Int J Primatol (2009) 30:367–386
DOI 10.1007/s10764-009-9349-y

Home Range Size and Use in *Allocebus trichotis* in Analamazaotra Special Reserve, Central Eastern Madagascar

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Received: 8 July 2008 / Accepted: 18 February 2009 /

Abstract No information is currently available on the space needs of hairy-eared dwarf lemurs (*Allocebus trichotis*), classified as Data Deficient. The data are crucial for their conservation and comparison with other nocturnal primates. I conducted the first radiotracking study of the species from January to December 2007 in the Analamazaotra Special Reserve of Central Eastern Madagascar. I used nocturnal focal individual follows and daytime nest locations to determine home ranges. I followed 1 full sleeping group (4 adults) for 8 mo and 1 partial sleeping group (2 females) for 3 mo. Group home ranges, calculated via 100% minimum convex polygons (MCP), were 35.5 ha and 16.0 ha, respectively. The 95% kernel method of analysis yielded group home ranges of 15.2 ha and 7.1 ha respectively. The mean home range size for individuals was 15.4 ha (MCP) and 5.4 ha (kernel). This is much larger than for other Cheirogaleidae and could be due to a more insectivorous diet or the use of patchily distributed gum-producing trees. There were small nonsignificant monthly variations in home range size. The mean home range size per individual per month was 5.2 ha (MCP) and 2.2 ha (kernel). Important individual differences in overall and monthly home range size could be due to variations in the individual reproductive cycles and survival strategies. Overlap analyses and the lack of sexual difference in home range size suggest the social unit is a family or multimale/multifemale sleeping group with monogamous or promiscuous mating. The Analamazaotra Special Reserve probably holds *ca.* 100 adult individuals. Additional research is urgently needed to clarify the habitat needs of this rare species.

Keywords conservation · habitat use · population estimate · seasonal variation · social structure

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Introduction

The study of the behavior and ecology of the Cheirogaleidae is important for the understanding of human and primate origins because these species have often been suggested to have niches similar to that of the ancestral primate (Bearder *et al*. 2006; Charles-Dominique and Martin 1987; Crompton 1995; Napier and Walker 1987). Most studies on this family have focused on species living in dry forests on the west coast of Madagascar and very few on species of the eastern rain forest. One rain forest species, the hairy-eared dwarf lemur (*Allocebus trichotis*), was believed to be extinct until its rediscovery in 1989 (Meier and Albignac 1989). Since then, only a few researchers have focused on the species (Meier and Albignac 1991; Rakotoarison *et al*. 1997). Moreover, the home range size of only 8 of 26 cheirogaleid species (Mittermeier *et al*. 2006) have been reported (Table I). At the generic level, *Allocebus* is the only taxon for which home range information is missing. I here address this gap in our knowledge.

Allocebus trichotis is a small nocturnal strepsirrhine that is classified as Data Deficient (IUCN 2008). Little is known about the behavior and ecology of the species. Individuals travel alone or in pairs and researchers have found ≤6 sleeping together in tree holes (Goodman and Raselimanana 2002; Meier and Albignac 1991; Rakotoarison *et al*. 1997). Captive animals eat insects (Meier and Albignac 1991) and dental and nail morphology suggest a diet of gum and nectar (Petter *et al*. 1977). Although some authors suggested a hibernation period during the austral winter (Rakotoarison *et al*. 1997; Yoder 1996), 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). An understanding of home range size and use is crucial for the conservation assessment of the habitat needs of this rare species.

Specifically, an animal's home range is defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943, p. 351). Because most habitats are heterogeneous, it is likely the animal will not use all of its home range in equal proportion. One can use the study of home ranges to determine a species' spacing system, which is important to determine its social organization (Bearder 1987; Müller and Thalmann 2000), and to indicate its habitat and space needs (Burt 1943; Haskell *et al*. 2002) as well as its extinction risk (Haskell *et al*. 2002).

The size of an animal's home range can vary according to the species' weight, diet, sex, and age and according to the season, population density and weather variables (Burt 1943; Clutton-Brock and Harvey 1979; Harestad and Bunnel 1979; Haskell *et al*. 2002). Home range size tends to increase with the species' size, mass, and the amount of animal matter in its diet (Clutton-Brock and Harvey 1979; Harestad and Bunnel 1979; Haskell *et al*. 2002). Home range sizes for other cheirogaleids are between 0.7 and 9 ha (Table I). A linear regression based on the available data shows a nonsignificant tendency for a linear relationship between the species' body mass and home range size (n=16, r^2=0.22, p=0.069). If the home range size of *Allocebus trichotis* is related to its weight, as expected from comparative studies of other mammals, and as is probably the case in the Cheirogaleidae, then I expect a home range size between 1.1 ha and 3.3 ha, based

Table I Previous home range studies in the Cheirogaleidae and comparison with the results from this study

Species	Average weight (g)	Staple diet	Location of study and forest type	Home range analysis	Average home range (ha)	Reference
Microcebus berthae	30.7	Unknown *	Kirindy, dry deciduous forest	MCP of sleeping sites	3.5	Schwab 2000
M. berthae	33.0	Unknown *	Kirindy, dry deciduous forest	MCP	3.7	Dammhahn and Kappeler 2005
M. griseorufus	52.5	Gumivore, Frugivore	Berenty, spiny forest	MCP	0.7	Génin 2008
M. murinus	62.5 *	Insectivore *	Ankarafantsika, dry deciduous forest	MCP	2.8	Radespiel 2000
M. murinus	62.5 *	Insectivore *	Kirindy, dry deciduous forest	MCP	1.8	Eberle and Kappeler 2004
M. murinus	62.5 *	Insectivore *	Mandena, littoral rainforest	MCP	2.4	Lahann 2008
M. ravelobensis	71.5 *	Unknown *	Ankarafantsika, dry deciduous forest	MCP	0.6	Weidt et al 2004
Mirza coquereli	310 *	Omnivore *	Morondava, dry deciduousforest	Not specified	9.0	Pages 1978
M. coquereli	300.0	Omnivore *			2.5	Kappeler 1997
Cheirogaleus major	357.0	Frugivore *	Mandena, littoral rainforest	MCP	4.4	Lahann 2007
C. major	357.0	Frugivore *	Mandena, littoral rainforest	MCP	4.2	Lahann 2008
C. medius	130.0	Frugivore *	Kirindy, dry deciduous forest	MCP	1.6	Fietz 1999
C. medius	192.8	Frugivore *	Ampijoroa, dry deciduous forest	MCP	1.6	Müller 1999a, b
C. medius	357.0	Frugivore *	Mandena, littoral rainforest	MCP	1.5	Lahann 2008
Phaner pallescens	327.0	Gumivore, Insectovore	Kirindy, dry deciduous forest	MCP	4.8	Schülke 2003
P. pallescens	300.0	Gumivore	Beroboka, dry deciduous forest	MCP	4.0	Charles-Dominique and etter 1980
Allocebus trichotis	65.3	Insectivore	Analamazaotra, rainforest	100% MCP	15.4	This study
				95% Kernel	5.4	This study

Note the much larger home range in the hairy-eared dwarf lemur compared to other cheirogaleids

*Mittermeier *et al.* (2006).

on the resulting equation from the linear regression wherein $y = (1.74 \pm 0.82) + (0.007 \pm 0.004)\,x$, wherein y = home range size in ha and x = species body mass in g. In addition to body mass, I also examine other factors that may influence home range size and use. Specifically, I discuss the influence of diet, reproductive state, seasonality, and habitat type on home range parameters.

The details of the social organization of the Cheirogaleidae are variable but, overall, the social system is either a dispersed family group (*Cheirogaleus major* and *C. medius*: Fietz 1999; Lahann 2007; Müller 1998, 1999b) or a dispersed multimale/multifemale social system (most *Microcebus* species: Atsalis 2000; Dammhahn and Kappeler 2005; Eberle and Kappeler 2004; Radespiel 2000; Weidt *et al*. 2004). Based on sleeping group composition, previous authors suggested that hairy-eared dwarf lemurs live in family groups and have a monogamous mating system (Meier and Albignac 1991; Rakotoarison *et al*. 1997). If this is true, I expect home ranges of individuals of the same sleeping group to overlap to a large extent and to exclude the members of other sleeping groups. I also expect the home ranges sizes of males and females to be the same.

Materials and Methods

I 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. The small village of Andasibe lies between the capital Antananarivo and the shores of the east coast, *ca*. 30 km east of Moramanga (Dolch 2003). Previously covered with continuous forest, the region now has only fragments of forest (Dolch 2003). The climate is humid with an average annual rainfall of 1700 mm over 210 d, an annual average temperature of 18°C, and atmospheric humidity >70% (ANGAP 2002). The forest of the study area is disturbed midaltitude primary eastern rain forest at altitudes of 850–950 m. Mean canopy cover is 87.6±4.3%. Dense forest makes direct observations of small nocturnal species difficult.

My team and I captured 11 individuals (Table II) and radiocollared 6 (Table III). Capturing the first individuals was very difficult and took *ca.* 2.5 mo. We caught 2 adult males and 1 juvenile using hand-held bamboo noose poles. Juveniles were smaller than adults and weighed up to 50 g. Once we captured a first individual and located its sleeping hole, 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 followed the first social group from April to November. I am confident that this is a complete social group because we observed no other individuals in this group's home range. Attempts to locate and catch a second sleeping group also took longer than expected, and we succeeded only in September. However, this second social group was most likely not complete because we captured no males, but observed unknown adult individuals leaving the radiocollared females' tree holes on several occasions. I radiocollared all individuals with masses >65 g (TW-4 transmitter, 3.2 g, Biotrack Ltd.) and tracked them via a TR-4 receiver and RA-14 antenna (Telonics Inc.). I fitted the first collared individual with a leather collar that lasted only a few hours (Table II). I subsequently fitted individuals with cable-tie collars that lasted throughout the study and were never lost. I recaptured radiocollared individuals

Table II Captured individuals

Group	ID	Age class	Sex	Head and body length (mm)	Tail length (mm)	End of rainy season captures		End of dry season captures		Start of rainy season captures and radio-collar removal	
						Date	Weight (g)	Date	Weight (g)	Date	Release Mass (g)
	AM 1	adult	M	134	139	23-Mar	80				
Group 1	AF 1	adult	F	133	135	2-Apr	87	27-Aug	82	14-Dec	95
	AF 2	adult	F	134	134	13-Apr	82	27-Aug	69	14-Dec	79
	AM 2	adult	M	133	147	30-Mar	74	27-Aug	81	14-Dec	78
	AM 5	adult	M	141	130	2-Apr	82	27-Aug	82	7-Dec	91
	AM 3	juvenile	M?	117	118	2-Apr	43	27-Aug	50	14-Dec	63
	AM 4	juvenile	M?	119	111	2-Apr	44			4-Dec	66
Group 2	AF 4	adult	F	135	123			7-Sep	69	3-Dec	67
	AF 5	adult	F	132	140			7-Sep	67	21-Nov	70
	AF 3	juvenile	F?	119	120			6-Sep	50	21-Nov	48
	AM 6	juvenile	M?	117	121			7-Sep	44		

Adult male AM1 lost his radiocollar on the first night. Group 1 was a full social sleeping group. Group 2 was a partial sleeping group. There was no sexual dimorphism. Juveniles were distinguished by their smaller size and weight. Female AF1 was the heaviest female and male AM5 the larger male. Weight varied seasonally. Females in particular lost weight over the dry season whereas males were not affected or gained weight. We removed all radiocollars at the end of the study and most individuals gained weight between the first capture at the end of the rainy season and their release

Table III Focal individuals

ID	Radio-tracked		Total number of sleeping site locations	Total number of nocturnal follows	Total follow time	Total number of GPS Waypoints (including nest locations)	Total number of GPS Waypoints (excluding nest locations)
	From	To					
AF1	2 April	30 November	148	64	163 hrs 24 min	1025	818
AF2	13 April	30 November	141	46	104 hrs 51 min	680	525
AF4	7 September	30 November	47	30	70 hrs 15 min	450	381
AF5	7 September	21 November	42	21	54 hrs 16 min	345	283
AM2	30 March	30 November	152	61	158 hrs 14 min	941	722
AM5	3 April	28 November	101	30	81 hrs 45 min	406	258
TOTAL			631	252	632 hrs 45 min	3847	2987

We radiocollared only adult individuals with masses >65 g. We followed individuals of group 1 (AF1, AF2, AM2, and AM5) for 8 mo. We followed individuals from group 2 for 3 mo. The delay between the start of the study in January and the start of the follows as well as the gap between group 1 and group 2 were due to the difficulty in catching a first individual in a sleeping group. We located individuals in their tree holes during the day 4 or 5 times a week. The total number of sleeping site locations is the number of days in which we located an individual in its sleeping site. By contrast, the total number of GPS waypoints (including nest locations) also includes location points where the individual was in its tree hole during the night and the total number of GPS waypoints (excluding nest locations) excludes all the nest locations (during the day or at night) where the individual was inactive. Average follow time per individual per follow was 2.5 h. We collected GPS waypoints every 10 min whenever possible. The differences in data collection between individuals were due to difficult weather conditions on certain nights/days, problems with individual radiocollars, or the inability to locate a particular individual because it moved far away from its usual home range area or because the terrain prevented continuous follow, e.g. large river every 2–3 mo to replace the collars with expired battery. I weighed and checked the reproductive state of recaptured individuals, i.e., observation of nipples, vulva and palpation in females; measurement of testicle length and breadth in males. I removed all the radiocollars at the end of the study.

I used radiotracking of focal individuals during nocturnal follows and daytime nest locations of all radiocollared individuals to determine an individual's range (Dammhahn and Kappeler 2005; Fietz 1999; Lahann 2007; Müller 1999b). My team and I conducted partial nocturnal follows 5 nights per week, adhering to the following schedule: on 3 nights, we located the first focal individual in its tree hole and followed it from the time it left its nest for *ca.* 2 h, then we located a second focal individual and also followed it for *ca.* 2 h; on 2 nights, we entered the forest at *ca.* 2100 h and sought a first individual that we then followed for *ca.* 3 h; then we located a second individual and followed it until it entered its tree hole at dawn. The average follow time per individual was *ca.* 2.5 h and the mode was 1 h (n=253 follows). Although I originally tried full-night follows, these were very difficult to maintain in the long term owing to difficult terrain and weather conditions. The schedule reported here worked best to maintain observers' concentration and stamina.

We recorded the subject's position every 10 min via a handheld GPS Map60 CSX. We took GPS waypoints under the tree where we had seen the individual or where it was believed to be based on close range triangulation. We monitored behavior every 5 min and feeding events *ad libitum* whenever possible. However, direct observations were often hampered by difficult weather conditions, dense vegetation, and the fact that individuals often moved at heights >10 m above ground. We located radiocollared individuals in their nests during the day 4 or 5 times a week (minimum result twice, maximum 7 times; Müller 1999a; Radespiel 1998). We conducted point-quarter vegetation sampling in 6 1-ha plots to determine tree genus composition (Ganzhorn 2003).

I conducted analyses of home range size and location via Ranges 7 (Anatrack Ltd.). For comparability to previous studies I estimated the overall home range per individual (n=6) via 100% minimum convex polygons (MCP) with harmonic means centers using all the location points, i.e., daytime nest locations and nocturnal follow locations, range n=345 to 1025 waypoints per individual: Table III (Dammhahn and Kappeler 2005; Fietz 1999; Lahann 2007; Müller 1999b). The method creates a polygon including all the locations where an individual was recorded (Mohr 1947). Although it is a quick and easy method, it is also well known to overestimate home range size (Barg *et al.* 2005; Burgman and Fox 2003; Mohr 1947; Pimley *et al.* 2005). I therefore also used 95% adaptive core weighted kernel analyses with least square cross validation using only the location points collected during nocturnal follows, i.e., excluding all locations during which the individuals were inactive in their nests, range n=258 to 818 waypoints per individual: Table III (Pimley *et al.* 2005; Seaman and Powell 1996; Worton 1989). The method is based on the actual amount of use of different areas by an individual (the utilization distribution) and therefore produces much more accurate home range estimates, excluding outliers (Aebischer *et al.* 1993; Barg *et al.* 2005; Pimley *et al.* 2005; Seaman and Powell 1996; Worton 1989). I used the resulting home range edges to determine the percentage home range overlap between individuals, which I represented graphically in a sociogram.

To detect monthly variations in home range size I first checked for correlations between the number of location points per individual per month and the resulting home range estimate. The results of the 2-tailed Pearson correlations are not significant for either the MCP estimates ($n=37$, $p=0.10$) or the kernel estimates ($n=34$, $p=0.39$). I therefore used all the location points, excluding localization in the nest for kernel, for all individuals with >10 locations per month. I used a Friedman test for related samples to detect differences in home range size between months ($n=3$ individuals for MCP and kernel) and Mann-Whitney *U*-tests to detect differences between sexes in individual monthly home range size (for MCP $n_{\text{males}}=15$, $n_{\text{females}}=22$; for kernel $n_{\text{males}}=12$, $n_{\text{females}}=22$). I used SPSS 16.0 (SPSS Inc.) for all statistical analyses. I set $\alpha=0.05$. I used visual inspection of home range maps to determine the position of nests and particular behaviors: feeding, moving, resting, grooming, calling, and social interactions.

As there was a large amount of overlap between individuals of the same sleeping group, I used group home ranges to determine individual space needs for the species. I used similar home range analyses with the group as a unit, estimating group MCP and kernel home range size.

Results

Group Home Ranges

Group 1 was composed of 4 adults and group 2 of 2 adults (Table II). The group home ranges estimated via MCP are 35.5 ha and 16.0 ha, respectively, for kernel they are 15.2 ha and 7.1 ha, respectively (Fig. 1). Although there is some overlap between the 2 MCP group home ranges, the kernel group home ranges were mostly exclusive (Fig. 1).

Individual Home Ranges

Mean individual home ranges are 15.4 ha for MCP and 5.4 ha for kernel (Table IV). There is no difference between sexes (Table IV); however, there is important individual variation (Table IV; Fig. 2).

Seasonal Change in Home Range

There is no significant difference between months for either the MCP or the kernel home range sizes: for MCP: $n=3$, χ^2 $(7)=3$, $p=0.92$; for kernel: $n=3$, χ^2 $(7)=6.44$, $p=0.54$. There is no significant difference between monthly male and female home range size: $n_{\text{males}}=15$, $n_{\text{females}}=22$, $U=120$, $p=0.17$ (2-tailed) for MCP home ranges; $n_{\text{males}}=12$, $n_{\text{females}}=22$, $U=110$, $p=0.44$ (2-tailed) for kernel home ranges. The mean monthly home range is 5.2±3.0 ha for MCP (range: 0.2–12.9 ha) and 2.2±1.6 ha (range: 0.2–6.6 ha) for kernel. Visual inspection of home range maps showed monthly home range shifts.

The hairy-eared dwarf lemurs were active throughout the study and did not hibernate, but interindividual variation in monthly home range size is large. Males

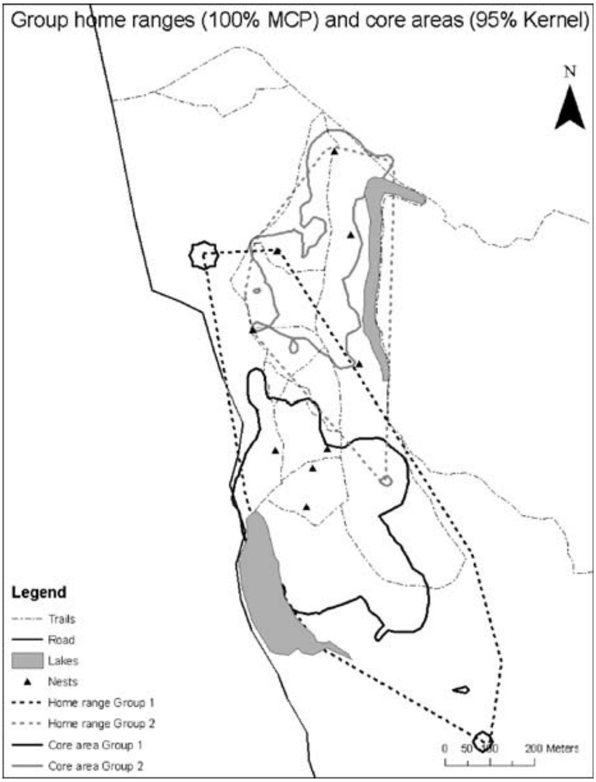

Fig. 1 Group home ranges. MCP estimated home ranges are represented as dotted lines (black for group 1, gray for group 2) and kernel home ranges are represented in full lines (black for group 1, gray for group 2). Although there is overlap between the MCP home ranges, kernel home ranges are mostly exclusive. Kernel home ranges show excursion areas to the north and south in group 1 and to the south in group 2.

AM2 and AM5 did not follow similar fluctuation patterns (Fig. 3). The home range of AM2 peaked in September–October (Fig. 3). He made 2 excursions in late August and early September, to an area 400–500 m north of his normal area of activity (Fig. 2). Conversely, male AM5 had no such peak in home range size (Fig. 3). His home range was largest in April–May, dropped until July, and then remained small (<2 ha for MCP; Fig. 3).

Female home range sizes also followed different fluctuation patterns (Fig. 3). The home range of female AF1 was largest in April (Fig. 3). It decreased in May and increased only slightly during the colder season (May–August; Fig. 3). Her range decreased again in September and increased gradually until November (Fig. 3). Female AF2 followed a different pattern. She often made excursions to an area 600–700 m from her closest sleeping hole (Fig. 2), especially in May–August, which explains her larger overall home range compared to that of AF1 (Table IV; Fig. 2). Her home range peaked in May and then again in September–October (Fig. 3). It decreased gradually during the colder season, from May to August (Fig. 3).

Table IV Individual home range sizes

ID	Home range size (ha)	
	100% MCP	95% Kernel
AF1	9.6	5.5
AF2	30.1	7.5
AF4	11.9	5.5
AF5	10.1	2.1
AM2	20.7	6.1
AM5	10.2	5.5
Overall mean ± SD (n=6)	15.4±8.3	5.4±1.8
Male mean ± SD (n=2)	15.4±7.4	5.8±0.4
Female mean ± SD (n=4)	15.4±9.8	5.1±2.2

There is no sexual difference in home range size but individual differences are large

Weight and Home Range

There is no major difference between male and female morphology or mass (Table II). Juveniles are distinguished from adults by their smaller size and body weight (Table II).

Female AF1 was the heaviest female throughout the study (Table II) and the only gravid one in December. She was still lactating in April (I observed swollen nipples) but no longer in June. This female lost 4.5 g (about 5% of her body mass) during the dry season (mass in April: 86.5 g; in August: 82 g; Table II). Female AF2 lost *ca.* 16% of her body mass during the colder season, *ca.* 3 times more than AF1 (mass in April: 82 g; in August: 69g; a 13-g loss; Table II).

Male AM5 was the heavier of the 2 males (Table II). His weight did not change during the dry season (Table II). Male AM2 gained 7 g (*ca.* 9% of his body weight) during the colder season (mass in April: 74 g; in August: 81 g; Table II).

Diet and Home Range

During focal follows, I observed hairy-eared dwarf lemurs feeding on 27 occasions. In 14 cases the individual caught, or tried to catch, small moths and in 5 cases it fed on gum. Individuals also ate fruit, flowers, and leaves in 5 cases. In 3 cases, I could not identify the food item. The hairy-eared dwarf lemurs most often ate gum from *Terminalia* trees. During point quarter vegetation sampling, I measured 1468 trees with a diameter at breast height >10 cm belonging to 113 different genera within 6 1-ha plots. I located only 5 *Terminalia* trees (0.3% of trees).

Reproductive State and Home Range

The size of the testicles varied seasonally in both males but asynchronously. Between late March and late May, after the end of the rainy season, the testicle area, measured height (mm) × breadth (mm), of male AM2 decreased by 48%, from 357 mm^2 to 185 mm^2. It then increased almost 3-fold to reach its highest at the end of the dry season (in August: 532 mm^2). His testicles then regressed again by 67%

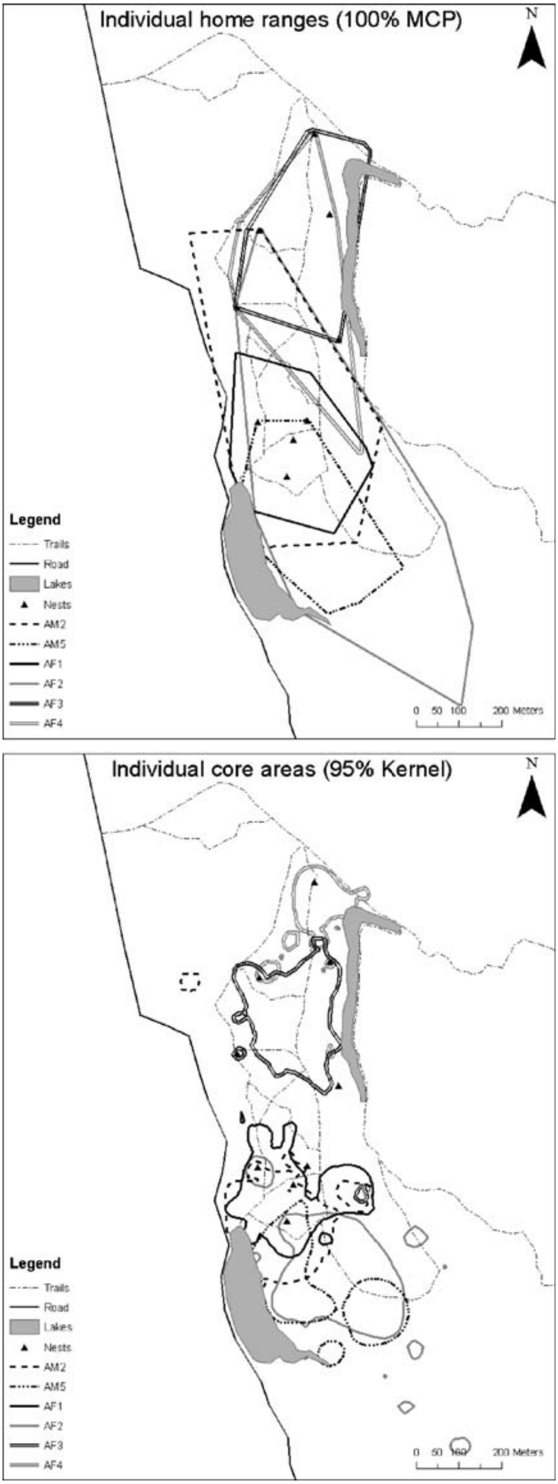

Fig. 2 Individual home ranges. Dotted lines represent males; full lines, females. Intragroup overlap was greater than intergroup overlap, especially for kernel estimated home ranges (bottom). MCP home range estimates include excursion areas rarely visited. Kernel home ranges include areas used most often or where a substantial amount of time was spent even if related to only a few excursions. There was inter- and intrasexual overlap. Male AM2 made occasion excursions north of his usual home range and female AF2 did so south of her usual home range. There are important individual variations in home range size.

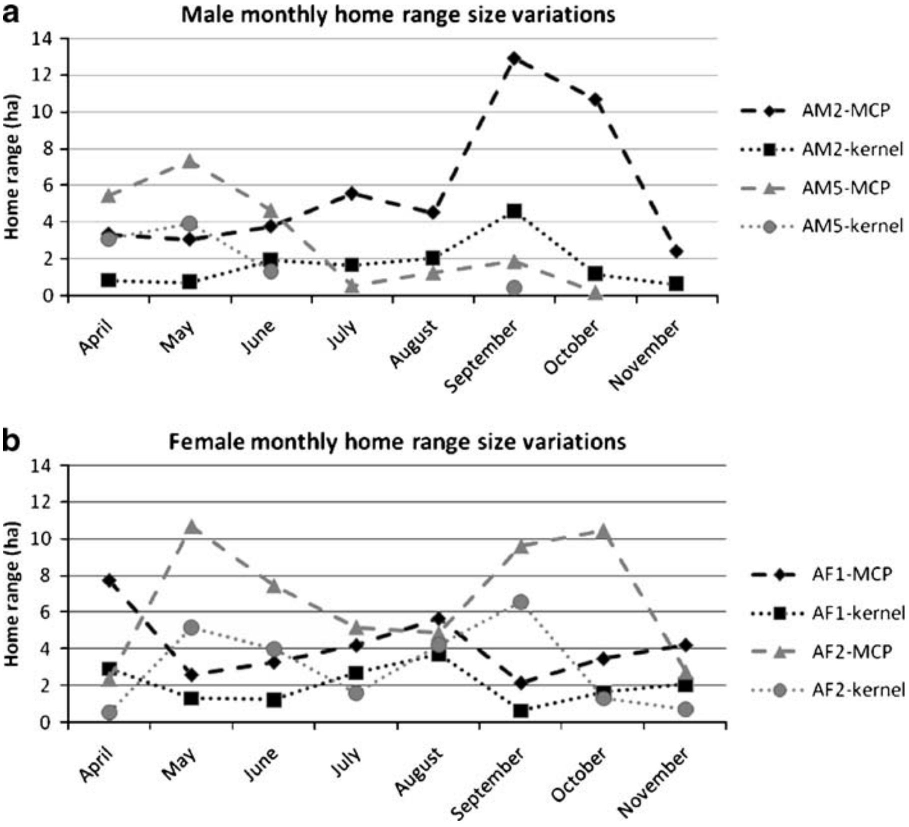

Fig. 3. Individual monthly home range size variations. Striped lines represent MCP home range variations; dotted lines, kernel home range variations. Individuals did not follow similar fluctuation patterns. **(a)** Males: The home range of AM2 was largest in September and October. AM5 had a larger home range in April–May that decreases and stays low after May. **(b)** Females: The home range of AF1 was largest in April, decreased in May and increased slowly during the colder season (May–August) before shrinking again in September and rising afterward. The home range of AF2 was largest in May and again in September-October. It decreased during the dry season from May to August and again after October.

until December (175 mm^2). Male AM5 had a similar testicle area from March to May (237 mm^2 and 273 mm^2). His testicles increased by 54% until August (421 mm^2) and reached their highest in December (465 mm^2).

Home Range Use

Although certain feeding areas were exclusive to a particular individual, most were shared by members of the same sleeping group. Calls often took place near home range edges (43% of calls were <10 m from kernel home range edges; 24% were <10 m from MCP edges) but I also heard them near tree holes (14%) and in other parts of the home range (n=51). Nests were generally away from the home range edge. All or most nests used by AF1, AF2, AF4, and AM2 were >10 m away from the MCP edge and all or most of the nests used by AF1, AF2, AF5, and AM5 were >10 m away from the kernel edge (Fig. 2). Social encounters recorded for group 2 were generally between a female and a juvenile (most likely mother and offspring) but I recorded inter- and intrasexual nocturnal encounters between adults of group 1. These social encounters generally took place in the central area of this group's range, where the kernel home ranges of all individuals overlap.

Home Range Overlap and Social Interactions

Male MCP home ranges overlapped with those of 2–4 females while their kernel home ranges overlapped with those of 2–3 females (Table V; Figs. 2 and 4). Female home ranges overlap with those of ≤2 males. Male and female home ranges overlap with each other.

The sociogram (Fig. 4) shows the high degree of overlap in MCP estimated home ranges of individuals of the same sleeping group (group 1: AF1, AF2, AM2, and AM5; group 2: AF4 and AF5). Sleeping groups overlap as well (Fig. 1), but the percentage of overlap between and within sexes is higher within groups (Table V; Fig. 4). Kernel home ranges also overlap largely between members of group 1 (Table V; Figs. 2 and 4). Again, although there is a limited amount of overlap between the 2 groups (Fig. 1), the intra- and intersexual overlap is larger within a sleeping group (Table V; Figs. 2 and 4).

Within group 1, the 2 pairs AF1/AM2 and AF2/AM5 have a higher degree of overlap (Fig. 4), confirmed by the number of times I saw individuals together at night, at least for AM2/AF1. These 2 individuals met most often (72 observed interactions throughout the study period). Female AF2 met males AM2 and AM5 a

Table V Home range overlap between individuals

	AF1	AF2	AM2	AM5	AF4	AF5
a. Percentage overlap between MCP home ranges						
AF1		88.7	99.9	51.4	6.8	0.0
AF2	28.2		52.5	32.2	18.1	7.6
AM2	46.2	76.3		31.3	28.8	12.0
AM5	48.4	95.2	63.8		0.0	0.0
AF4	5.4	45.7	49.9	0.0		65.9
AF5	0.0	22.4	24.4	0.0	77.6	
b. Percentage overlap between kernel home ranges						
AF1		19.7	67.8	16.7	1.3	0.0
AF2	14.3		24.0	47.3	0.1	0.0
AM2	61.1	29.8		33.3	1.1	0.0
AM5	16.5	64.4	36.5		0.0	0.0
AF4	1.3	0.1	1.3	0.0		3.3
AF5	0.0	0.0	0.0	0.0	8.5	

Lines in the table show how much the home range of the line individual overlaps with the column individual, e.g., 88.7% of the home range of AF1 overlaps with the home range of AF2 but only 28.2% of the home range of AF2 overlaps with AF1

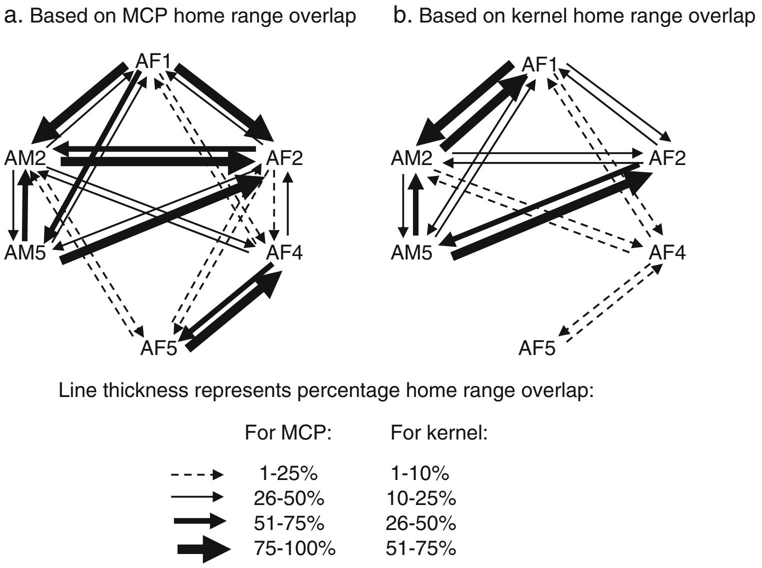

Fig. 4 Sociograms based on MCP and kernel home range overlaps. Arrows indicate the direction of the overlap and line thickness indicates the percentage overlap, e.g., 26–50% of the home range of AM2 overlaps with the home range of AF1 but 75–100% of the home range of AF1 overlaps with the home range of AM2.

roughly equal amount of times (8 and 9 respectively) and female AF1 rarely met male AM5 (3 sightings). The kernel-based sociogram (Fig. 4) also shows a higher amount of overlap between males than between females of group 1. Males also met much more often at night than females (14 vs. 2 sightings). Although home ranges overlapped between groups (Fig. 1), showing inter- and intrasexual overlap, certain individuals (AM5 and AF5) have no or very limited intergroup overlap (Fig. 4).

Discussion

Habitat Needs and Conservation Assessment

My results clearly show that hairy-eared dwarf lemurs need a much larger home range than other cheirogaleids do (Table I), and this should be taken into account in conservation management. To estimate the minimum number of individuals potentially living in the Analamazaotra Special Reserve, I used the group home range estimate because there is a large amount of overlap between individuals of group 1. I used the MCP estimate (35.5 ha) to include all the visited areas, even occasional excursion areas, which could also be important for the species' survival. I estimate a minimum, i.e., excluding overlap between groups, of 23 groups of 4 adult individuals each or 92 breeding adults in the 810-ha Analamazaotra Special Reserve ($810 \div 35.5 = 22.8 \approx 23$; $23 \times 4 = 92$). To estimate the maximum number of individuals in the Analamazaotra Special Reserve, I used the smallest available home range value, which is the mean individual kernel home range estimate (5.4 ha). In this case, I expect a maximum of 150 adult individuals (810 ÷ 5.4=150). However, this maximum value will most likely not be attained owing to unsuitable habitat within the reserve, e.g., clearing, forest edges, lakes, etc. This means that the 810-ha Analamazaotra Special Reserve probably holds *ca.* 100 individuals and explains why *Allocebus* is so much harder to find than *Microcebus* or *Cheirogaleus* because it has much lower population densities (*ca.* 11–19 individuals/km^2) (Meier and Albignac 1991; Rakotoarison 1998; Yoder 1996). In comparison, densities of the sympatric *Cheirogaleus major* and *Microcebus rufus* have been estimated at *ca.* 75–110/km^2 (Fietz 2003) and 110/km^2 (Kappeler and Rasoloarison 2003), respectively.

Why Is the Hairy-eared Dwarf Lemur's Home Range So Large?

Microcebus murinus, which is similar in mass and size to *Allocebus trichotis* (Lahann *et al.* 2006; Rasoloarison *et al.* 2000) and also has a diet high in invertebrates (Mittermeier *et al.* 2006), has home ranges of 0.6–4.8 ha, depending on the individual's sex and the reproductive cycle (Eberle and Kappeler 2004; Lahann 2008; Radespiel 2000). *Allocebus trichotis* has a mean MCP home ranges of 15.4 ha, much larger than that of other Cheirogaleidae. What are the possible causes of this difference?

Climatic conditions could account for variations in home range size. In *Microcebus murinus*, home ranges were slightly smaller in the littoral rain forest, where mean annual temperature is lower and annual rainfall is higher, than in the dry deciduous forest (0.6 ha for females and 4.2 ha for males in the littoral rain forest vs. 0.7–1.6 ha for females and 2.8–4.8 ha for males in the dry deciduous forest: Eberle and Kappeler 2004; Lahann 2008; Radespiel 2000). In the Analamazaotra Special Reserve, where the mean temperature is lower (18°C) and the annual rainfall higher (1700 mm/yr; ANGAP, 2002) than in the littoral rain forest (23°C, 1600 mm/yr: Lahann *et al.* 2006), I would expect even smaller home ranges. However, the opposite is true.

A much more insectivorous diet in hairy-eared dwarf lemurs or the use of very patchily distributed food resources, e.g. gum trees, could explain larger home ranges (Clutton-Brock and Harvey 1979; Harestad and Bunnel 1979; Haskell *et al.* 2002). Indeed, my observations show a diet high in moths (*ca.* 52%) and gum (19%) and the *Terminalia* trees on which the species feeds could indeed be a limiting resource because they represented only 0.3% of all the trees measured during point quarter sampling. To investigate the effect of diet on home range size, I compared my results with those on other nocturnal primates with similar diets. The bush-babies *Otolemur garnetti* and *Galago moholi* have a similar percentage of animal prey in their diet (*ca.* 50%: Bearder 1987). When home range sizes are adjusted for body mass, i.e., home range size is divided by body mass, then the values for *Allocebus trichotis* (0.24 for MCP and 0.08 for kernel) are generally higher [for *Otolemur garnetti*: 0.02; for *Galago moholi*: 0.02–0.06 for females, 0.05–0.11 for males, calculated from values reported in Bearder (1987)]. Only the kernel value falls within the range of male *Galago moholi*. In *Perodicticus potto*, as in *Allocebus trichotis*, gum contributes *ca.* 20% of the diet (Bearder 1987). When adjusted for body mass, the home range values for central pottos, *Perodicticus potto edwardsi*, are 0.02–0.03 for kernel and 0.09–0.17 for MCP [calculated based on body weight reported in Bearder (1987) and on home range size reported in Pimley *et al.* (2005)]. Again, the values for hairy-eared dwarf lemurs are higher, suggesting diet composition alone cannot explain the larger home ranges in this species.

Comparisons between home range estimates of different species are very difficult because of the different methods used, e.g., number of individuals, length of study, home range estimate used, etc., and the many factors influencing home range size, e.g., diet, body mass, habitat characteristics, etc. In most cases, the information currently available is too scarce to enable exact comparisons. Additional research on the ecology of hairy-eared dwarf lemurs and other nocturnal primates is therefore needed.

Seasonality

Although statistical analyses showed no significant difference in home range size between months, probably due to the small sample size ($n=3$ individuals), it is clear that, at the individual level, there were important variations. Changes in individual monthly home range size and location could be related to the onset of the reproductive season, to a change in resource availability at the end of the drier colder months, or to a shift in diet due to the change in resource availability. For example, the increase in home range size in male AM2 in September is probably due to the onset of the reproductive season because its testicles were largest in August. This was also the case in *Microcebus murinus*, wherein testes volume was highest in August and home range size was highest in September (Schmelting *et al.* 2000).

Female AF1 probably increased her home range in April to increase her food intake and gain mass before the cold season. It is possible that depleting resources forced her to increase her home range gradually during the colder season to meet her needs. This would also explain the decrease in September, when more resources become available. In *Microcebus rufus* the mating season occurred in October–November with births in the second and third week of December (Blanco 2008). If the gestation period is similar in *Allocebus trichotis* (57 d), it is likely that this female mated late October and was about to give birth when released on December 14.

The peak in home range size in female AF2 in May could also be related to her efforts to gain mass before the colder season. She might have followed a pattern similar to that of male AM2 by increasing her home range in September and October in preparation for reproduction.

Male testicle size varied asynchronously. Testicles were most developed in August for 1 male and in December for the other. This contradicts the results of Rakotoarison *et al.* (1997), who found that testes regressed in May to August and started to increase in volume only in September. In *Microcebus murinus* and *M. ravelobensis*, testes volume was also at a maximum in August and in *M. murinus* it also increased a second time in November (Schmelting *et al.* 2000). I therefore suggest temporal variations in individual reproductive cycles might be found in future research and that, as for *Microcebus murinus* (Schmelting *et al.* 2000), a long mating season with asynchronous female estrus might be found.

Spacing System

My results suggest that the sleeping group is the basic social unit for the species. Because only males of group 1 were radiocollared, it is unfortunately impossible to say how much interaction occurs between males of different groups, between the males and females of group 2, and between females of group 1 and extragroup males.

Home range sizes were similar in male and female hairy-eared dwarf lemurs. Previous studies also found similar home range sizes in male and female *Cheirogaleus major* (Lahann 2007), *C. medius* (Schwab and Ganzhorn 2004), and *Microcebus ravelobensis* (Weidt *et al*. 2004). Researchers found sexual differences in *Mirza coquereli*, *Microcebus berthae*, *Microcebus murinus*, and *Microcebus myoxinus* (Dammhahn and Kappeler 2005; Eberle and Kappeler 2004; Pages 1978; Radespiel 2000; Schwab 2000; Schwab and Ganzhorn 2004). The lack of sexual differences in hairy-eared dwarf lemurs could be the results of a family group social system similar to those of *Cheirogaleus major* and *C. medius* (Fietz 1999, 2003; Lahann 2007; Müller 1998) or a multimale/multifemale social system similar to that of *Microcebus ravelobensis* (Weidt *et al*. 2004). Further research using parentage analysis should be conducted to determine the mating system, which I suspect to be either monogamous (2 pairs sharing a home range) or promiscuous (males or females looking for mates within or between groups).

In conclusion, it is clear that much more research is needed to clarify the home range needs and social structure of *Allocebus trichotis*. Because the species is very difficult to locate and capture, I suggest additional research in the Andasibe area at first. Local guides are now well aware of the tree holes and forest areas used by the individuals we studied and know how to identify and catch the species. Hairy-eared dwarf lemurs also occur in other forests of the area (Mantadia National Park, Analamazoatra Forest Station, and Maromiza forest; Biebouw 2006; Marquart and Garbutt *pers. comm*). The study of additional groups over a whole year cycle should help to clarify home range needs, individual or group differences, seasonal variations, and inter- and intragroup interactions. As the minimum convex polygon method overestimates home range size (Barg *et al*. 2005; Burgman and Fox 2003; Mohr 1947; Pimley *et al*. 2005) and my MCP estimates included areas that an individual visited only rarely, I suggest that the kernel estimate be used for a more realistic home range area estimate.

Acknowledgments This research was funded by Primate Conservation Inc., Conservation International's Primate Action Fund, The Linnean Society's Systematics Research Fund, Primate Society of Great Britain and Oxford Brookes University. MICET helped with research permits, visas, and logistics in Madagascar. The local ANGAP and Association Mitsinjo in Andasibe helped with logistics, access to the field sites, and support staff. Field assistants included Miss Tiana Andrianoelina and Mr. Laingoniaina Rakotonirina from the Department of Paleontology and Biological Anthropology at the University of Antananarivo; conservation agents from the local ANGAP office (Richard, Nono and Simon); local guides from Association Mitsinjo (Play, Nasoavina, Justin-Claude, Alain, Pierre, and Olivier) and Association Tambatra (Justin), and 2 European volunteers (Anna Stangl and Jason Mann). This project was conducted as part of my Ph.D. at Oxford Brookes University and I also thank my supervisors: Dr. Anna Nekaris and Prof. Simon Bearder for their support and advice throughout this study and for comments and reviews on the paper. Finally, I thank the anonymous reviewers who helped improved the manuscript with their comments.

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