann et al., 2005; Lahann, 2008]. Tree holes in particular have been proposed to be better for antipredator defence and thermoregulation [Schmid, 1998; Radespiel et al., 2003; Lahann, 2008]. However, the antipredator advantage of using tree holes has been questioned as several authors reported predation events where animals were removed from their sleeping site during the day [Wright and Martin, 1995; Schmelting, 2000; Schülke and Ostner, 2001; Fietz and Dausmann, 2003]. Furthermore, the risk of predation in 'low-quality' sleeping sites (i.e. leaf nests or dense vegetation) can be compensated for by behavioural adaptations such as frequent change of sleeping sites, crypsis and flight responses [Radespiel, 1998; Radespiel et al., 2003; Schülke and Ostner, 2005].

The hairy-eared dwarf lemur (*A. trichotis*) was believed to be extinct until its rediscovery in 1989 [Meier and Albignac, 1989]. Since then, only a few studies have focused on the species [Meier and Albignac, 1991; Rakotoarison et al., 1997]. This small nocturnal strepsirrhine is currently classified as 'data deficient' [IUCN, 2008]. Individuals most often travel alone or in pairs and sleep together in groups of 2–4 in tree holes [Meier and Albignac, 1991; Rakotoarison et al., 1997; Goodman and Raselimanana, 2002]. It is possible that they have a social system similar to *Cheirogaleus* spp. and share sleeping sites with family members [Meier and Albignac, 1991; Rakotoarison et al., 1997]. The tree holes reported in previous studies were in dead trees of at least 30 cm diameter, at heights of 1.4–2.2 m [Meier and Albignac, 1991; Rakotoarison et al., 1997]. Hairy-eared dwarf lemurs seemed to have high nest fidelity [Meier and Albignac, 1991]. As Meier and Albignac [1991] observed allogrooming in the nest, it is likely that the use of such structures plays an important role in the social life of the species. Some authors suggested a hibernation period during the aus-

tral winter [Rakotoarison et al., 1997], but Meier and Albignac [1991] found no obvious fat reserves to prepare animals for dormancy, and Schütz and Goodman [1998] observed active individuals during the winter (June). The aims of this study were to expand upon these preliminary observations by describing (1) tree hole characteristics to determine habitat needs for conservation, (2) tree hole utilisation to identify the potential functions of tree holes and (3) sleeping group composition to clarify the species' social system.

Materials and Methods

K.B. conducted this study between January and December 2007 in the Analamazaotra Special Reserve of central eastern Madagascar (18°56' S, 48°25' E), near Andasibe/Périnet. The village of Andasibe lies between the capital Antananarivo and the shores of the east coast, about 30 km east of Moramanga [Dolch, 2003]. The Analamazaotra Special Reserve was created in 1970, and its high biodiversity made it a hot spot for tourists [Dolch, 2003]. Previously covered with continuous forest, this region now has only fragments of forest [Dolch, 2003]. The climate is humid with an average annual rainfall of 1,700 mm over 210 days, an annual average temperature of 18°C and atmospheric humidity over 70% [ANGAP, 2002]. The study area was in disturbed, mid-altitude, primary, eastern rain forest at altitudes of between 850 and 950 m.

Aided by local guides, K.B. captured 11 individuals and radio-collared 6 (table 1). At first capture, adults weighed between 67 and 87 g (males: $n = 3$, mean = 78 g; females: $n = 4$, mean = 76 g). Capturing the first individual was difficult and took about 2.5 months. We caught 2 adult males and 1 juvenile using hand-held bamboo noose poles. Once the first individual was captured and its sleeping site located, it was relatively easy to trap the other members of its sleeping group by fitting a net in front of their tree hole at dusk. We radio-collared all individuals with weights over 65 g (TW-4 transmitter, 3.2 g, Biotrack Ltd.) and tracked them using a TR-4 receiver and RA-14 antenna (Telonics Inc.). We fitted the first captured individual with a leather collar, which the animal removed after only a few hours (AM1 in table 1). We subsequently fitted individuals with cable-tie collars with protective rubber coating which lasted throughout the study and were never lost. We recaptured the radio-collared individuals every 2–3 months to replace the collars with expired batteries. We removed all the radio-collars at the end of the study. At release, the study animals weighed between 67 and 95 g (males: $n = 2$, mean = 85 g; females: $n = 4$, mean = 78 g).

Radio-collared individuals were located in their tree hole during the day on 159 days [Radespiel, 1998; Müller, 1999a, b]. Each time a new sleeping site was discovered, we recorded its GPS location, tree hole height, genus and diameter at breast height (DBH) of the tree, whether the tree was alive or dead, and the maximum height and width of the entrance hole [Radespiel, 1998; Schmid, 1998].

We calculated the proportion of use for each tree hole as the number of days of occupation (i.e. the number of location days when the tree hole was occupied by at least 1 individual divided by the total number of location days when at least 1 individual was located in a nest, $n = 159$). We determined the proportion of tree hole use per individual as the number of days an individual used a particular tree hole divided by the total number of days that individual was located. We established the tree hole re-use and change rates as the number of days an individual re-used or changed its sleeping site on consecutive days divided by the total number of consecutive days on which it was located [Radespiel, 1998]. This calculation was completed per individual and for all individuals.

We set up six 1-ha vegetation plots and thirty 25-m² microhabitat plots at random within the study individuals' home ranges to determine tree density and tree diameter and genus composition. We used the point quarter sampling method following Ganzhorn [2003] to determine the density of trees with a DBH over 10 cm in the vegetation plots. In the microhabitat plots, we measured all trees with a DBH over 1 cm. To determine the tree diameter composition, we

Table 1. List of captured and radio-collared individuals showing their age group, sex and morphological measurements

ID	Age class	Sex	Head and body length mm	Tail length mm	First capture weight g	Release or last capture weight g	Radio-collared
AF1	adult	F	133	135	87	95	x
AF2	adult	F	134	134	82	79	x
AF3	juvenile	?	119	120	50	48	
AF4	adult	F	135	123	69	67	x
AF5	adult	F	132	140	67	70	x
AM1	adult	M	134	139	80		
AM2	adult	M	133	147	74	78	x
AM3	juvenile	?	117	118	43	63	
AM4	juvenile	?	119	111	44	66	
AM5	adult	M	141	130	82	91	x
AM6	juvenile	?	117	121	44		

F = Female; M = male; ? = unknown. Males could be distinguished by their testes. AF1 had swollen nipples at first capture but not afterwards. Sex was very difficult to determine in juveniles as testes were not developed. Head and body length: head length (from tip of nose to most distal point on occipital soft tissue) + body length (from base of skull to base of tail). Tail length: from base of tail to tip excluding hairs. First capture was March 23 for AM1, March 30 for AM2, April 2 for AF1, AM3, AM4 and AM5, April 13 for AF2, September 6 for AF3 and September 7 for AF4, AF5 and AM6. Release (when radio-collars were removed) and last capture (for juveniles) was November 21 for AF3 and AF5, December 3 for AF4, December 4 for AM4, December 7 for AM5 and December 14 for AF1, AF2, AM2 and AM3. We fitted AM1 with a radio-collar but retrieved it on the forest floor the next day. AM6 was not recaptured. AF1 was pregnant at release on December 14 (determined by palpation).

counted the number of trees in each diameter class (in 5-cm increments) using data from the vegetation plots on the one hand and the microhabitat plots on the other hand [White and Edwards, 2000]. To determine the tree genus composition, we calculated the basal area of each tree using data from the vegetation plots following White and Edwards [2000]. The sums of the basal areas per genus were used to determine the relative importance of each taxon. To compare used and available trees, we calculated the expected frequency for each used genus based on the taxon composition and calculated a χ^2 test to detect significant differences between the observed and expected usage frequencies (significance level $p < 0.05$).

The composition of the sleeping group was determined from the identity of individuals sleeping in the same sites, using individual radio-collar signals as well as direct observations of animals leaving and entering the tree hole at dusk and dawn [Radespiel, 1998; Müller and Thalmann, 2000]. We counted the number of times pairs of individuals slept together and calculated Coles' index of association [Cole, 1949; Pimley et al., 2005; Nekaris, 2006]. To determine the importance of social sleeping and sleeping group size and composition (all-male, all-female or mixed), we counted the number of times each group size and type occurred divided by the total number of sleeping sites located ($n = 294$).

Table 2. Tree hole characteristics emphasising the importance of large live trees

Nest No.	Tree genus	State of tree	DBH cm	Nest height m	Height of entrance cm	Width of entrance cm
1	<i>Uapaca</i>	partly dead	54	1.1	5.5	2.5
2	<i>Abrahamia</i>	live	31	2.0	7.0	3.8
3	<i>Cryptocarya</i>	live	49	4.4	4.5	3.0
4	<i>Eugenia</i>	live	42	9.3	6.0	4.0
5	<i>Eugenia</i>	live	26	7.2	13.5	2.5
6	<i>Eugenia</i>	live	42	unknown ¹	unknown ¹	unknown ¹
7	<i>Cryptocarya</i>	live	27	8.0	12.0	3.5
8	<i>Ilex</i>	live	32	8.8	22.0	7.5
9	<i>Syzygium</i>	live	31	5–10 ¹	unknown ¹	unknown ¹

Nest height: from ground level to base of tree hole.

¹ The tree of nest 6 was identified, but the hole could not be located precisely because it was too high and hidden from view. Nest 9 was located but the exact tree hole height was only estimated, and the entrance height and breadth were never measured because we did not catch animals in that tree hole and did not climb the nesting tree.

Results

Tree Hole Characteristics

In total, 9 different tree holes in 9 trees were located (table 2). Only 1 tree hole was in a partially dead *Uapaca* tree (Euphorbiaceae); all the others were in live trees. The live trees used belonged to 5 different genera: *Eugenia* (Myrtaceae, $n = 3$), *Cryptocarya* (Lauraceae, $n = 2$), *Abrahamia* (Anacardiaceae, $n = 1$), *Ilex* (Aquifoliaceae, $n = 1$) and *Syzygium* (Myrtaceae, $n = 1$). The DBH of the nesting trees varied between 26 and 54 cm (median: 31.9 cm). The tree holes were 1.1–8.8 m above ground (median: 7.2 m). The smallest tree hole entrance was 4.5×3.0 cm and the largest was 22.0 cm high and 7.5 cm wide (median 7.0×3.5 cm).

Tree Hole Use

We located study animals in their tree hole during the day 4–5 times a week (minimum twice, maximum 7 times). We located at least 1 radio-collared animal in its tree hole on 159 days, including 92 days where all the radio-collared animals were found. This yielded a total of 631 individual sleeping site locations. Nests 2, 3 and 4 were used most often (table 3). Nests 7 and 8 were used to a lesser extent. Nests 1, 5, 6 and 9 were used least often.

Table 4 shows the percentage use of each tree hole per individual. Each individual used between 4 and 5 different tree holes but used 1 or 2 more than the others. Nest 1 was used only briefly by female AF1 and males AM2 and AM5 at the beginning of the study, before AF2 had been caught. Nests 2–4 were used exclusively by AF1, AF2, AM2 and AM5. Nests 5, 6 and 9 were used exclusively by females AF4 and AF5. Male AM2 and female AF2 slept together with female AF5 in nest 7 on 1 occasion, and female AF2 slept once with female AF4 in nest 8.

Table 3. Tree hole use in number of days and percentage use per tree hole demonstrating high nest fidelity

	Nest No.								
	1	2	3	4	5	6	7	8	9
Number of days	7	54	77	80	9	6	33	26	2
Percentage use	4	34	48	50	6	4	21	16	1

Number of days: total number of days on which at least 1 individual was found in the nest. Percentage use: calculated as the proportion of the total number of location days in which at least 1 animal was found in at least 1 nest (n = 159).

Table 4. Percentage tree hole use per individual showing individual preference for 1 or 2 tree holes

ID	Nest No.									n
	1	2	3	4	5	6	7	8	9	
AF1	3	27	51	19	0	0	0	0	0	149
AF2	0	24	36	39	0	0	1	1	0	140
AF4	0	0	0	0	6	11	28	53	2	47
AF5	0	0	0	0	21	2	67	5	5	42
AM2	4	20	38	38	0	0	1	0	0	152
AM5	4	21	34	42	0	0	0	0	0	101

The proportion for each nest was calculated as the number of days the individual used that nest divided by the total number of days that individual was located (n in the last column).

An individual was located on consecutive days in 438 cases. In 69% of cases animals re-used the tree hole of the previous day, and in 31% of cases they changed hole. Each individual showed the same pattern with re-use days always exceeding days with a change of hole. One individual was observed to use the same cavity for at least 8 consecutive days.

Hairy-eared dwarf lemurs lined their tree holes with fresh leaves. On November 14, we observed nesting behaviour in female AF4. She returned to nest 8 around 00.30 h and made 5 excursions to collect leaves from an adjacent *Erythroxylum* tree (Erythroxylaceae) and bring them back to her tree hole. The return trips lasted until about 01.00 h. She then stayed in this tree hole until 01.45 h.

Response to Disturbances at the Tree Hole

After being captured at a sleeping site, at least one captured individual returned to the same tree hole on average within 3 days (n = 6 captures). After being captured in a tree hole, some individuals moved to higher nests (in 4 captures) with smaller entrances (3 captures) in larger trees (3 captures) or to unknown nests (2 captures).

The sleeping group made loud disturbance calls when a twig was inserted in the tree hole during the day.

Comparison between Used and Available Trees

Trees with a DBH of 26–54 cm, used as sleeping sites by the hairy-eared dwarf lemurs, represented 11% of trees with a DBH over 10 cm ($n = 1,468$) and 0.5% of trees with a DBH over 1 cm ($n = 1,184$). There was a significant difference between the used and available tree genera [$\chi^2(4) = 76$, $p < 0.01$]. All 5 live tree genera (*Eugenia*, *Cryptocarya*, *Abrahamia*, *Ilex* and *Syzygium*) were used more than expected. Although attempts were made to detect available tree holes in the microhabitat plots, we found only 1 tree hole that was a known nest.

Sleeping Group Composition and Social Interactions

Individuals slept alone in 36% and socially in 64% of cases ($n = 294$). When sleeping socially, the most common group size was 3 individuals (42%, $n = 187$). Hairy-eared dwarf lemurs also slept in groups of 2, 4, 5 and 6 (31, 18, 6 and 3% of cases, respectively). Sleeping groups were most often mixed (82%). All-female and all-male groups were much rarer (15 and 3%, respectively). Individuals sleeping alone were most often females (75%, $n = 107$).

Cole's index of association (table 5) showed that AF1/AM2, AF1/AF2 and AF2/AM2 shared sleeping sites in at least 3 out of 4 days. AM5 associated with these individuals about every other day but more with AM2 and AF2 than with AF1. AF4 and AF5 slept together about every third day but never associated with AF1 or AM5. AM2 and AF2 associated with AF5 on only 1 occasion, and AF2 and AF4 also slept together once.

Juveniles were found in adult sleeping holes on 29 days. In 11 cases, 1 or 2 juveniles were found to sleep with individuals AF1, AF2, AM2 and AM5. In 5 cases, 1 or 2 juveniles slept with AF1 and AM2. In 4 cases, 1 or 2 juveniles slept with AF4 and AF5. In 3 cases, 1 or 2 juveniles slept with AF1, AF2 and AM2. In 2 cases, 2 juveniles slept with AF1, AM2 and AM5. In 1 instance each, at least 1 juvenile slept with AM2 and AM5, and at least 1 juvenile slept with AF1, AF4 or AF5.

In 6 cases, unknown adult individuals were seen sharing radio-collared individuals' sleeping sites. One and on another day 2 adults shared a nest with AF5. One and on another day 2 adults shared a nest with AF1, AF2 and AM2. One adult was found in the same nest as AF1, AF2, AM2 and AM5. Two individuals shared a nest with AF4, AF5 and at least 1 juvenile.

Several types of social activity were observed at the sleeping site. These included allogrooming between an adult and a juvenile on leaving the tree hole and calling at dispersal and reunion. Groups also made 'disturbance calls' if a small twig was inserted into the entrance hole. During dispersal, animals usually left one after another with varying time intervals. Individuals either returned to their sleeping site alone or were observed to enter the sleeping site shortly one after another.

Interspecific Associations

We observed 7 instances of a sleeping association between hairy-eared dwarf lemurs and white-tailed tree rats (*Brachytarsomys albicauda*). A rat was first observed using the same tree hole as male AM2 (nest 1) on March 30. It was sitting at the hole entrance and emitted high-pitched alarm calls, while the hairy-eared dwarf

Table 5. Results of Cole's index of association for each pair of individuals sleeping together

	Group 1			Group 2	
	AF2	AM2	AM5	AF4	AF5
Group 1					
AF1	0.77	0.78	0.45	0.00	0.00
AF2		0.74	0.57	0.01	0.01
AM2			0.59	0.00	0.01
AM5				0.00	0.00
Group 2					
AF4					0.29

The index was calculated using the formula: $I = 2AB/(A + B)$, where I = Cole's index of association, AB = number of days individuals A and B slept in the same tree hole, A = number of days individual A was located in a tree hole and B = number of days individual B was located in a tree hole. The closer the index is to 1, the more frequently the two individuals slept together. High associations between adults suggest two sleeping groups.

lemur was observed with an endoscope, sleeping at the bottom of the cavity. A rat was located together with members of AM2's sleeping group again in the same tree hole on April 3, 5 and 6. On April 6, using the endoscope, we were able to observe a rat with 1 juvenile hairy-eared dwarf lemur on either side of it, curled up together, sleeping. On June 5, while capturing some members of the same sleeping group to re-fit radio-collars in nest 3, we found *B. albicauda* again, sleeping together with 2 adult and 2 juvenile *A. trichotis*. On June 10, we observed 2 rats, one smaller than the other, leaving the same tree hole as members of this group (nest 3). We also observed this interspecific nest association in the other sleeping group. On November 7, we observed the 2 radio-collared females AF4 and AF5 leaving nest 7. A white-tailed tree rat slept together with them in this tree hole in addition to 2 unknown individuals and 1 juvenile *A. trichotis*.

Discussion

Sleeping Site Characteristics

Hairy-eared dwarf lemurs used tree holes in living trees from 5 different genera with diameters over 26 cm (median 32 cm), at heights of 1–9 m above ground (median 7 m). Our results contradict the use of dead trees previously observed [Meier and Albignac, 1991; Rakotoarison et al., 1997]. The sleeping site found by Meier and Albignac [1991] near Mananara fits within the tree diameter sizes found in this study. Tree holes measured by Rakotoarison et al. [1997] in Vohidrazana forest, although geographically close and similar in structure to the current site, were in larger trees (minimum tree diameter at the hole: 63.7 cm). Previous research found lower tree holes (1.2–2.2 m) [Meier and Albignac, 1991; Rakotoarison et al., 1997] but this could be due to the fact that high tree holes are hard to detect and animal presence is difficult to confirm without radio-tracking.

Although studied in a different area, the sympatric *M. rufus* was reported to use leaf nests at 1–10 m above ground as well as tree holes; while the sympatric *C. major* was observed to build leaf nests at 12–20 m height and to use tree holes at 8–10 m height in trees with diameters over 47 cm [Wright and Martin, 1995; Lahann, 2007; Deppe et al., 2008]. K.B. also observed leaf nests of *Microcebus lehilahytsara* at approximately 2 m height. This leads us to suggest potential niche differentiation among these species but interspecific competition for access to shelters is also possible. Generally the size of the nest varied with the size of the animal. *C. major*, for example, used very large leaf nests of 30 cm in diameter [Wright and Martin, 1995]. When using tree holes, the size of the sleeping tree also depended on the size of the animal. In Mandena, for example, *C. major* used larger trees than *C. medius* (49 vs. 37 cm DBH), and *M. murinus* used the thinnest trees (13–15 cm DBH) [Lahann, 2008]. There was also a vertical stratification of sleeping sites depending on the species. *C. major* used higher sleeping sites than *M. murinus* and *C. medius* (9.7 vs. 4.1 and 3.9 m) [Lahann, 2008]. On the other hand, Schwab [2000] suggested interspecific resource competition for access to a limited number of suitable tree holes between the small *M. berthae* and larger sympatric species such as *M. murinus*, *C. medius*, the dormouse tufted-tail rat (*Eliurus myoxinus*), as well as reptiles. We also observed the white-tailed tree rat (*B. albicauda*) using the same tree holes as *A. trichotis*, simultaneously and consecutively, but never observed any aggressive behaviour that could have suggested competition. It is possible that both species gained thermoregulatory or antipredatory advantages through this interspecific association, which will need to be investigated in further research. Simultaneous follows of *M. rufus*, *C. major*, the recently described *M. lehilahytsara* and *Cheirogaleus crossleyi* should also be conducted to clarify the amount of niche separation or competition between the sympatric nocturnal Cheirogaleidae of the Andasibe region.

Sleeping Site Use

Hairy-eared dwarf lemurs re-used the tree hole of the previous day in 69% of cases. This result confirmed the high sleeping site fidelity suggested by Meier and Albignac [1991]. *C. major* and *C. medius* also had high tree hole fidelity [Müller, 1999a, b; Lahann, 2007]. *C. major* family groups repeatedly used 1 or 2 group-exclusive tree holes, while *C. medius* family groups re-used their tree holes from 1 year to the next. Female grey mouse lemurs also had a high sleeping site fidelity and often returned to the site of the previous day while males preferred to change sleeping sites frequently [Radespiel, 1998; Radespiel et al., 2003; Lahann, 2008]. In the dry season however, male *M. murinus* greatly increased their sleeping site fidelity [Schmelting, 2000].

Hairy-eared dwarf lemurs used 4 or 5 tree holes each. A similar number of sleeping sites was found in *M. ravelobensis* during a study of similar length (8 months) [Radespiel et al., 2003]. In comparison, individual *C. medius* used between 4 and 15 different sleeping sites within 6 months [Müller, 1998, 1999a], *M. murinus* used 1–18 tree holes within 8 months [Radespiel et al., 2003] and *P. pallescens* used between 8 and 38 sleeping sites during a 2-year study [Schülke and Kappeler, 2003]. The small number of tree holes used by *A. trichotis* could be a sign that the types of trees used are a limiting resource and that hairy-eared dwarf lemurs are forced to re-use these sites frequently because they are the only available tree holes. The observation that used tree sizes were rare in the habitat and that all 5 used tree genera where sleeping

sites were located were used more than expected by their availability alone adds strength to this hypothesis. Due to the small sample sizes of our study, further research should aim to confirm this theory.

Tree Hole Functions

The choice of a good sleeping site can strongly influence predation pressure [Martin, 1973; Goodman, 2003]. Although some tree holes used by the hairy-eared dwarf lemur had good antipredator characteristics (high above ground, small entrances, no cracks in the trunk), others seemed a poor choice (very low to the ground or larger openings). Predators known to break into cheirogaleid tree holes during the day include the fossa (*Cryptoprocta ferox*), the ring-tailed mongoose (*Galidia elegans*), the narrow-striped mongoose (*Mungotictis decemlineata*), the harrier hawk (*Polyboides radiatus*) and boas (e.g. *Sanzinia madagascariensis*) [Goodman et al., 1993; Wright and Martin, 1995; Gilbert and Tingay, 2001; Schülke and Ostner, 2001; Fietz and Dausmann, 2003]. The fossa, ring-tailed mongoose, harrier hawk, and other diurnal raptors and snakes are known to be present in the Analamazaotra Special Reserve [ANGAP, 2002; Garbutt, 2007]. We also observed other potential predators of the hairy-eared dwarf lemur: the fanaloka (*Fossa fossana*) and a snake (*Ithycyphus perineti*). Although all these predators could potentially attack hairy-eared dwarf lemurs in their tree hole during the day, we never observed any signs of destruction or direct predation attempts, and all the followed animals survived throughout the study.

Behavioural adaptations such as escape reactions, crypsis and frequent change of sleeping site can diminish the chances of being preyed upon [Bearder, 1987; Radespiel et al., 2003]. However, escape reactions seem impossible if the tree hole has only one entrance which is blocked by the predator [Schülke and Ostner, 2005]. Furthermore, hairy-eared dwarf lemurs had high nest fidelity and preferred to use the same tree hole for at least 8 consecutive days rather than change sleeping site and returned to the same tree hole even after having been disturbed by a human capture.

Hairy-eared dwarf lemurs therefore seemed to rely heavily on the physical characteristics of their tree holes for protection against predators. The height of the sleeping site might not be as important as the structure of the cavity itself. Indeed, higher nests can still be accessed by viverrids, diurnal raptors and snakes. Small entrances, strong walls and deep cavities are probably better at protecting against diurnal raptors and viverrids, delaying their break-in and limiting their access. The observation that some individuals changed tree holes after being captured suggests a possible antipredator strategy of moving to higher nests with smaller entrances. Additionally, some nests had a long and narrow tunnel leading to the chamber where the hairy-eared dwarf lemurs were resting (nest 1) and in most nests, the cavity was not just a cylindrical hole but had a more complex internal structure. Although difficult to study, the internal structure of the tree holes should also be taken into account when determining sleeping sites' quality in terms of predator defence. A nest hidden behind dense vegetation could also provide additional security. This seemed to be the case especially for the higher nests which were hidden from view by lianas or epiphytes. As a last resort, the loud and noisy grunt heard in the hairy-eared dwarf lemur and in other cheirogaleids in response to a disturbance in their nests could startle a predator trying to break into the tree hole [Scheumann et al., 2007].

Individuals used large live trees which are known to have better insulating properties than small dead trees [Radespiel, 1998; Schmid, 1998; Lahann, 2008]. Although all the study animals were active throughout the study, even during the colder, drier season from May to August, 1 adult male (AM5) did spend 1 full night in his tree hole in July, suggesting that short periods of torpor could occur. All the other members of his sleeping group had left the sleeping site however, suggesting that the tree hole alone offered enough thermal protection without the additional need of huddling to keep warm [Vickery and Millar, 1984; Perret, 1998; Müller, 1999a; Radespiel et al., 2003; Schülke and Ostner, 2005]. Individuals were also observed to return to a tree hole during periods of heavy rain, suggesting that holes were also used for protection against adverse weather conditions.

Social System

Cole's index of association (table 5) revealed 2 potential social groups: group 1 composed of 2 females (AF1 and AF2) and 2 males (AM2 and AM5); group 2 composed of 2 females (AF4 and AF5). Group members usually slept together in group-exclusive sleeping sites but intergroup sleeping associations were also observed. The proposed grouping pattern confirmed results found for the spacing system and observations of nocturnal interactions [Biebouw, 2009]. There was large home range overlap within members of group 1 (AF1, AF2, AM2 and AM5) and group 2 (AF4 and AF5) but only limited overlap between groups [Biebouw, 2009]. Members of a group also met occasionally at night but intergroup encounters were never observed [Biebouw, 2009]. We therefore suggest a dispersed multi-male/multi-female social system.

Up to 2 juveniles regularly associated with members of group 1. As these juveniles most often slept with AF1 and/or AM2, we propose that the 2 young were this pair's offspring. As Biebouw [2009] showed that these 2 adult individuals had the highest amount of home range overlap (95% kernel) and met most often at night, and as our study showed that they had the highest sleeping association index, we suggest a potential pair bond between AF1 and AM2.

AF2 and AM5 could have been offspring from previous years. AF1 was heavier than AF2 and the only pregnant female in December, supporting the possibility that female AF2 was younger and not yet sexually active. However, AM2 was lighter than AM5 and both males had well-developed testes, contradicting the hypothesis of a family group social system [Meier and Albignac, 1991; Rakotoarison et al., 1997] as both males were sexually active and inbreeding would occur.

The 2 females of group 2 slept together about every third day and seemed less social than members of group 1. However, 2 unknown adults were observed to sleep with these 2 females, and their sociality could have been underestimated if these 2 individuals were part of their social group. Up to 2 juveniles also associated with the 2 females of group 2. When the females slept apart, only 1 juvenile was found with each female, suggesting they both had 1 offspring. It is therefore possible that group 2 actually had a composition similar to that of group 1, with 2 adult males, 2 adult females and 2 juveniles; however, this remains to be confirmed. In either case, it was clear that these 2 females slept together much less often than those of group 1 and that they most likely both had young.

Sleeping groups have often been used to partly describe the social system of solitary foragers [Müller and Thalmann, 2000; Sterling et al., 2000]. In the Cheiro-

galeidae, the social system is usually either a dispersed multi-male/multi-female group (*M. berthae*, *M. ravelobensis*, *M. rufus* and *M. zaza*) or a dispersed or gregarious family group composed of an adult pair with or without offspring (*Cheirogaleus* spp. and *P. pallescens*) [Charles-Dominique and Petter, 1980; Atsalis, 1998, 2000; Müller, 1998, 1999a, b; Fietz, 1999, 2003; Schwab, 2000; Schülke, 2002; Radespiel et al., 2003; Schülke and Kappeler, 2003; Weidt et al., 2004; Braune et al., 2005; Dammhahn and Kappeler, 2005; Kappeler et al., 2005; Lahann, 2007, 2008]. Male or female uni-sex pairs (*M. griseorufus*), female groups with solitary males (*M. murinus*) or solitary females with offspring and solitary males (*M. coquereli*) have also been observed [Martin, 1973; Pagès, 1978; Kappeler, 1997a, b; Radespiel, 1998, 2000; Schmelting, 2000; Schwab, 2000; Eberle and Kappeler, 2002; Wimmer et al., 2002; Radespiel et al., 2003; Génin, 2008; Lahann, 2008]. A longer study with larger sample sizes and direct observations of matings or genetic analysis are necessary to clarify the social organisation of the hairy-eared dwarf lemur.

Recommendations for Conservation

As our results suggest tree holes could be a limiting resource, conservation management strategies should ensure the maintenance of trees with diameters over 25 cm, with or without visible holes. Further research into sleeping hole availability, nest use and the degree of niche separation or competition between sympatric *Cheirogaleidae* as well as other tree hole users (e.g. endemic rodents) should enable a better assessment of the conservation needs of these species.

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