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**Revealing the behavioural ecology
of the elusive hairy-eared dwarf lemur
(*Allocebus trichotis*)**

**by
Karla BIEBOUW**

Degree awarded by Oxford Brookes University

**Thesis submitted in partial fulfilment of the requirements of the award of
Doctor of Philosophy**

May 2009

**APPENDIX
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ABSTRACT

In this study we followed hairy-eared dwarf lemurs (*Allocebus trichotis*), a small nocturnal strepsirrhine primate, using radio-tracking during a one year study. Our aim was to clarify the behavioural ecology of the species and in particular to determine habitat use, social organisation and seasonal activity cycle. We conducted field work between January and December 2007 in the Analamazaotra Special Reserve, Andasibe, central eastern Madagascar. After capturing and measuring eleven individuals, we followed two males and two females for eight months and two additional females for three months. Adults weighed about 77 g, measured 13-14 cm and had a 12-15 cm tail. The much larger home range of *Allocebus trichotis* compared to other Cheirogaleidae (mean: 15 ha (MCP), 5 ha (kernel)) could be due to the highly insectivorous diet or the use of patchily distributed gum-trees. Each focal animal used four or five different tree holes and shared these with conspecifics and occasionally with white-tailed tree rats (*Brachytarsomys albicauda*). Tree holes were in living trees with average diameters at breast height of 32 cm, at median heights of 7 m. Tree holes could have anti-predator and thermoregulatory functions and might be a limiting resource. Hairy-eared dwarf lemurs mainly used the small branch niche, five to ten meters above ground. Their diet was gummivore-insectivore. We propose a dispersed pair-bonded multi-male/multi-female social system with a monogamous or slightly promiscuous mating system. During the colder drier season, most animals decreased activity and entered periods of daily torpor, especially the heavier ones. The mating season probably lasted from October to December with births between December and February. Although this study presents crucial data on a rare nocturnal species, its small sample sizes call for additional research. Continued efforts are needed to assess the conservation status of this Data Deficient species. Fortunately, this and recent studies prove the feasibility of research on small nocturnal strepsirrhine primates in the eastern rainforests of Madagascar.

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Biebouw, K., Bearder, S. K. and Nekaris, K. A. I. (2009). Tree hole utilisation by the hairy-eared dwarf lemur (*Allocebus trichotis*) in Analamazaotra Special Reserve. *Folia Primatologica* **80**: 89-103.

GENERAL INTRODUCTION

The hairy-eared dwarf lemur (*Allocebus trichotis*) is a small nocturnal strepsirrhine primate belonging to the Cheirogaleidae. All the members of this family (5 genera, 29 species) are endemic to the island of Madagascar, situated off the South East coast of Africa (IUCN, 2008; Mittermeier et al., 2006). Cheirogaleidae contain the mouse lemurs (*Microcebus* spp., 15 species); the dwarf-lemurs (*Cheirogaleus* spp., 7 species); the giant dwarf-lemurs (*Mirza* spp., 2 species); the fork-marked lemurs (*Phaner* spp., 4 species); and the monotypic hairy-eared dwarf lemur (*Allocebus*) (IUCN, 2008). It includes the world's smallest primate (Madame Berthe's mouse lemur, *Microcebus berthae*) with a weight of about 30 g (Mittermeier et al., 2006). The largest cheirogaleids, the fork-marked lemurs, weigh around 330 g but can be surpassed in weight by the greater dwarf lemur (*Cheirogaleus major*), which can seasonally increase its body mass to up to 500 g (Mittermeier et al., 2006).

The taxonomic position of *Allocebus trichotis* within the Cheirogaleidae remains controversial. Although the species was originally named *Cheirogaleus trichotis* by Günther in 1875, Petter-Rousseaux and Petter created the new genus *Allocebus* in 1967. This change was based on morphological and dental differences compared to the other Cheirogaleidae (Petter et al., 1977). Although the cranial morphology and dentition resembles that of *Phaner*, this is most likely due to morphological adaptations to gum feeding (Petter et al., 1977). A cytogenetic study showed a closer affinity to *Microcebus*, *Cheirogaleus* and *Mirza* (Rumpler et al., 1995). Genetic data later revealed a closer affinity between *Allocebus* and a *Mirza/Microcebus* clade (Pastorini et al., 2001).

Although the family Cheirogaleidae was at some point believed to be more closely related to the loriformes and in particular to the Galaginae of Africa, it is now generally accepted that the lemurs of Madagascar form a monophyletic group: the lemuriformes (Charles-Dominique and Martin, 1987; Martin, 2000; Pastorini et al., 2003; Yoder, 1994; Yoder, 2003). The infraorder lemuriformes includes 5 living families, all endemic to Madagascar: the Lemuridae, Lepilemuridae, Indriidae, Daubentoniidae and Cheirogaleidae (Gould and Sauther, 2007; Yoder, 1994; Yoder, 1997). The systematic classification within lemuriformes is still controversial but it is generally agreed that the Daubentoniidae are the most basal (DeIpero et al., 2006; Matsui et al., 2009; Pastorini et al., 2003; Yoder, 2003). The phylogenetic relationships between the other families are still not resolved (DeIpero et al., 2006; Pastorini et al., 2003; Yoder, 2003). The infraorder lemuriformes forms, together with the loriformes (Galaginae and Perodictinae from Africa and Lorisinae of Asia) the suborder Strepsirrhini

(Martin, 2000; Matsui et al., 2009; Nekaris and Bearder, 2007; Yoder, 1997; Yoder, 2003). Although the exact origin of the primates of Madagascar is still discussed, most authors support the theory of an African origin either by rafting, island hopping or through a land bridge (Kappeler, 2000; Martin, 2000; Masters et al., 1995; Matsui et al., 2009; Yoder, 1997; Yoder, 2003). Hypotheses on how the ancestors of the lemurs reached Madagascar, which separated from Africa about 120 million years ago (mya), depends on the estimated divergence dates for the origin of the strepsirrhines (depending on authors from about 59 to 81 mya) and the split between lemuriformes and lorisiformes (estimated at between 54 and 77 mya) (Martin, 2000; Matsui et al., 2009; Yoder, 1997; Yoder and Yang, 2004).

In the latest IUCN species conservation status assessment of 2008, out of 120 strepsirrhine species (92 lemuriformes and 28 lorisiformes), most (36%) were classified as Data Deficient (i.e. the risk of extinction could not be assessed due to lack of information on the species' distribution and/or population status) (IUCN, 2008). This was mainly due to the lack of information on the recently discovered and/or re-classified Lepilemuridae and Cheirogaleidae (Andriaholinirina et al., 2006; Craul et al., 2007; Groves, 2000; IUCN, 2008; Kappeler et al., 2005; Lei et al., 2008; Louis et al., 2006a; Louis et al., 2006b; Louis et al., 2008; Olivieri et al., 2007; Rasoloarison et al., 2000; Yoder et al., 2000). If we exclude these species and focus on the 77 species for which an assessment could be made, we find that most (35%) were classified as Least Concern (i.e. the species is widespread and abundant); about one quarter (19 species, 25%) were Endangered (i.e. facing a very high risk of extinction in the wild) and another quarter (18 species, 23%) were classified as Vulnerable (i.e. facing a high risk of extinction in the wild) (IUCN, 2008). A total of 44 species were threatened (Vulnerable, Endangered or Critically Endangered (i.e. extremely high risk of extinction in the wild)) (IUCN, 2008). Overall, the lemuriformes and in particular members of the families Lemuridae, Lepilemuridae and Indriidae have a high risk of extinction (IUCN, 2008). Within the lorisiformes, the Galaginae and Lorisinae are most threatened (IUCN, 2008). During this assessment, the hairy-eared dwarf lemur was re-classified as Data Deficient, after decades of being Endangered, emphasizing the urgency of a behavioural ecology study of the species (IUCN, 2008).

For most strepsirrhine primates, the main threat is habitat destruction (IUCN, 2008). In Madagascar, this is either through illegal logging for valuable hardwood, charcoal production, fuel, timber and mining; and through bush fires to create new cattle pastures or agricultural land, often also as a consequence of slash-and-burn agricultural practices (IUCN, 2008; Mittermeier et al., 2006). Many species have a very limited geographical range and very

specific habitat requirements, making them very vulnerable to habitat destruction and fragmentation (IUCN, 2008; Mittermeier et al., 2006). Hunting for food and for the pet trade is also an issue in some areas (IUCN, 2008; Mittermeier et al., 2006). In Africa, habitat fragmentation is also the main threat to strepsirrhines (IUCN, 2008). Asian Lorisinae also have the added pressure of being hunted for traditional “medicines” and superstitious beliefs (IUCN, 2008).

1.1 A short history of the search for the hairy-eared dwarf lemur

1.1.1 Museum specimens

The first hairy-eared dwarf lemur specimen was collected in 1874 by Crossley (Meier and Albignac, 1991). It is still held at the Natural History Museum in London (BMNH 75.1.29.20 – Fig. 1.1) and was first described by Günther in 1875 (Petter et al., 1977). Further specimens were collected by Humblot in 1883 (an adult and a juvenile held at the Muséum National d’Histoire Naturelle in Paris: NMHN 1883.651 and NMHN 1883.650) and by Fritsche in 1926 (held at the Naturhistoriska Riksmuseet in Stockholm: NHRM A640302) (Meier and Albignac, 1991). The adult specimen from Paris was described by Petter and Petter-Rousseaux in 1956 but the specimen from Stockholm was not discovered until 1996 (Meier and Albignac, 1989; Meier and Albignac, 1991). None of the specimens had very clear localities, making an expedition to search for the species difficult. As no further captures were reported, the hairy-eared dwarf lemur was considered extinct (Meier and Albignac, 1991; Petter et al., 1977; Tattersall, 1982).

Fig. 1.1: Photographs of the type specimen of *Allocebus trichotis* held at the Natural History Museum in London



In 1964 Peyrieras found a live animal near Mananara, in north-eastern Madagascar, and kept it in captivity for a few days, observing its behaviour (Petter et al., 1977). The dead

specimen is now held at the Laboratoire d'Ecologie of Brunoy (France) and was described by Petter et al. (1977) (Meier and Albignac, 1991).

1.1.2 Field searches and first live captures

After the rediscovery of the species by Peyrieras in 1964, Petter et al. (1977) attempted another search for live animals, returning to the area of Peyrieras' capture, but without success. Yoder (1996) also attempted to relocate the species in the Mananara region in 1989 but also failed. The species was classified as Endangered in the 1986 IUCN Red list of threatened species (IUCN, 2008). Once again, the hairy-eared dwarf lemur was believed to be near extinction until its second rediscovery in 1989 by Meier and Albignac, only 40 km South of Peyrieras' original capture site.

1.1.3 First field research

In 1989 and 1990 Meier and Albignac (1991) captured five hairy-eared dwarf lemurs in the Mananara region. They kept the first captured individual in a mosquito net enclosure in the forest to observe its behaviour and organised housing for two pairs captured afterwards. They described habitat, sleeping site, sleeping group size and composition and morphology of wild animals for the first time. Their observations in captivity gave the first insights into the sleeping site and diet preferences, social behaviour, activity, locomotion and seasonality of this rare primate. As the species was believed to be limited to the Mananara region, it was given the "highest priority" rating in the 1992 action plan for the lemurs of Madagascar designed by the IUCN/SSC Primate Specialist Group (Mittermeier et al., 1994).

1.1.4 Opportunistic observations

In the following ten years, additional sightings regularly occurred (Fig. 1.2). The hairy-eared dwarf lemur was discovered in the Masoala Peninsula and Anjanaharibe-Sud Special Reserve around 1994 (Mittermeier et al., 1994; Schütz and Goodman, 1998); in the Vohidrazana forest near Andasibe and the Zahamena Integral Nature Reserve in 1995 (Rakotoarison, 1998; Rakotoarison et al., 1997); in the Analamazaotra Special Reserve near Andasibe in 1998 (Garbutt, 2001) and in Marojejy National Park in 2001 (Goodman and Raselimanana, 2002). Its presence was confirmed by photographic evidence in the Anjanaharibe-Sud Special Reserve in 1997 and by additional observations in the Masoala Peninsula in 1998 (Schütz and Goodman, 1998). These opportunistic observations added to the knowledge of the species' habitat, geographical and elevation range, morphology, activity, locomotion and support use (Garbutt, 2001; Goodman and Raselimanana, 2002; Schütz and Goodman, 1998). Although the hairy-

eared dwarf lemur was reclassified as Critically Endangered in the 1996 IUCN Red list, its status was reversed to Endangered again in the 2000 list (IUCN, 2008).

Fig. 1.2: Map showing the localities where the hairy-eared dwarf lemur is currently known to occur, based on studies in the last 20 years

1.1.5 Focussed research

Rumpler et al. (1995) studied the karyotype of the species for the first time and concluded that *Allocebus* was more closely related to *Microcebus/Mirza/Cheirogaleus* than to *Phaner*. Rakotoarison et al. (1997) discovered the species in a forest near Andasibe. They spotted four animals during a nocturnal census and found a tree hole used for sleeping during the day from which two occupants were caught. After comparing morphological measurements, the authors concluded possible geographic variations in morphology but this speculation was only based on one adult male. Furthermore, the authors claim to have found the hairy-eared dwarf lemur in a highland rainforest because of an altitude range of the studied forest of between 680 and 1,235 m, but the eight located animals were all found near the forest edge and exact altitudes of the sightings were not reported. Observed animals used sleeping holes in large dead trees at 1.4 to 2.2 m above ground. Two captured individuals were kept in captivity at the Parc Botanique et Zoologique de Tsimbazaza (PBZT) in Antananarivo. Observations in captivity confirmed a diet of insects, fruits and possibly nectar; vocalizations resembling those of *Mirza* and *Microcebus* (suggesting a closer affinity to this group than to *Phaner*); and a potential for reduced activity, increased weight and testes regression during the colder drier season. One

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has to be careful however when deducting seasonal activity cycles from observations in captivity as local variations in weather and food availability cannot be taken into account.

1.1.6 Our study

Based on this scarce information, we organised a pilot study from January to May 2006 aiming to locate a viable population of the hairy-eared dwarf lemur that could be studied. As the last sightings occurred in Marojejy National Park (Goodman and Raselimanana, 2002) and in the Analamazoatra Special Reserve (Garbutt, 2001), we set out to investigate these two sites. We started the field work in Andasibe and managed to confirm the species' presence in the Analamazoatra Special Reserve and discovered it in the Analamazoatra Forest Station (Biebouw, 2006). Although a short attempt was made to locate the species in Mantadia National Park, this was unsuccessful. The species was sighted there in 2007 by Nick Garbutt however (pers. comm.). While conducting this work, we had additional reports from Jörg Ganzhorn that Kathrin Marquart had caught four *A. trichotis* in Maromizaha forest, only a few kilometres South of Andasibe. Having found a study population in Andasibe, we cancelled the planned surveys in Marojejy.

Although it is becoming clear that the hairy-eared dwarf lemur has a much wider distribution than originally thought, there is still very limited information on its population size, density and behavioural ecology. The species has therefore very recently been reclassified as Data Deficient by the assessors of the last *IUCN Red list of threatened species* (IUCN, 2008).

1.2 Where are we now and what still needs to be done?

Although recent discoveries give a better idea of the geographical and altitudinal range of the hairy-eared dwarf lemur, still virtually nothing is known about its behavioural ecology. We know the species is exclusively nocturnal and spends the day in tree holes in groups of two to four (Meier and Albignac, 1991; Petter et al., 1977; Rakotoarison et al., 1997; Yoder, 1996). Animals usually travel alone at night (Garbutt, 2001; Goodman and Raselimanana, 2002; Meier and Albignac, 1991). Their diet is believed to include nectar, sap and/or gum based on morphological and cranial features (Meier and Albignac, 1991; Petter et al., 1977; Rakotoarison et al., 1997; Yoder, 1996). In captivity, *A. trichotis* ate insects, fruits and honey (Meier and Albignac, 1991; Rakotoarison et al., 1997).

Juveniles were reported in March but nothing is known about the reproductive cycle (Meier and Albignac, 1991). Meier and Albignac (1991) suggested oestrus could take place in November-December and births in January-February. *Allocebus trichotis* could hibernate

during the colder drier months between May and October (Mananara region) or from June to September (Andasibe region) (Petter et al., 1977; Rakotoarison et al., 1997; Yoder, 1996). Captive individuals from Mananara were less active between June and September but had no fat reserves to cope with hibernation (Meier and Albignac, 1991). Rakotoarison et al. (1997) did observe seasonal variations in weight. Between May and August, the testes of captive animals from the Andasibe region regressed and they decreased their activity.

Although originally believed to be only present in lowland primary forest, the species also seems to tolerate some levels of disturbance (Meier and Albignac, 1991; Petter et al., 1977; Schütz and Goodman, 1998). The species could be declining and threatened mainly because of habitat destruction (Meier and Albignac, 1991; Rakotoarison et al., 1997; Tattersall, 1982; Yoder, 1996). The hairy-eared dwarf lemur could be in low densities or only seem rare because of a particular ecology (Meier and Albignac, 1991; Petter et al., 1977; Rakotoarison, 1998; Tattersall, 1982; Yoder, 1996). Yoder (1996) suggested that a limiting resource could be crucial for its survival and explain its low densities. Garbutt (2001) believed the species to be more common than thought but to have been continuously mistaken for *Microcebus* spp. Goodman and Raselimanana (2002) also reported good densities of the species in Marojejy National Park. Long-term field studies are urgently needed to determine the distribution, population density, conservation status, life history, population variability, habitat needs, predation pressure, diet, social organisation, communication and taxonomic status of the hairy-eared dwarf lemur (Rakotoarison et al., 1997).

1.3 Thesis

1.3.1 Aims and objectives

In this study we aimed to clarify the behavioural ecology of the hairy-eared dwarf lemur by radio-tracking individuals of the Analamazoatra Special Reserve, near Andasibe, central eastern Madagascar, to enlighten its conservation needs. Our objectives were to:

- 1- Determine habitat use in terms of home range, sleeping site and vegetation
- 2- Establish the social organisation of the study animals
- 3- Uncover the seasonal activity cycle of the species and confirm whether or not the species hibernates.

1.3.2 Thesis structure

In the next section on materials and methods, we first describe the study site and the materials and methods used to capture, handle, measure and radio-track study animals. We also present how habitat and climate data were collected. We explain the materials and methods used for data analysis and in particular how we determined home range size, habitat use, social organisation, and overall and seasonal activity. We then present our results in the form of six thematic chapters dealing with the general description and morphology of the study animals, home ranges, sleeping sites, habitat use, social organisation and activity and seasonality.

In Chapter One, we present the results of our capture efforts and morphological measurements. We attempt to test two hypotheses suggested by previous research that: 1) there is no sexual dimorphism in the hairy-eared dwarf lemur; and 2) there are morphological differences between the northern and southern populations.

In Chapter Two, we present results from home range analysis and compare these with previous studies on cheirogaleids. We compare expected home range sizes for *A. trichotis* inferred from previous research with the results of our radio-tracking study and present data on home range use. We discuss the potential effects of body weight and size; diet; sex and social organisation; and weather variables, habitat characteristics and food availability, on home range size in the hairy-eared dwarf lemur.

In Chapter Three, we describe sleeping site characteristics and use. We attempt to identify the functions of these structures and the potential advantaged their use gives the species.

In Chapter Four, we combine results on microhabitat use based on direct observations of radio-collared focal individuals with data on habitat and microhabitat characteristics of the study site. We compare the used and available habitat to determine the needs of the species.

In Chapter Five, we use information on home range overlap, sleeping associations and nocturnal social encounters to assess the social and spacing system of the study animals. We discuss the potential social organisation of the species.

In Chapter Six, we first present results on the climate of Andasibe during the study period. We then reveal the overall nocturnal activity (dispersal and reunion times, activity duration, and activity budget) and the monthly variations in nocturnal activity, home range size, body weight and reproductive cycle. In the discussion, we compare our results to those of other

Cheirogaleidae, suggest how the species responds to the colder drier season, and propose a timing for the main parts of the reproductive cycle.

MATERIALS AND METHODS

M.1 Study site

This study was conducted between January and December 2007 in the Analamazaotra Special Reserve of central eastern Madagascar (18° 56'S, 48°25'E; 810 ha), near Andasibe. The village of Andasibe lies between the capital Antananarivo and the East coast, about 30 km East of Moramanga (Fig. M.1)(Dolch, 2003). The Analamazaotra Special Reserve was created in 1970 and is a hot spot for tourists, who mainly come to see the largest of all lemurs: *Indri indri* (Dolch, 2003). Although originally covered with continuous forest, the region now only has fragments left (Dolch, 2003). The Analamazaotra Special Reserve is part of the Andasibe-Mantadia National Park which was created in 1989 and is under the management of the Association Nationale pour la Gestion des Aires Protégées (ANGAP)(Dolch, 2003).

The climate of the region is humid with an average annual rainfall of 1,700 mm concentrated over 210 days, an annual average temperature of 18°C and atmospheric humidity over 70% (ANGAP, 2002). The warm rainy season lasts from December to March. The cold dry season takes place between June and September. The study area is comprised of disturbed mid-altitude primary eastern rainforest at altitudes between 850 and 950 m.

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Fig. M.1: Map of the study site

The 810-ha Analamazoatra Special Reserve lies between the capital Antananarivo and the shores of the East coast, about 30 km East of Moramanga (marked A on the map of Madagascar – right map). It is part of the Andasibe-Mantadia National Park (see middle map of the Andasibe area – Analamazoatra Special Reserve is indicated by the arrow). The large forest block in the North contains Mantadia National Park. The forest block in the South is Maromiza forest. The small fragment West is the Analamazoatra Forestry Station. Protected areas are stripped in green. The left map shows the main road leading to Andasibe (full black line), the trail system of the study area (dotted lines) and the two main water bodies in the area (blue areas: the ‘lac vert’ at the top and the ‘lac rouge’ at the bottom).

M.2 Captures

The difficulty of capturing hairy-eared dwarf lemurs may be a key factor that has precluded their study. Capturing the first individual was very difficult and took about two and a half months. Between 24 January and 23 March 2007 my team and I walked along existing trails and through the forest in search of hairy-eared dwarf lemurs in areas where they had been located during the pilot study, including new sighting areas as the search progressed. Walks generally took place from sunset to at least 2230 and occasionally at different times of the night or all night. During this period, we sighted the species on 17 nights (out of 34 nights work, i.e. about every other night). We originally attempted to catch individuals by hand using strong flashlights to dazzle the animal as had successfully been done for *Microcebus* spp. However, hairy-eared dwarf lemurs were not dazzled by white light and did not freeze as mouse lemurs did, so this method was considered ineffective. On 12 and 13 February, we set up small Sherman and mesh live traps baited with banana in a 25 x 25 m area of the forest where hairy-eared dwarf lemurs had been sighted on several occasions. As this first attempt was unsuccessful and traps had to be set-up in the afternoon and removed at the end of each capture session following ANGAP regulations, we decided to try other capture techniques that were less time consuming and might give better results. After several unsuccessful attempts with self-made butterfly-type trapping nets, my guides designed bamboo noose-poles of varying lengths with nooses of thick fishing wire. Although we first had several promising but unsuccessful trials, we finally caught an adult male on 23 March 2007. The technique consisted of carefully trying to wrap the noose around the torso of the animal to hold it in place and very quickly afterwards grab the individual by hand. After having fitted this first individual with a transmitter fixed on a leather collar, the animal was followed for a few hours and then left to relax. When we returned the next morning in the hope to locate this individual's sleeping site, we found the radio-collar on the forest floor. A second capture attempt, using the same technique was successful again one week later, on 30 March. This second adult male was fitted with a cable-tie radio-collar and its sleeping site was successfully located the next day.

Once this first individual was captured and its sleeping hole located by radio-tracking, 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 (Fig. M.2). A thin-meshed plastic net was set up a few hours before sunset around the nesting tree and sown together to form a tube out of which the animals could not escape. A small opening, held closed with rope, enabled the hand capture of the animal. After setting up the net, my team and I waited quietly near the tree hole for the

animals to come out. As soon as an individual left its sleeping site, the entrance hole was held shut by one team member while the other used the small opening in the bottom of the net to catch the individual by hand.

Fig. M.2: Set-up for tree hole capture

A net is set-up and sown to form a tube in front of the tree hole (in the tree on the right hand side). A small opening at the bottom of the net is held shut by rope. As soon as an animal exits its sleeping site, the tree hole entrance is obstructed and the animal is caught by hand using the opening in the bottom of the net.



Between 15 and 24 May, we started the search for a second sleeping group. Hairy-eared dwarf lemurs were much more difficult to see in this period and we did not manage to catch any individual. A second attempt was made from 28 August to 6 September and concluded successfully with the capture of a juvenile individual on 6 September using the bamboo noose-pole technique. For ethical reasons, this individual was fitted with a radio-collar for only a few hours, until its sleeping site could be located. Its sleeping group was captured the next evening by using the sleeping hole net technique and the juvenile's radio-collar was removed.

We recaptured radio-collared individuals every two to three months to replace the collars with expired battery. This was done using the tree hole trapping technique. As some nests were high in trees (the highest tree hole where captures were made was over nine meters

above ground) my team and I had to invent new ways to reach the nest for each tree hole. We used self-constructed wood platforms, safety ropes and climbing harnesses (Fig. M.3).

Fig. M.3: Set-up to reach high tree holes for captures

Two examples of wooden platforms built to access high nests are shown: a nest over 4 m high on the right and a nest over 7 m high on the left. The trapping net gives a clue of the position of the tree hole.



M.3 Handling and morphological measurements

As soon as an individual was captured it was placed in a cotton holding bag and processed. This bag was used to weigh the animal with a spring balance (100 g or 300 g, Pesola AG). The weight of the bag was later subtracted from the measured value. Animals were held by hand during measurements. At first capture, we used 200 mm electronic digital callipers to take the following measurements: 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), tail width (tail diameter at one centimetre from base), hind foot length (from heel to longest toe excluding nail), ear length (from subaurale to supraurale), ear breadth (from preaurale to postaurale), testicle length (top to bottom of scrotal sac) and testicle breadth (from left to right of scrotal sac). Although animals were not anaesthetised, they tended to relax when held by the skin on the back of their neck (enabling accurate measurements on the head, tail, hands and feet); and were held by their hand and feet to measure body length. We also determined sex and noted signs of reproductive activity (i.e. swollen nipples or vulva, pregnant females). We cut fur on individuals' tails for visual recognition and took photographs of each individual's front, back and face. All physical measurements were conducted by K. Biebow.

We calculated mean body weights per individual based on all the captures excluding those for pregnant females. These calculations were the basis for the calculation of the means for all adults, all juveniles, all adult males and all adult females. We also calculated the mean testicle breadth and width based on all captures in males. All calculations and analyses were conducted by K. Biebow.

We radio-collared all individuals with weights over 65 g (TW-4 transmitter, 3.2 g, Biotrack Ltd., Fig. M.4). We fitted the first collared individual with a leather collar which only stayed on for a few hours. We subsequently fitted individuals with cable-tie collars which lasted throughout the study and were never lost. We recaptured radio-collared individuals every two to three months to replace the collars with expired battery. When individuals were recaptured, we only weighed them and checked their reproductive state (i.e. swollen nipples or vulva and palpation in females; measurement of testicle length and breadth in males). Measurements never took more than 30 minutes. Animals were released at the place where they were captured. We removed all the radio-collars at the end of the study, in December 2007. By then most animals had gained weight compared to their first capture, suggesting that wearing radio-collars did not have a significant negative effect on their health.

Fig. M.4: TW-4 transmitters and collars used for radio-tracking

The left picture shows the TW-4 transmitter with the cable-tie collar and rubber coating. The right picture shows a hairy-eared dwarf lemur with radio-collar. Radio-collar weight (3.2 g) was at the recommended 5% of animal body mass. The lightest radio-collared individual weighed 67 g so the 3.2 g radio-collar was 4.8% of its body mass.



M.4 Radio-tracking

We used a TR-4 receiver and RA-14 antenna (Telonics Inc.) to follow focal individuals at night and locate all individuals in their sleeping site during the day. My team and I conducted partial nocturnal follows five nights per week, adhering to the following schedule: on three nights, we located the first focal animal in its tree hole and followed it from the time it left its nest for about two hours, then we located a second focal individual and also followed it for about two hours; on two nights, we entered the forest at around 9 pm and sought a first individual which, once located, was followed for about three hours, then we located a second individual and followed it until it entered its tree hole at dawn. My assistant, Miss Tiana Andrianoeliana, and I were responsible for behavioural data collection. For the first weeks of the study, we scored behaviour together to guarantee inter-observer reliability.

Although we originally tried full-night follows, these were very difficult to maintain in the long-term due to difficult terrain and weather conditions. The schedule reported here, although resulting in more observations in the first part of the night, worked best to maintain observers' concentration and stamina. As animals were observed at all times of the night, we believe it still allows an accurate picture of the species' behaviour and activity to be drawn. Although focal individual follows produce more auto-correlated data than sequential localisations, we preferred this method because individuals were often difficult to locate at first and focal follows permitted more detailed behavioural observations. It also allowed us to follow animals on unusual excursions which would otherwise not have been detected.

During nocturnal follows, we recorded the focal animal's position every ten minutes using a handheld GPS Map60 CSX (Garmin Ltd.). We took GPS waypoints under the tree where the animal had been seen or where it was believed to be based on close range triangulation. We monitored behaviour every five minutes 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 over ten meters above ground. Whenever possible, we recorded the focal animal's behaviour, posture, height, type and size of support and genus of used tree. When individuals met conspecifics at night, we tried to determine the identity of the focal animal's partner by scanning all the known radio-collar frequencies. When its identity could be determined, we logged the GPS location of the interaction for both animals. When the interacting animal was a captured juvenile, it could be identified from its tail fur-cuts.

Radio-collared individuals were located in their sleeping site on average five days per week (at least twice and up to every day) (Müller, 1998; Radespiel, 1998; Radespiel et al., 2003a; Schmelting, 2000; Weidt et al., 2004). Each time a new sleeping site was discovered, we recorded its GPS location, entrance hole height from ground level to the base of the cavity, genus and diameter at breast height (DBH) of the tree, whether the tree was alive or dead, and the height and width of the entrance hole at its largest point (Lahann, 2007a; Lahann, 2008; Radespiel, 1998; Radespiel et al., 2003a; Rakotoarison et al., 1997; Schmelting, 2000). 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 (Müller and Thalmann, 2000; Radespiel, 1998).

M.5 Habitat characteristics

M.5.1 Vegetation plots for tree density

We set up six one-hectare vegetation plots within the study individuals' home ranges to determine tree density. Each plot was divided using 25 m interval lines. We used the point quarter sampling method following Ganzhorn (2003). Sampling points were located at 25 m interval, at each intersection of the grid lines. At each sampling point, a long stick was set-up at random in the ground to locate the central point. We used a compass to determine the North-South direction and to subsequently divide the sampling point in four quarters. In each quarter we measured the distance from the central point to the centre of the nearest tree with a diameter over ten centimetres. We measured the tree diameter at breast height (DBH) and recorded the tree's genus.

M.5.2 Microhabitat plots

We set up five random 25 m² microhabitat plots per individual home range, giving a total of 30 plots. In each plot we measured all trees with a DBH over one centimetre and recorded their height class (in five-meter increments). We used the threshold of one centimetre because hairy-eared dwarf lemurs are known to use the small branch niche (Garbutt, 2001; Goodman and Raselimanan, 2002; Rakotoarison et al., 1997). We counted the number of lianas, recorded their thickness class relative to the size of the hairy-eared dwarf lemurs (small: hands and feet fit around the support, medium: support less wide than the width of the animal, large: support wider than the width of the animal), their height class, and their orientation. We counted the number of tangles, arborescent ferns and *Pandanus* (endemic spiky shrub or tree from the

family Pandanaceae) and recorded their height class. We also checked for usable tree holes. We used five photographs of the canopy per plot (one central to the plots and one in each corner) to determine the percentage canopy cover (see analysis below).

M.5.3 Other habitat characteristics

We recorded gum producing trees and their genus whenever one was encountered in the habitat. We also noted signs of degradation in the reserve (clearings, large paths, invasive plants) based on presence/absence.

M.6 Climate

General weather data were collected to determine general seasonal changes in climate in the region. A minimum/maximum thermometer was set-up in the shade at about two meters height against the wall outside our house in the village (Mayes, 2003). A 50 mm rain gauge was also set up in the garden, on a pole, at about one meter height, away from vegetation or buildings that could interfere but shaded from strong wind (Mayes, 2003). We noted the minimum and maximum temperature at least once a week. The amount of rainfall was recorded at least once a week, soon after a period of rainfall to limit evaporation, or more often during periods of heavy rainfall where the rain gauge was emptied regularly to avoid overflow. This provided the minimum and maximum temperatures and the total rainfall per month.

M.7 Data analysis

M.7.1 Home range

M.7.1.1 On choosing the analysis method

All the previous studies on cheirogaleids have used the Minimum Convex Polygon (MCP - (Mohr, 1947)) method to estimate home range size (Charles-Dominique and Petter, 1980; Dammhahn and Kappeler, 2005; Eberle and Kappeler, 2004; Fietz, 1999; Fietz, 2003a; Génin, 2008; Kappeler, 1997a; Kappeler, 1997b; Lahann, 2007a; Lahann, 2008; Müller, 1998; Müller, 1999b; Radespiel, 2000; Schmelting, 2000; Schmelting et al., 2000; Schülke and Kappeler, 2003; Schwab, 2000; Weidt et al., 2004). This is also the case for many other nocturnal prosimian primates (Pimley et al., 2005; Sterling et al., 2000). This choice is most likely due to the simplicity of the method, its robustness with auto-correlated data and its alleged comparability (Kernohan et al., 2001; Sterling et al., 2000; Swihart and Slade, 1997). However,

this method has been highly criticised because of its sensitivity to sample size and outliers and its tendency to overestimate home range size (Börger et al., 2006; Boulanger and White, 1990; Burgman and Fox, 2003; Girard et al., 2002; Hansteen et al., 1997; Kernohan et al., 2001; Pimley et al., 2005; Swihart and Slade, 1997). Its comparability has also been questioned because of these flaws (Hansteen et al., 1997; Kernohan et al., 2001; Seaman et al., 1999).

An alternative method that has often been proposed as the preferred home range estimate is the kernel analysis in which the density of data points is used to create a probability function of the animal's location (the utilization distribution) (Worton, 1987; Worton, 1989). This method has been recommended because of its higher precision, its robustness to auto-correlated data, outliers and changes in spatial resolution and because it enables detailed description of space use and can be used even with small sample sizes (Börger et al., 2006; Garton et al., 2001; Hansteen et al., 1997; Kernohan et al., 2001; Pimley et al., 2005; Swihart and Slade, 1997; Worton, 1987; Worton, 1995). There are mixed reports about its sensitivity to sample size however: some studies suggest the method still performs well with small samples (e.g. 10 fixes per month (Börger et al., 2006) or less than 50 locations (Kernohan et al., 2001)) but others warn for home range overestimates at small sample sizes (typically < 100) (Garton et al., 2001; Girard et al., 2002; Seaman et al., 1999).

When applying kernel analysis, the choice of the type of kernel (fixed or adaptive) and of the smoothing parameter are very important (Börger et al., 2006; Gitzen and Millspaugh, 2003; Hemson et al., 2005; Seaman et al., 1999; Seaman and Powell, 1996; Swihart and Slade, 1997; Worton, 1989; Worton, 1995). In the fixed kernel method, the kernel probability function estimates the density of data points and uses a fixed value for the smoothing parameter (Worton, 1989). The smoothing parameter controls the detail of the data (Worton, 1989). A small smoothing parameter will give fine detail while a large value will smoothen the peaks of the distribution most (Worton, 1989). In the adaptive kernel method, the smoothing parameter varies to give more detail to areas of low density and smoothen areas of high concentration of data points (Worton, 1989). Worton (1989) promotes the use of the adaptive kernel while Seaman et al. (1999) and Seaman and Powell (1996) encourage the use of the fixed kernel. Most researchers advocate the use of the least-square cross-validation method for selecting the smoothing parameter (Gitzen and Millspaugh, 2003; Seaman et al., 1999; Seaman and Powell, 1996; Worton, 1989).

M.7.1.2 On the use of auto-correlated data

Since Swihart and Slade (1985a, 1985b) showed that auto-correlated data tend to underestimate home range size and proposed a statistical test for independence and showed how to calculate the time to independence, many researchers have tried without success to subsample their data to reach statistical independence (De Solla et al., 1999; McNay et al., 1994; Rooney et al., 1998). Most researcher now agree that biological independence is more important than statistical independence (De Solla et al., 1999; Lair, 1987; McNay et al., 1994; Rooney et al., 1998). Locations are biologically independent when the sampling interval is long enough for the animal to move from any point of its home range to any other point (Lair, 1987; McNay et al., 1994; Rooney et al., 1998; Swihart and Slade, 1997). Indeed, statistically auto-correlated data are inherent to the home range concept because if animals use a home range area, they will return to the same area repeatedly and no point will ever be completely independent of another (De Solla et al., 1999; Otis and White, 1999; Rooney et al., 1998). Additionally, a lot of useful biologically relevant information is lost when sub-sampling to attain statistical independence and home ranges tend to be underestimated (De Solla et al., 1999; Hansteen et al., 1997; McNay et al., 1994; Rooney et al., 1998). Swihart and Slade (1997) also showed that although the bias of home range estimators increase with increasing autocorrelation and lower sample sizes, kernel and MCP methods were robust enough to cope with auto-correlated data and that a minor violation of independence could easily be resolved by slightly increasing the study duration and hence the sample size.

M.7.1.3 Home range analysis

K. Biebow conducted analyses of home range size, location, and overlap using Ranges 7 (Anatrack Ltd.)(Gallerani Lawson and Rodgers, 1997; Génin, 2008; Larson, 2001; Radespiel, 2000; Schmelting, 2000; Schmelting et al., 2000; Weidt et al., 2004). For comparability to previous studies we estimated the overall home range per individual using 100% Minimum Convex Polygons (MCP) with harmonic means centres using all the location points (i.e. daytime nest locations and nocturnal follow locations) (Dammhahn and Kappeler, 2005; De Solla et al., 1999; Génin, 2008; Kernohan et al., 2001; Lair, 1987; Mohr, 1947; Radespiel, 2000; Rooney et al., 1998; Weidt et al., 2004). We 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 animals were inactive in their nests) (Garton et al., 2001; Gitzen and Millsbaugh, 2003; Horne and Garton, 2006; Kernohan et al., 2001; Pimley et al., 2005; Seaman et al., 1999; Seaman and Powell, 1996; Sterling et al., 2000; Swihart and Slade, 1997; Worton, 1987; Worton, 1989; Worton, 1995). The ten-minute interval of

localisations was large enough for biological independence because animals can move fast and reach any point within their home range within this time frame (see above). We used Pearson correlations to disprove any association between the number of location points and the estimated home range value. We calculated the percentage home range overlap between individuals based on the MCP and kernel estimated home ranges.

M.7.2 Home range use

We used visual inspection of home range maps to determine the position of nests and particular behaviours (feeding, moving, resting, grooming, calling and social interactions). These were not mutually exclusive and if several behaviours were observed in the same place, this location was recorded for all behaviours observed. We counted the number of feeding and social interaction locations in the overlap areas and compared them to those outside overlap areas. We compared the number of call locations in overlap areas to those outside overlap areas; near home range edges (< 10 m) or more than ten meters from home range edges; and near tree holes (< 10 m) or away from tree holes (> 10 m). We counted the number of nests near home range edges (< 10 m) and more than ten meters away from home range edges.

M.7.3 Sleeping site use

We calculated the proportion of use for each sleeping site as the number of days of occupation (i.e. the number of location days where the sleeping site was occupied by at least one individual divided by the total number of location days on which at least one individual was located in a sleeping site)(Radespiel, 1998; Radespiel et al., 2003a). We determined the proportion of sleeping site 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 (Radespiel, 1998; Radespiel et al., 2003a). We established the sleeping site 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; Radespiel et al., 2003a). This calculation was completed per individual and for all individuals. We recorded the response of disturbances at the nest. After a group of individuals had been captured, we noted how long it took for at least one individual to return to that tree hole and where animals slept if they did not return to the disturbed nest. We calculated the mean number of days before an individual returned to the captured tree hole and checked the differences in physical characteristics between the disturbed cavity and the tree hole to which animals moved.

M.7.4 Behaviour and microhabitat use

We calculated the proportion of five-minute instantaneous scan samples for which each behaviour was used to determine the activity budget. We calculated the proportion of five-minute instantaneous scan samples for which each type of microhabitat (tree, liana, tangle, etc.) and size (small, medium or large) and orientation (horizontal, vertical or oblique) of support was used. Support size was determined relative to the size of the animal (small: hands and feet fit around the support, medium: support less wide than the width of the animal, large: support wider than the width of the animal) (Nekaris, 2001). We conducted the same calculation to determine the genus and family of the used trees. We calculated the average height at which individuals were seen and the proportion of five-minute instantaneous scan samples at which animals were at different height intervals (in 5 m increments). We calculated diet composition based on the number of feeding events for each type of food item. We used a Mann-Whitney U-test to compare heights at which individuals fed on animal prey or gum (SPSS 16.0., $\alpha = 0.05$).

M.7.5 Habitat characteristics

M.7.5.1 Tree density and composition from point-quarter sampling plots

Tree density was calculated using the formula from Ganzhorn (2003): $D = 10,000/d^2$; in which D is the tree density, in number of trees per hectare, and d is the mean distance from the central point to the nearest tree in meters. To determine the tree diameter composition, we counted the number of trees in each diameter class (in five centimetre increments) and plotted the results on a histogram (White and Edwards, 2000). To determine the tree genus and family composition we calculated the basal area of each tree following the formula from White and Edwards (2000): $BA = (d/2)^2 * \pi$; in which BA is the basal area in square centimetres and d is the tree diameter at breast height in centimetres. The sums of the basal areas per genus or family were used to determine the relative importance of each genus and family.

M.7.5.2 Microhabitat composition

Plant densities per hectare were calculated by dividing the total number of plants in each group by the total area surveyed, i.e. 30 times 25 m² = 0.075 ha. We used the same calculation for the different types of lianas (small, medium or large). Tree diameter composition was determined as for the tree density plots (see previous paragraph). We used the same method to determine tree, liana, tangle, arborescent fern and *Pandanus* height composition. We determined canopy cover by using Photoshop to calculate the proportion visible sky on each of the five pictures per plot. Using the magic wand tool, we selected all the areas of visible sky.

Under the 'Image' tab we selected 'histogram' to get the total number of pixels in the picture and the number of pixels selected (visible sky). Canopy cover for each picture was then one minus the proportion visible sky. We calculated the mean canopy cover per plot using the result from all five pictures and the mean for all plots based on canopy cover per plot.

M.7.6 Comparisons between used and available trees

Based on the tree genus and family composition, determined from point-quarter sampling (see above), we calculated the expected usage frequency for each genus used by the hairy-eared dwarf lemurs during the night (based on microhabitat use, see above), for nesting, or for feeding, using the formula: $E = p \times n$, where E = expected usage frequency, p = proportion available in the habitat, and n = total number of observations (i.e. total number of trees used during the night, for nesting or for feeding) (Neu et al., 1974). We then calculated a χ^2 -test using the formula:

$$\chi^2 = \sum \frac{(O - E)^2}{E}$$

where χ^2 = calculated value of the χ^2 -test, O = observed usage frequency, and E = expected usage frequency (Fowler et al., 1998). The calculated χ^2 value was compared to the critical value from the χ^2 -distribution at the 0.05 and 0.01 levels of significance (Fowler et al., 1998). If the calculated value was higher than the critical value, we rejected the null hypothesis that the observed and expected frequencies agree (Fowler et al., 1998). If the difference was significant ($\alpha = 0.05$), we used the differences between the observed and expected usage frequencies to detect which genera were used more-, less-, or as expected by their availability in the habitat. We also calculated the proportion of available trees with diameters at breast height within the range of tree sizes used as nesting trees, based on data from the point-quarter sampling plots for the proportion of tree with a DBH over 10 cm that could be used as sleeping trees and on data from the microhabitat plots to determine the proportion of trees with a DBH over 1 cm that could be used as sleeping trees.

M.7.7 Sleeping associations

We counted the number of times pairs of individuals slept together and calculated Coles' index of association (Cole, 1949; Nekaris, 2006; Pimley et al., 2005). 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.

M.7.8 Activity and seasonality

We calculated the overall activity budget as the proportion of five-minute instantaneous scan samples for each type of behaviour. We determined the range, mean and median dispersal and reunion times (i.e. time after sunset at which animals left their sleeping site and time before sunrise at which they entered it). We calculated the total activity time as the difference between the mean and median dispersal and reunion times (in local time). These calculations were conducted for the whole study period and per month and included all the followed individuals. To detect monthly variations, we plotted the minimum, maximum and median dispersal, reunion and nocturnal activity times. If animals had not left their tree hole four hours after sunset, they were assumed to be in torpor. To detect torpor phases, we noted when individuals returned to their sleeping site during the night as well as the length of time during which they stayed in their tree hole. We most often waited for up to 30 minutes to see if the animal would leave its nest again before searching for another focal individual to follow. In some cases we remained with the inactive animal to determine the length of its stay in the tree hole. To determine monthly variations in torpor periods, we counted the number of times individuals returned to their sleeping site during the night, regardless of duration. We also looked the identity of inactive animals and the duration of their stay if it was known and descriptively compared these between months. We ran simple multivariate regression analyses to determine the effect of weather variables (monthly rainfall, mean monthly temperature), night length and moon phase on activity.

To determine monthly variations in home range size, we estimated monthly individual MCP and kernel home ranges following the same methods as for the overall home ranges (see above, Section 7.1). We plotted the individual MCP and kernel home ranges on a graph to describe monthly changes. We only used data from the four adult individuals that were followed for eight months. We also compared weights for these individuals per month. Finally, in addition to information on the female reproductive cycle collected during captures (i.e. lactation, pregnancy), we also calculated male testicular volume for each capture as the volume of an ellipsoid using the formula: $V = (\pi \times L \times W^2)/6$, where V = volume in mm^3 , L = testes length in mm, and W = testes width in mm (Dammhahn and Kappeler, 2005; Fietz, 1999).

Calculations, analyses, maps and graphs were conducted by K. Biebouw. We used Excel, SPSS 16.0 and ArcView GIS. The significance level was set at $\alpha = 0.05$.

CHAPTER 1:

GENERAL DESCRIPTION AND MORPHOLOGY

1.1 Introduction

The hairy-eared dwarf lemur was well described by Meier and Albignac (1991) who also published the first photographs of a live specimen (Fig. 1.1). The hairy-eared dwarf lemur is brownish-grey on the back and whitish-grey on the ventrum. The dense fur is dichromatic with a dark hair base and lighter ends. There is a darker median line on the back. Here and there, longer sensory hairs protrude from the basal fur coat. The tail is brown, with darker longer hairs towards the tip. The forearms and legs are greyer than the back. Hands and feet are pink and covered in whitish hairs. Nails are keeled. The snout is long and pointy. There is a lighter median line from the tip of the rostrum to between the eyes and thin dark rings surround the eyes. The tip of the nose and lips are pink. Ears are very small and hidden in conspicuous long brown ear tufts that give the species its name.

Fig. 1.1: First published photographs of *A. trichotis* by B. Meier (Meier and Albignac, 1989; Meier and Albignac, 1991)



In this chapter, we present the results of our capture efforts and morphological measurements. We attempt to find out whether there are sexual and/or geographical morphological differences.

Morphological measurements of live animals from previous studies showed no obvious sexual dimorphism (Table 1.1). Adult individuals ($n = 6$) weighed on average 85 g and were 30 cm long. Head and body length was around 14 cm. The tail was longer than the body (16 cm). The small ears were wider than long (about 1.9 cm wide and 1.7 cm long).

Table 1.1: Morphological measurements from live *A. trichotis* captured in previous studies and reported in the literature

We calculated the mean morphological measurements per age-class (sub-adults or adults), per sex (adult males or females) and per geographical region (northern and southern adults) based on measurements reported in the literature. Data from studies conducted in the northern part of the species' range (Mananara, Marojejy and Zahamana) are from Meier and Albignac (1991) and Goodman and Raselimanana (2002); data from studies conducted at the southern end (Vohidrazana near Andasibe) are from Rakotoarison et al. (1997); see Fig. 2 in the General Introduction for a map of these locations.

	Means					
	Sub-adults (n = 3)	Adults (n = 6)	Adult males (n = 4)	Adult females (n = 2)	Adults north (n = 5)	Adult south (n = 1)
Body weight (g)	46	85	85	85	88	69
Head length (mm)	35	38	38	38		38
Head width (mm)	23	26	26	26		26
Body length (mm)	68	120	120	120		120
Tail length (mm)	123	161	163	158	165	140
Head/body length (mm)	115	139	140	138	136	158
Total length (mm)	238	300	303	295	301	298
Ear length (mm)	16	17	17		17	18
Ear width (mm)	13	19	19			19
Ear tuft length (mm)		10	9	11	10	
Ear tuft width (mm)	13	16	17	15	16	
Hindfoot length (mm)	30	32	32		38	26
Hindleg:						
Tarsus (mm)	30	32	33	31	32	
Tibia (mm)	40	44	44	45	44	
Femur (mm)	25	36	37	36	36	
Third digit including nail (mm)	11	8	8	8	8	
Claw of second digit (mm)	4	4	4	4	4	
Foreleg:						
Carpus (mm)	19	22	22	21	22	
Ulna (mm)	21	29	31	26	29	
Humerus (mm)	25	29	30	29	29	
Third digit including nail (mm)	10	11	9	12	11	
Testes width (mm)			10			
Testes length (mm)			10			

Rakotoarison et al. (1997) suggested the southern population could be larger with shorter tails. Mean weight for animals captured in the northern part of the species' range (i.e. Mananara region and Marojejy National Park – n = 5) was 88 g (Table 1.1). Animals had a mean head and body length of around 14 cm and a 17 cm tail. In comparison, the adult male captured in Vohidrazana (southern part of the species range) was lighter (69 g on average), larger (about 16 cm head and body length), and had a shorter tail (14 cm).

1.2 Results

1.2.1 General description

The overall appearance of individuals closely matched the description by Meier and Albignac (1991) (Fig. 1.2). The back was brownish-grey with a darker median line in some individuals. The underparts were whitish-grey. The white colour spread up on the flanks and under the chin. Forearms, legs and tail were darker than the rest of the body. The hairs on the tail became darker towards the tip and were bushier towards the end in some individuals. The face was a little more reddish than the dorsum. A white line could be seen from the tip of the nose to between the eyes. The snout was short and pointy with a round pink nose. The rosy tinge extended around the nose and lips. The large dark eyes were surrounded by a thin dark brown circle. The ears were concealed in long brown hairs. The hands and feet were pink with sparse white fur on the back and obvious pads on the inside (Fig. 1.2 – Foot). The tips of the fingers and toes were flattened and widened, resembling suck pads. The nails were rounded and short but a triangular keel was present (Fig. 1.2 - Hand). There was a long grooming claw on the first digit of the foot. Juvenile animals were difficult to sex. In adults, males had obvious testicles while females did not. During lactation, the nipples were swollen and could easily be used to sex the animal but these regressed afterwards. Juveniles could be recognised by their smaller size.

Fig. 1.2: Overall appearance of the hairy-eared dwarf lemurs captured during this study

Female AF1 with radio-collar:



Female AF2 moving:



Male AM1:



Hand:



Foot:



1.2.2 Morphology

In total my team and I captured 11 individuals: three males, four females and four juveniles (Table 1.2). Adult individuals weighed between 68 and 84 g (mean 77 ± 6 g) and measured 26 to 28 cm (mean 270 ± 7 mm). Their head and body was 13 to 14 cm long and their tail was generally longer- than or as long as the body (12 to 15 cm). Juveniles weighed about 60% of the adults (mean 47 ± 3 g) and were slightly smaller (mean total length: 236 ± 4 mm). Juveniles had a head and body length around 12 cm with a tail generally longer than the body of 11 or 12 cm. Tail diameter, hind foot length and ear height and breadth were similar in adults and juveniles. Tail diameter varied between 4 and 5 mm for adults and between 3 and 5 mm for juveniles. Hind feet of adults were 29 to 35 mm and 28 to 32 mm in juveniles. Ears were generally wider than high. Ear height ranged from 10 to 15 mm in adults and from 10 to 16 mm in juveniles. Ear breadth was between 7 and 14 mm in adults and between 11 and 13 mm in juveniles.

Table 1.2: Morphological measurements from individuals captured during this study

Table 1.2.a: Per individual

In total my team and I captured 11 individuals (four adult females, three adult males and four juveniles). Sex (F = female, M = male, ? = unknown) was determined based on the presence or absence of testicles and/or nipples. The assumed sex of juveniles causing their ID name (either AF for females or AM for males) was later removed because of their immaturity and difficulty in sexing them. Juveniles were distinguished from adults by their smaller size and weight. See Materials and methods for details of how measurement were taken. Weight, testicle length and breadth were measured each time an individual was captured (number of captures in parentheses). Total length = head and body length + tail length.

Table 1.2.b: Means and standard deviations

We calculated means and standard deviations per age-class (adults and juveniles) and per sex (adult males and adult females). The number of individuals used for each mean calculation is reported in parenthesis. To calculate mean weight we used the mean values per individual reported in Table 1.1.a. Note the size and weight differences between adults and juveniles and the lack of sexual dimorphism.

Table 1.2: Morphological measurements from individuals captured during this study

Table 1.1.a: Per individual

ID	sex	age class	weight (g)	head length (mm)	body length (mm)	head and body length (mm)	tail length (mm)	total length (mm)	tail diameter (mm)	hind foot length (mm)	ear height (mm)	ear breadth (mm)	testicle length (mm)	testicle breadth (mm)
AF 1	F	adult	84 (n = 3)	39	94	133	135	268	4	29	10	11		
AF 2	F	adult	77 (n = 3)	36	98	134	134	268	4	31	11	12		
AF 3	?	juvenile	49 (n = 2)	37	82	119	120	239	5	32	11	12		
AF 4	F	adult	68 (n = 2)	40	95	135	123	257	5	30	15	11		
AF 5	F	adult	69 (n = 2)	39	93	132	140	272	5	34	12	14		
AM 1	M	adult	80	39	95	134	139	273	4	32	11	7	19	13
AM 2	M	adult	77 (n = 6)	39	93	133	147	279	4	35	11	11	21 (n = 4)	14 (n = 4)
AM 3	?	juvenile	45 (n = 3)	34	83	117	118	235	3	28	10	12		
AM 4	?	juvenile	49 (n = 2)	35	84	119	111	230	3	31	10	13		
AM 5	M	adult	84 (n = 4)	39	102	141	130	271	4	32	12	13	23 (n = 4)	15 (n = 4)
AM 6	?	juvenile	44	37	80	117	121	238	4	31	16	11		

Table 1.1.b: Means and standard deviations

	weight (g)	head length (mm)	body length (mm)	head and body length (mm)	tail length (mm)	total length (mm)	tail diameter (mm)	hind foot length (mm)	ear height (mm)	ear breadth (mm)
Adults (n = 7)	77 ± 6	39 ± 1	96 ± 3	135 ± 3	135 ± 8	270 ± 7	4 ± 0.4	32 ± 2	11 ± 2	11 ± 2
Juveniles (n = 4)	47 ± 3	36 ± 1	82 ± 2	118 ± 1	118 ± 4	236 ± 4	4 ± 1	31 ± 2	12 ± 3	12 ± 1
Adult males (n = 3)	80 ± 4	39 ± 0.2	97 ± 4	136 ± 5	139 ± 8	274 ± 4	4 ± 0.2	33 ± 2	11 ± 0.5	10 ± 3
Adult females (n = 4)	75 ± 8	38 ± 1	95 ± 2	134 ± 1	133 ± 7	266 ± 6	5 ± 0.4	31 ± 2	12 ± 2	12 ± 1

There were no major differences in male and female morphology. Males were on average slightly heavier than females (means: 80 g vs. 75 g) but of similar size (mean total length: 27 cm vs. 26 cm). Tails were slightly longer in males (14 cm vs. 13 cm). There were larger inter-individual weight variations in females than in males (standard deviation of 8 g in females vs. 4 g in males).

1.3 Discussion

1.3.1 No sexual dimorphism in *A. trichotis*

Our results confirm that there is no obvious sexual dimorphism in the hairy-eared dwarf lemur. Morphological measurements from live animals previously captured by Meier and Albignac (1991), Rakotoarison et al. (1997) and Goodman and Raselimanana (2002) already suggested the lack of difference between males and females (Table 1.1). The slightly higher weight of males in our study is most likely related to inter-individual rather than sexual differences (Table 1.2). Indeed, females had broader weight ranges than males.

Sexual dimorphism was also lacking in *Microcebus berthae*, *M. rufus*, *M. ravelobensis*, *Cheirogaleus major* and *C. medius* (Atsalis, 1999b; Dammhahn and Kappeler, 2005; Fietz, 1999; Fietz, 2003a; Groves, 2000; Kappeler, 1991; Lahann, 2007a; Randrianambinina et al., 2003; Schwab, 2000). Results for *M. murinus* are controversial. Some authors found no differences between sexes (Fietz, 1998; Schmid and Kappeler, 1998) while others found that females were larger than males (Kappeler, 1991). When studied in captivity, there were sexual differences in monthly weights all year round for *M. murinus* and between January and September for *M. rufus* (Wrogemann et al., 2001). Females were heavier. Contradicting results were also found in *Mirza coquereli*. Kappeler (1991) originally found no sexual dimorphism but later discovered that males were heavier than females (Kappeler, 1997b). This difference could be due to the fact that the first study was based on captive animals while the second was conducted in the wild. Sexual dimorphism was also present in *Phaner pallescens* (Schülke et al., 2004). Females were slightly heavier than males. Several studies also found seasonal variations in sexual dimorphism (Dammhahn and Kappeler, 2005; Fietz, 1998; Fietz, 1999; Randrianambinina et al., 2003; Schmid, 1999; Schmid and Kappeler, 1998; Schwab, 2000).

1.3.2 Variations between the northern and southern populations

Our findings did not confirm the hypothesis of Rakotoarison et al. (1997) that individuals of the South are larger. The mean weight of the animals we captured in the South was 77 g, while animals caught in Mananara and Marojejy (northern Madagascar) had a mean weight of 88 g

(Table 1.1 and 1.2). Both populations had a similar head and body length around 14 cm. We can however confirm the suggestion by Rakotoarison et al. (1997) that animals from the South have shorter tails. On average, our animals had tails that were 14 cm long while animals from the North had tails that were 17 cm long on average. We therefore conclude that individuals of the southern population are lighter and smaller than those of the northern population. Although their head and body size is similar, the difference is mainly due to the longer tail of the northern population. Additional captures in the area of occurrence of the species should be conducted to confirm this trend or determine whether there is a gradual change in morphology between the northern and southern end of the species' range.

The male captured by Rakotoarison et al. (1997) in Vohidrazana, another forest of the Andasibe area, was much lighter (mean: 69 g) than the males we captured (mean: 80 g). This individual also had a longer head and body (16 cm vs. 14 cm mean for this study's males) but a similar tail length (14 cm). It is possible that this was a particularly large male (the largest male in our study had a head and body length of 14 cm). Rakotoarison et al. (1997) measured this male's weight in captivity over six months, from April to September. During this period, his weight ranged between 60 g (in August and September) and 85 g (in June). During our study, the lowest recorded male weight was 74 g (late March and early June) and the highest was 91 g (early December). Late August we recorded weights of 81 and 82 g. It seems remarkable that the male studied by Rakotoarison et al. (1997) had a lowest weight in August/September and a highest weight in June when the opposite happened in our study: male weights were lowest in June and higher in August. As this animal was studied in captivity, it is likely that its diet was highly altered compared to wild individuals, which would explain why it was heaviest in the middle of the drier colder season (June) while wild animals were at their lightest due to potentially depleting food resources. We suggest results from captive studies be used with caution when trying to draw conclusions on seasonality in wild animals, as many ecological factors most likely influence these variations and are hardly ever replicable in captivity.

Lahann et al. (2006) also found geographic variations in the morphology of *Microcebus murinus*. They compared mouse lemur populations of Mandena (an evergreen littoral forest on the South East coast of Madagascar), Kirindy (a dry deciduous forest in central western Madagascar) and Ampijoroa (a dry deciduous forest in North western Madagascar). These three sites vary in the amount of annual rainfall and mean annual temperatures. They found a gradient in weight from South to North (individuals from Mandena were heavier than those of Kirindy and animals from Kirindy were heavier than those from Ampijoroa). Individuals with the longest tails were found at the intermediate Kirindy site and animals from the far South

(Mandena) had longer tails than those from the North (Ampijoroa). This pattern does not fit our findings for *A. trichotis* where individuals from the South were lighter with shorter tails.

1.3.3 Concluding remarks

Its is clear that hairy-eared dwarf lemurs present no sexual dimorphism. The question of whether there are geographical variations within the population will need to be further investigated. Additional surveys in the species' area of occurrence should enable a more accurate picture of these variations and genetic analyses could also confirm whether sub-species occur.

CHAPTER 2:

HOME RANGE

2.1 Introduction

The notion of 'home range' was first mentioned by Seton (1909): "No wild animal roams at random over the country; each has a home-region, even if it has not an actual home" (p. 26). Burt (1943) first defined an animal's home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (p. 351). As most habitats are heterogeneous however, it is likely than the animal will not use all of its home range in equal proportions (Hayne, 1949).

Several factors can affect the size of an animal's home range. Home range size tends to increase with the species' size, weight and the amount of animal matter in its diet (Harestad and Bunnell, 1979; Haskell et al., 2002; Kelt and Van Vuren, 2001; Seton, 1909). It can also vary depending on the individual's sex and age and fluctuate according to the season, reproductive cycle, habitat characteristics, food availability, weather variables, population density and social organisation (Burt, 1943; Clutton-Brock and Harvey, 1979; Harestad and Bunnell, 1979; Haskell et al., 2002; Hemingway and Bynum, 2005; Matthiopoulos, 2003; Milton and May, 1976).

Most studies on the Cheirogaleidae have focused on species living in dry forests on the West coast of Madagascar; only few focused on species of the eastern rainforest. A quick literature search on the PrimateLit database (<http://primatelit.library.wisc.edu>), using species' Latin names as keywords, revealed 45 references for species of the East coast vs. 455 for species of the West coast (with *M. murinus* dominating with 334 references). The home range sizes of only nine out of 26 recognized cheirogaleid species (Mittermeier et al., 2006) have been reported (Table 2.1). Nothing is currently known about home range size or use in the hairy-eared dwarf lemur. This knowledge is important to determine the habitat needs of the species and enable comparisons of the socio-ecology of nocturnal primates in general (Sterling et al., 2000).

Table 2.1: Summary of previous studies on home range size in the Cheirogaleidae

For each species we report the source reference focussing on home range size, the location of the study and it's type of habitat, the type of data and analysis method used to estimate the home range (MCP: Minimum Convex Polygon), the home range size, whether the study found sexual differences in home range size ($\sigma^7 > \text{f}$: male home ranges larger than female's, $\text{f} > \sigma^7$: female home ranges larger than male's, =: no sexual difference in home range size, MS: mating season) and the number of animals used for home range analysis (Sample size). When information on head and body length or weight was not reported in the source reference, we used complementary references (in brackets next to the values in head and body length or weight columns).

Used references: 1: Dammhahn and Kappeler (2005); 2: Schwab (2000); 3: Génin (2008); 4: Eberle and Kappeler (2002); 5: Eberle and Kappeler (2004b); 6: Lahann (2008); 7: Radespiel (2000); 8: Schmelting (2000); 9: Schmelting et al. (2000); 10: Weidt et al. (2004); 11: Wright and Martin (1995); 12: Kappeler (1997b); 13: Kappeler (1997a); 14: Pagès (1978); 15: Pagès (1980); 16: Lahann (2007a); 17: Fietz (1999); 18: Fietz (2003a); 19: Müller (1998); 20: Müller (1999b); 21: Charles-Dominique and Petter (1980); 22: Schülke and Kappeler (2003); 23: Rasoloarison et al. (2000) ; 24 : Louis et al. (2006a); 25: Kappeler et al. (2005); 26: Groves (2000); 27: Mittermeier et al. (2006).

Table 2.1: Summary of previous studies on home range size in the Cheirogaleidae

Species	Source	Location and habitat	Head and body length (mm)	Weight (g)	Data	Analysis	Home range size (ha)	Sexual difference	Sample size
<i>Microcebus berthae</i> Madame Berthe's mouse lemur	1	Kirindy Central West dry deciduous	males: 119 females: 127	33	capture sites, sleeping sites, direct observations and radio-tracking	MCP	males: 4.9, females: 2.5	♂ > ♀	4 ♀ 5 ♂
	2	Kirindy Central West dry deciduous	139	31	radio-tracking of sleeping sites	MCP of sleeping sites	males: 4.3; 7.3 (mean: 5.8) females: 1.4; 1.0 (mean: 1.2)	♂ > ♀	2 ♀ 2 ♂
<i>Microcebus griseorufus</i> Reddish-grey mouse lemur	3	Berenty South spiny forest	123 (23)	wet year: males: 51 females: 59 dry year: males: 43 females: 56	radio-tracking	MCP	wet year: 0.9 ± 0.2 dry year: 0.4 ± 0.1	=	14 ♀ 14 ♂
	4	Kirindy Central West dry deciduous	129 (23)	60	-	-	males: 1.9, females: 1.3	♂ > ♀	27 ♀ 30 ♂
<i>Microcebus murinus</i> Grey mouse lemur	5	Kirindy Central West dry deciduous	129 (23)	60	capture locations, direct observations, location data	MCP	during mating season: males: 2.8, females: 0.7	♂ > ♀ during MS	14 ♀ 14 ♂
	6	Mandena Southeast littoral rainforest	129 (23)	81	radio-tracking, triangulation	MCP	males: 4.2, females: 0.6	♂ > ♀	4 ♀ 5 ♂
7	Ankarafantsika Northwest dry deciduous	129 (23)	62 (23)	radio-tracking, triangulation	MCP	outside first mating season: males: 2.8, females: 1.8 within first mating season: males: 4.8, females: 2.0	♂ > ♀		
8, 9	Ampijoroa Northwest dry deciduous	129 (23)	62 (23)	radio-tracking, triangulation	monthly MCP	Males only: monthly mean: 1.7	NA	11 ♂	

Species	Source	Location and habitat	Head and body length (mm)	Weight (g)	Data	Analysis	Home range size (ha)	Sexual difference	Sample size
<i>Microcebus ravelobensis</i>									
Golden-brown mouse lemur	10	Ankarafantsika Northwest dry deciduous	127 (23)	72 (23)	radio-tracking, triangulation	MCP	before mating season: males: 0.4; 0.6 (mean: 0.5) females: 0.6; 0.5 (mean: 0.5) during mating season: males: 0.5; 0.8 (mean: 0.7) females: 0.6; 0.5 (mean: 0.6)	=	6 ♀ 7 ♂
<i>Microcebus rufus</i>									
Brown mouse lemur	11	Ranomafana Central East rainforest	119 (24)	46	marked with bird-bands	-	1	=	30
<i>Mirza coquereli</i>									
Coquerel's giant mouse lemur	12	Kirindy Central West dry deciduous	307 (25)	males: 295-320 females: 285-300	capture sites, sleeping sites, radio-tracking and direct observations	MCP	during mating season: males: 17.0, females: 4.0 outside mating season: males: 4.0, females: 2.5	during MS: ♂ > ♀ outside MS: =	10 ♀ 8 ♂
	13	Kirindy Central West dry deciduous	307 (25)	males: 295-320 females: 285-300	capture sites, sleeping sites, radio-tracking and direct observations	MCP	males: 4.2 females: 3.9	♂ > ♀	69
	14	Central West dry deciduous	307 (25)	300	radio-tracking	-	central area: males: 2.0, females: 3.0 total home range: males: 8.0, females: 10.0 central area: males: 1.5, females: 2.5-3.0 peripheral area: males: 4.0, females: 4.5	♀ > ♂	2 ♀ 2 ♂
	15	Central West dry deciduous	307 (25)	300	radio-tracking	-		♀ > ♂	6
<i>Cheirogaleus major</i>									
Greater dwarf lemur	16	Mandena Southeast littoral rainforest	males: 282 females: 288	357	radio-tracking, triangulation	MCP	4.4	=	3 ♀ 4 ♂
	6	Mandena Southeast littoral rainforest	males: 282 females: 288	362	radio-tracking, triangulation	MCP	males: 4.4, females 4.0	=	3 ♀ 4 ♂

Species	Source	Location and habitat	Head and body length (mm)	Weight (g)	Data	Analysis	Home range size (ha)	Sexual difference	Sample size
	11	Ranomafana Central East rainforest	males: 282 females: 288 (16)	235-470	radio-tracking	-	4	=	12
<i>Cheirogaleus medius</i>									
Fat-tailed dwarf lemur	17	Kirindy Central West dry deciduous	184 (26)	males: 124 females: 136	radio-tracking	MCP	1.6 ± 0.5	=	14 ♀ 22 ♂
	18	Kirindy Central West dry deciduous	184 (26)	males: 124 females: 136	radio-tracking	MCP	1.6 ± 0.5 male floaters: up to 11.0	=	14 ♀ 22 ♂
	6	Mandena Southeast littoral rainforest	184 (26)	183	radio-tracking, triangulation	MCP	males: 1.6, females: 1.4	=	14 ♀ 13 ♂
	19, 20	Ampijoroa Northwest dry deciduous	184 (26)	males: 141-275 females: 141-214	capture sites, sleeping sites, tracking and direct observations	MCP	1.0-2.4 (mean: 1.6)	=	4 ♀ 4 ♂
<i>Phaner pallescens</i>									
Pale fork-marked lemur	21	Marosalaza Central West dry deciduous	230-290 (27)	300	recorded itineraries	MCP	4	=	5 ♀ 5 ♂
	22	Kirindy Central West dry deciduous	230-290 (27)	300	radio-tracking	MCP	males: 5.0 ± 1.9 females: 4.7 ± 1.5	=	8 ♀ 7 ♂

In this chapter, we compare expected home range size for *A. trichotis*, inferred from previous research in the Cheirogaleidae, with those resulting from our radio-tracking study and present data on home range use. We discuss the potential effect of body weight and size; diet; sex and social organisation; and weather variables, habitat characteristics and food availability on home range size in the hairy-eared dwarf lemur.

2.1.1 Inferences from previous studies

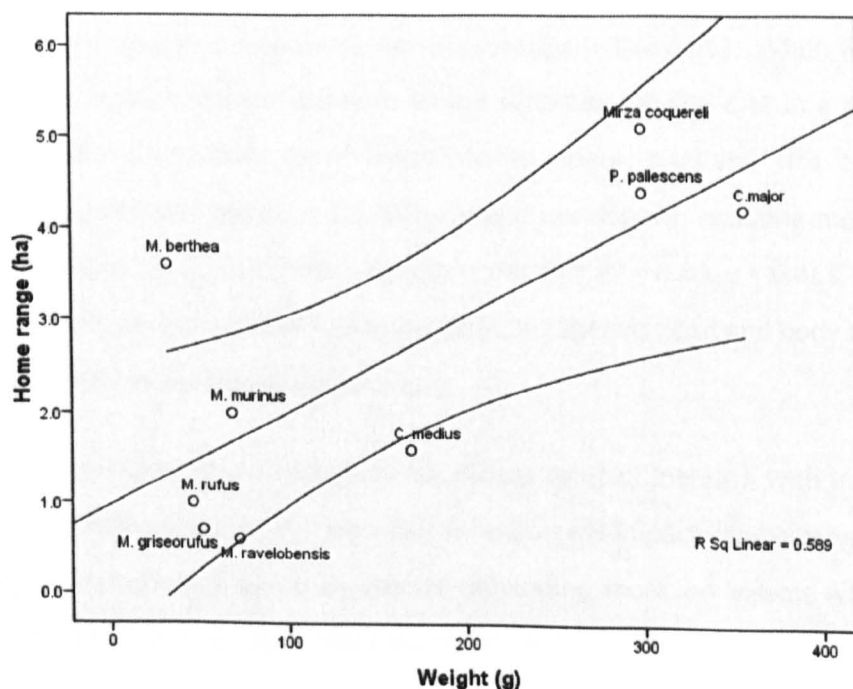
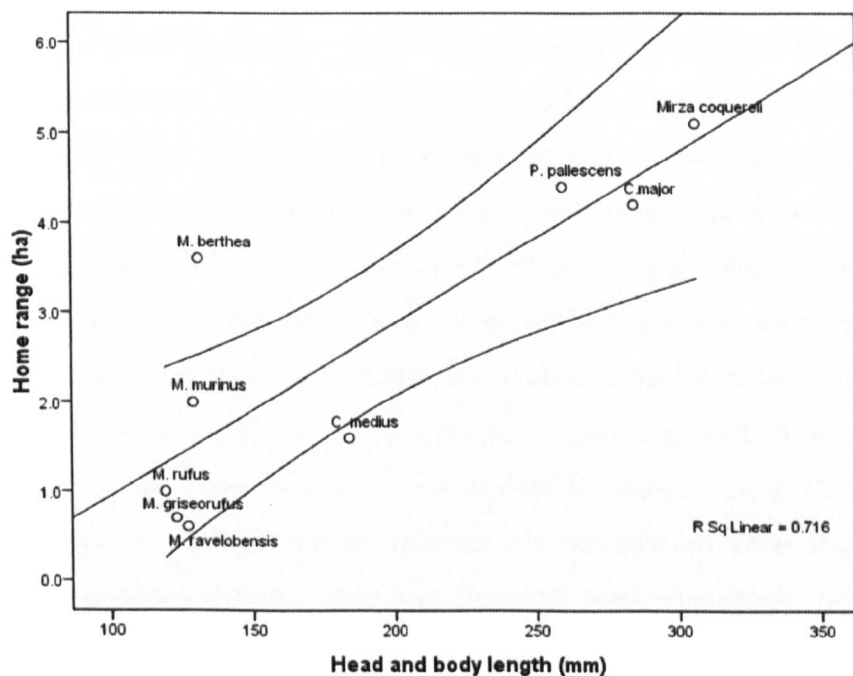
2.1.1.1 Based on size and diet

When comparing home ranges of sympatric *Microcebus murinus*, *Cheirogaleus major* and *C. medius*, Lahann (2008) found that the larger species had larger home ranges. To test the hypothesis that home range size is related to size and/or weight of the species, we conducted a Pearson correlation analysis using the available data (Table 2.1). We calculated average head and body lengths, weights and home range sizes per study and then per species ($n = 9$). We excluded values taken during the mating season as these can be exceptionally large, especially in males, due to an increase in home range related to male mating strategies. We also excluded male floaters (sexually mature surplus males that do not associate with a given female – (Fietz, 2003a)) for similar reasons.

Home range size was positively correlated with the species' size ($p < 0.01$, $r^2 = 0.72$) and weight ($r^2 = 0.59$, $p = 0.02$) (Fig. 2.1). A 95% mean confidence interval around the line of best fit revealed two outliers: *M. berthae* and *C. medius*. *Microcebus berthae* is the smallest of all mouse lemurs but had the largest home range of all *Microcebus* species. The fat-tailed dwarf lemur is larger than all *Microcebus* species but had a smaller home range than *M. murinus* and *M. berthae*.

Fig. 2.1: Correlation between home range size and species size (head and body length) or weight in the Cheirogaleidae

We calculated average head and body lengths, weights and home range sizes per study and then per species ($n = 9$), using data from previous studies and excluding values taken during the mating season and from floater males (see Table 2.1). Pearson correlation showed that home range size was positively correlated with the species' size ($p < 0.01$, $r^2 = 0.72$) and weight ($r^2 = 0.59$, $p = 0.02$). The figures show the resulting regression lines with a 95% confidence interval. Note that *M. berthae* and *C. medius* fall outside the confidence interval. Species above the regression line tend to rely more on insect food sources (prey or exudates) while species below the regression line tend to rely more on fruits.



The species above the regression line are omnivore/insectivore (*M. murinus* and *Mirza coquereli*), gummivore (*P. pallescens*), or feed mainly on insect secretions (*M. berthae*) (Charles-Dominique and Petter, 1980; Dammhahn, 2008; Dammhahn and Kappeler, 2008a; Dammhahn and Kappeler, 2008b; Hladik et al., 1980; Martin, 1973; Pagès, 1978). All these species rely on Homopteran larvae secretions, particularly during the winter or spring (Charles-Dominique and Petter, 1980; Corbin and Schmid, 1995; Dammhahn, 2008; Dammhahn and Kappeler, 2008a; Pagès, 1978; Radespiel et al., 2006). The species below the regression line eat mainly fruits, flowers and nectar (*C. medius* and *C. major*) or are frugivore-gummivore (*M. griseorufus*) or frugivore-insectivore (*M. rufus*) (Atsalis, 1999a; Fietz and Ganzhorn, 1999; Ganzhorn, 1988; Génin, 2008; Lahann, 2007b; Wright and Martin, 1995).

To further investigate the effect of size, weight, climate and diet on the size of the home range in the Cheirogaleidae, we conducted a multivariate regression analysis using the information listed in Table 2.1. Each study resulted in one or more cases depending on whether the study found significant differences in home range size between males and females or between wet and dry years (in the case of *M. griseorufus*). We excluded data from floater males and taken only during the mating season. As far as possible, we gathered data on weather (minimum and maximum temperature and annual rainfall) and diet (when available: percent animal matter, homopteran larvae secretions, gum and fruits/flowers or nectar) specific to the study site. The stepwise linear regression analysis using all the available information revealed the importance of size and percent homopteran larvae secretions in the diet for the determination of home range size (stepwise linear regression: resulting model included size and percent homopteran larvae secretions in the diet, $r^2 = 0.39$, $p = 0.014$, $y = 0.021 x + 0.023 z - 1.613$ where y = home range size in hectares, x = species head and body length in mm and z = percent homopteran larvae secretion in the diet.). When we combined the percent animal matter and homopteran larvae secretions in the diet in a new variable representing the percent matter from insect/animal origin, size and this new variable remained the only significant variables (stepwise linear regression: resulting model included size and percent matter from insect/animal origin in the diet, $r^2 = 0.40$, $p = 0.013$, $y = 0.022 x + 0.024 z - 2.029$ where y = home range size in hectares, x = species head and body length in mm and z = percent matter from insect/animal origin).

We therefore conclude that although home ranges tend to increase with increasing size and weight in the Cheirogaleidae, diet also has an important impact. Home ranges are larger than expected by morphology alone in species depending more on insects while they are smaller than expected in species depending mainly on fruit.

2.1.1.2 Based on sexual differences

Male home ranges were larger than those of females in *M. berthae* and *M. murinus* (Dammhahn and Kappeler, 2005; Eberle and Kappeler, 2002; Eberle and Kappeler, 2004; Lahann, 2008; Radespiel, 2000; Schwab, 2000). These two species live in multimale/multifemale individualized neighbourhoods and have a promiscuous mating system (Dammhahn and Kappeler, 2005; Eberle and Kappeler, 2002; Lahann, 2008; Radespiel, 2000; Schwab, 2000).

There are contradicting reports for *Mirza coquereli*: the first study of the species reported larger home ranges for females than for males but a more recent study found that home ranges were larger in males than in females during the mating season but did not differ outside of the reproductive period (Kappeler, 1997b; Pagès, 1978; Pagès, 1980). Coquerel's giant mouse lemurs are solitary and have a promiscuous mating system (Kappeler, 1997a; Kappeler, 1997b).

There were no sexual differences in home range size in *M. griseorufus*, *M. ravelobensis*, *M. rufus*, *C. major*, *C. medius* or *P. pallescens* (Charles-Dominique and Petter, 1980; Fietz, 1999; Fietz, 2003a; Génin, 2008; Lahann, 2007a; Lahann, 2008; Müller, 1998; Müller, 1999b; Schülke and Kappeler, 2003; Weidt et al., 2004; Wright and Martin, 1995). Most of these species (*Cheirogaleus* spp. and *P. pallescens*) live in monogamous family groups (Charles-Dominique and Petter, 1980; Fietz, 1999; Fietz, 2003a; Lahann, 2007a; Lahann, 2008; Müller, 1998; Müller, 1999b; Schülke and Kappeler, 2003) but some live in multimale/multifemale sleeping groups with promiscuous mating (*M. ravelobensis* - (Weidt et al., 2004)) or are female philopatric with low promiscuity (*M. griseorufus* - (Génin, 2008)).

Sexual differences in home range size therefore seem to be closely related to social organization. In species with a multimale/multifemale social system and a promiscuous mating system males tend to have larger home ranges than females, most likely as a mating strategy, to increase their access to females. However, there is increased scramble and/or sperm competition in these species (Dammhahn and Kappeler, 2005; Eberle and Kappeler, 2002; Eberle and Kappeler, 2004; Kappeler, 1997a; Kappeler, 1997b; Radespiel, 2000; Schwab, 2000). In monogamous species on the other hand, there is no sexual difference in home range size as the pair shares a home range. This social organisation does not prevent extra-pair copulations however (Fietz, 2003a; Schülke et al., 2004).

Resulting predictions:

- 1) Based on the hairy-eared dwarf lemur's mean head and body length (135 mm) and an estimated 50-75 % animal matter in its diet (Meier and Albignac, 1991), we expect home ranges of 2.1 ha to 2.7 ha (values based on the equation resulting from the multivariate stepwise linear regression: $y = 0.022 x + 0.024 z - 2.029$).**
- 2) 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 the case, we do not expect sexual differences in home range size.**

2.2 Results

2.2.1 Radio-collared individuals and follow time

In total my team and I radio-collared six adults (Table 2.2). We radio-tracked four adults (two males and two females) for eight months, from April to November 2007; and two adult females for three months, from September to November 2007 (Table 2.2). The average follow time per individual was around 2.5 hours and the mode was one hour (n = 252 follows).

Table 2.2: Radio-collared individuals and follow time

We followed six individuals in total: two males (AM) and two females (AF) for 8 months (April to November 2007) and two females for three months (September to November 2007). The discrepancy between the start of the study date and the beginning of the follows was due to the difficulty in capturing a first individual (see Materials and methods). The 'Total number of sleeping site locations' is the number of days in which an individual was located in its sleeping site. By contrast, the 'Total number of GPS waypoints (including nest locations)' also includes location points where the animal was in its sleeping site during the night and the 'Total number of GPS waypoints (excluding nest locations)' excludes all the sleeping site locations (during the day or at night) where the animal was inactive. The differences in data collection between individuals were due to difficult weather conditions on certain nights/days; problems with individual radio-collars 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).

4

Radio-tracked									
ID	From	To	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)		
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		

2.2.2 Individual home ranges

Mean individual home ranges were 15.4 ha for 100% MCP and 5.4 ha for 95% kernel (Table 2.3). There was no difference between sexes (Table 2.3). There was important individual variation however (Table 2.3, Fig. 2.2). The number of location points collected (Table 2.2) did not influence the home range estimates (Table 2.3): Pearson correlations: Total number of GPS waypoints (including nest locations) vs. 100% MCP home range estimate: $p = 0.28$ $n = 6$; Total number of GPS waypoints (excluding nest locations) vs. 95% kernel home range estimate: $p = 0.38$, $n = 6$.

Table 2.3: Individual home range sizes

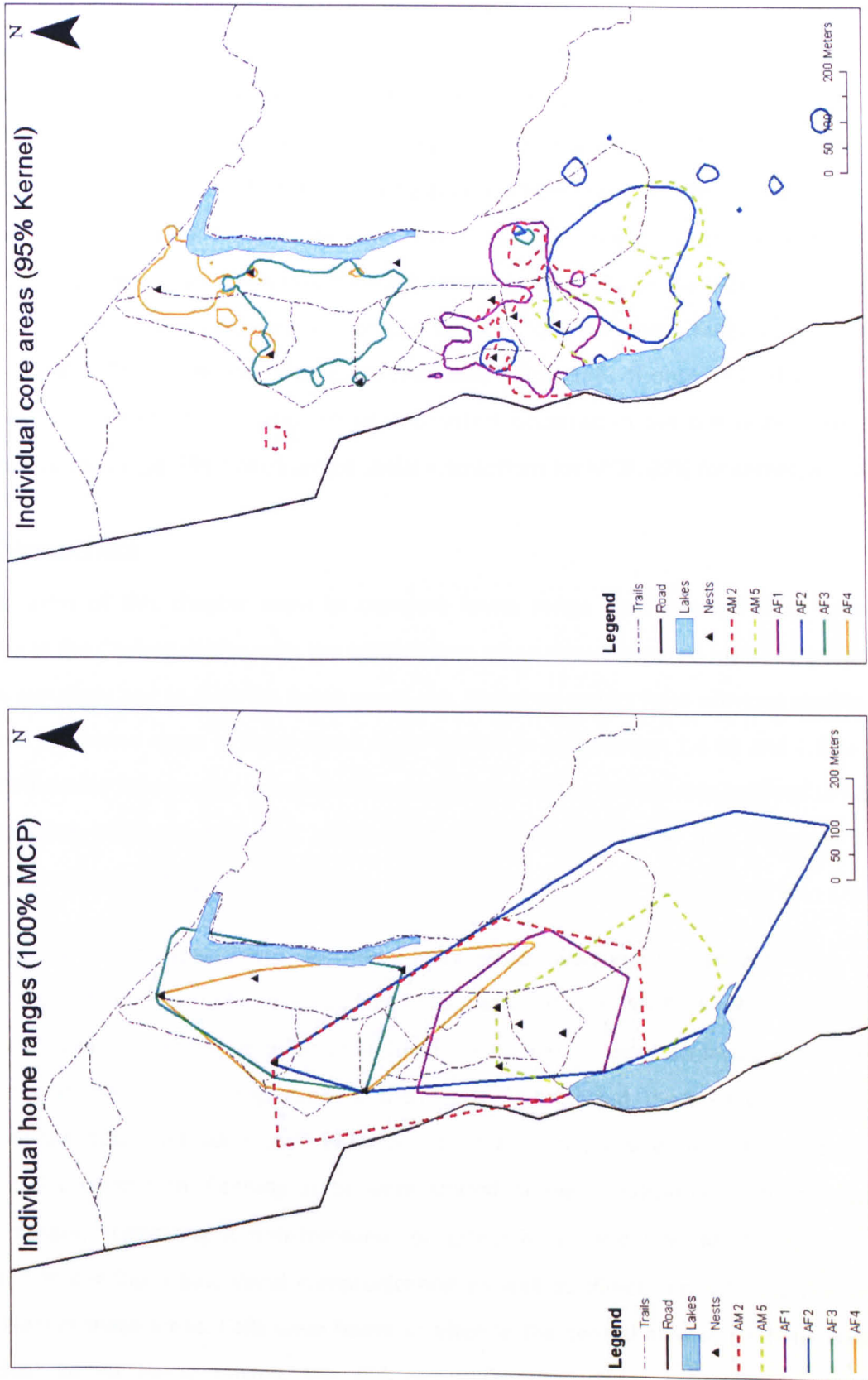
Individual home range sizes were estimated using 100% MCP (Minimum Convex Polygon) based on all recorded locations. Note the large inter-individual variations and the lack of sexual differences.

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 \pm SD (n = 6)	15.4 \pm 8.3	5.4 \pm 1.8
Male mean \pm SD (n = 2)	15.4 \pm 7.4	5.8 \pm 0.4
Female mean \pm SD (n = 4)	15.4 \pm 9.8	5.1 \pm 2.2

Fig. 2.2: Individual home range maps

Dotted Lines represent males; full lines, females. Sleeping site locations are represented by black triangles. Intragroup overlap was greater than intergroup overlap, especially for kernel estimated home ranges (left figure). 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 occasional 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. 2.2: Individual home range maps



2.2.3 Home range use

Behaviours recorded during scan samples were plotted on home range maps (see Materials and methods, Section M.7.2). Although certain feeding locations were exclusive to a particular individual, especially when looking at kernel home ranges, most were shared by members of the same sleeping group (8% of feeding observations exclusive for MCP; 46% for kernel; $n = 24$). Calls almost exclusively occurred in overlapping areas (100% of observed calls for MCP, 94% for kernel, $n = 51$). When looking at kernel home ranges, calls were as often less than ten meters from the home range edge than they were more than ten meters from the edge (51% were less than 10 meters from the home range edge). In the case of MCP home ranges, calls were more often more than ten meters from the home range edge (69% of observed calls). Calls were not often made near tree holes (18% of observed calls were less than ten meters from a nest site). Social encounters occurred in the overlapping areas of individual home ranges (98% of observed social interactions for MCP, 89% for kernel, $n = 54$).

2.3 Discussion

The aims of this chapter were to compare home range sizes inferred from previous research in the Cheirogaleidae with the actual home range sizes estimated from radio-tracking data in our study and to describe home range use. Based on results from previous studies, we expected the home range of hairy-eared dwarf lemurs to be between 1.5 ha and 2.8 ha. We predicted similar home range sizes for males and females as the species was believed to have a monogamous mating system and associate in family groups (Meier and Albignac, 1991; Rakotoarison et al., 1997)

Contrary to our expectations, individual hairy-eared dwarf lemurs had very large home ranges. Our estimates were between 10 and 30 ha, based on 100% MCP (mean: 15 ± 8 ha); and between 2 and 7 ha, based on 95% kernel (mean: 5 ± 2 ha). There were important individual variations, as shown by the large range of the results. As predicted, there were no differences between the sexes but additional research with larger sample sizes are recommended to confirm this conclusion. Feeding areas were shared between individuals with overlapping home ranges, suggesting a non-territorial or group-living tendency. Most social contact occurred in overlap areas. Vocal communication as well as direct contact occurred almost exclusively in these areas. Calls were heard as often in the central area as near the edges of individual kernel home ranges. We did not make distinctions between the types of vocalizations and it is possible that some calls may have a territorial function while others serve intra-group coordination (as in *Microcebus ravelobensis*, *Phaner pallescens* and *Mirza*

coquereli (Braune et al., 2005; Charles-Dominique and Petter, 1980; Pagès, 1978)) or advertise reproductive status (as in *Microcebus murinus* and *Mirza coquereli* (Buesching et al., 1998; Pagès, 1978)).

2.3.1 Why are the hairy-eared dwarf lemur's home ranges so large?

The effects of size and weight cannot explain the large home range size of the hairy-eared dwarf lemur compared to other cheirogaleids. Its estimated home range size is larger than that recorded so far for any species (Table 2.1).

Microcebus berthae is the only other small cheirogaleid with much higher home range size than expected from its size and weight alone (Fig. 2.1) (Dammhahn, 2008). This is mainly due to large male home ranges and could therefore be related to the males' mating strategy (Dammhahn and Kappeler, 2005; Schwab, 2000). Schwab and Ganzhorn (2004) showed that this species has more specific habitat needs than *M. murinus* or *C. medius*; and Dammhahn (2008) and Dammhahn and Kappeler (2008a, b) showed that Homopteran larvae secretions represent up to 82% of its diet. *Microcebus berthae* therefore seems to be the most specialized of all mouse lemurs and its specific needs could explain its larger home range. In addition, as stated previously, species that depend highly on insects tend to have larger home ranges. We therefore suggest that a highly insectivorous diet in the hairy-eared dwarf lemur or the use of patchily distributed food resources (e.g. gum trees), could explain larger home ranges (Clutton-Brock and Harvey, 1979; Harestad and Bunnell, 1979; Haskell et al., 2002).

Climatic conditions and habitat characteristics could also explain these large home ranges. The effect of habitat characteristics can be deduced from studies of *M. murinus*, *C. major* and *C. medius*, as all three species have been studied at different locations. *Microcebus murinus* and *C. medius* were studied in the dry deciduous forests of Kirindy and Ankarafantsika/Ampijoroa and in the littoral rainforest of Mandena. *Cheirogaleus major* was studied in the littoral rainforest of Mandena and in the eastern rainforest of Ranomafana. Mean annual temperatures increase from Ranomafana (18°C) to Mandena (23°C), Kirindy (25°C) and Ankarafantsika/Ampijoroa (27°C) (Atsalis, 1998; Atsalis, 1999a; Lahann et al., 2006). Annual rainfall increases from Kirindy (800 mm) to Ankarafantsika/Ampijoroa (1,200 mm), Mandena (1,600 mm) and Ranomafana (4,485 mm) (Atsalis, 1998; Atsalis, 1999a; Lahann et al., 2006). The home ranges of *M. murinus* males increased with increasing rainfall (at Kirindy: 1.9 ha, Ankarafantsika: 2.8 ha and Mandena: 4.2 ha); while those of females increased with increasing temperature (at Mandena: 0.6 ha, Kirindy: 1.3 ha and Ankarafantsika: 1.8 ha) (Eberle and Kappeler, 2002; Lahann, 2008; Radespiel, 2000). There was only a small difference between the home range sizes recorded for *C. major* at Ranomafana (4.0 ha) and Mandena

(4.4 ha) (Lahann, 2007a; Wright and Martin, 1995), but it is possible that home range size increases with increasing temperature and decreasing rainfall in this species. The home ranges of *C. medius* were similar for all three locations (Mandena: 1.5 ha, Kirindy: 1.6 ha, Ampijoroa: 1.6 ha - (Fietz, 1999; Lahann, 2008; Müller, 1998; Müller, 1999b)), so temperature and rainfall did not seem to affect home range size in this species.

We conclude that home range size can increase with increasing temperature and rainfall. However, geographic variations in the diet could explain variations. Hladik et al. (1980) and Martin (1973) studied the grey mouse lemur in the dry deciduous forest and describe it as omnivorous while Lahann (2007b) reported a diet rich in fruits (63%) and flowers (22%) at Mandena. The higher proportion of fruits and flowers in this species' diet in the littoral rainforest and the temporal and spatial patchiness of fruiting and flowering trees could explain the increased home range size in Mandena. Alternatively, the differences between locations could be related to differences in forest structure and tree species composition. Littoral forests, for example, have lower canopy heights than other rainforest (10-15 m) and a specific flora with many endemic plant species (de Gouvenain and Silander, 2003).

Further research will need to elucidate why the hairy-eared dwarf lemurs have such large home ranges. Additional studies of the diet and the distribution of food and shelter resources should be able to clarify the hypotheses presented here.

2.3.2 Inferences on the potential social organisation of the hairy-eared dwarf lemur

Home range sizes were similar in male and female hairy-eared dwarf lemurs. This was also the case in *M. griseorufus*, *M. ravelobensis*, *M. rufus*, *C. major*, *C. medius* and *Phanerpallescens* (Charles-Dominique and Petter, 1980; Fietz, 1999; Fietz, 2003a; Génin, 2008; Lahann, 2007a; Lahann, 2008; Müller, 1998; Müller, 1999b; Schülke and Kappeler, 2003; Weidt et al., 2004; Wright and Martin, 1995). Most of these species (*Cheirogaleus* spp. and *P. pallescens*) live in monogamous family groups (Charles-Dominique and Petter, 1980; Fietz, 1999; Fietz, 2003a; Lahann, 2007a; Lahann, 2008; Müller, 1998; Müller, 1999b; Schülke and Kappeler, 2003) but some live in multimale/multifemale sleeping groups with promiscuous mating (*M. ravelobensis* - (Weidt et al., 2004)) or in female philopatrics with low promiscuity (*M. griseorufus* - (Génin, 2008)). Further research should aim to clarify the social and mating system of the hairy-eared dwarf lemur which will be discussed in detail in Chapter Five.

2.3.3 Concluding remarks

It is clear that hairy-eared dwarf lemurs have larger home ranges than expected by their size and diet alone. Further research should aim to determine the causes of these large home ranges. Additional focus on the diet, effect of weather variables, food availability and nest availability should help to answer this question.

CHAPTER 3:

SLEEPING SITES

3.1 Introduction

We currently have information on sleeping site use for only 11 cheirogaleids. All species use some kind of shelter to rest during the day. Four species use exclusively leaf/branch nests which can be assumed to be self-constructed or that are naturally occurring tangles in the vegetation (*Microcebus griseorufus*, and both *Mirza* species (*M. coquereli* and *M. zaza*) (Génin, 2008; Kappeler, 1998; Kappeler et al., 2005). Tree holes only are used in *C. medius* and *C. major* although Lahann (2008) also observed *C. medius* sleeping in the spiny *Pandanus* plant in Mandena (but in only 4 and 8% of cases respectively for males and females), and Wright and Martin (1995) observed *C. major* using leaf nests during their active period and tree holes for hibernation in Ranomafana (Dausmann et al., 2005; Fietz, 1999; Fietz, 2003a; Fietz and Dausmann, 2003; Lahann, 2007a; Lahann, 2008; Müller, 1999b; Wright and Martin, 1995). The other five species (*M. berthae*, *M. murinus*, *M. ravelobensis*, *M. rufus* and *P. pallescens*) use a mixture of leaf nests and tree holes in varying proportions (Dammhahn and Kappeler, 2005; Deppe et al., 2008; Eberle and Kappeler, 2006; Lahann, 2008; Martin, 1973; Radespiel, 1998; Radespiel et al., 2003a; Rasoazanabary, 2006; Schmelting, 2000; Schmid, 1998; Schülke and Kappeler, 2003; Schwab, 2000; Wright and Martin, 1995). Both *M. murinus* and *M. ravelobensis* seemed to prefer tree holes over leaf nests (Radespiel, 1998; Radespiel et al., 2003a). However, there were important sexual and seasonal variations: male *M. murinus* from Mandena preferred leaf nests over tree holes, while the opposite was true for females (Lahann, 2008); and in Ankarafantsika, male *M. murinus* preferred to use tree holes during the dry season while they used leaf nests more in the rainy season (Schmelting, 2000).

In this chapter we present results on sleeping site characteristics and how hairy-eared dwarf lemurs use them. We attempt to identify the functions of these structures and the potential advantages their use gives the hairy-eared dwarf lemur.

Hairy-eared dwarf lemurs were observed to sleep together in groups of two to four in tree holes (Goodman and Raselimanana, 2002; Meier and Albignac, 1991; Rakotoarison et al., 1997). The tree holes used in previous studies were in dead trees of at least 30 cm diameter, at heights of 1.4 to 2.2 m (Meier and Albignac, 1991; Rakotoarison et al., 1997). Meier and Albignac (1991) suggested that *A. trichotis* had high nest fidelity.

Although hairy-eared dwarf lemurs have 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). Indeed, 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 (Dausmann et al., 2005; Eberle and Kappeler, 2006; Fietz, 1999; Fietz, 2003a; Fietz and Dausmann, 2003; Kappeler, 1998; Müller, 1999b; Rasoazanabary, 2006; Schmid, 1998; Wright and Martin, 1995). 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 (Dausmann et al., 2005; Kappeler, 1998; Lahann, 2008; Radespiel, 1998; Radespiel et al., 2003a; Schmid, 1998). Tree holes in particular have been proposed to be better for anti-predator defence and thermoregulation (Lahann, 2008; Radespiel et al., 2003a; Schmid, 1998). However, the anti-predator advantage of using tree holes have been questioned as several authors reported predation events where animals were removed from their sleeping site during the day (Fietz and Dausmann, 2003; Schmelting, 2000; Wright and Martin, 1995). Furthermore, the risk of predation in “low quality” sleeping sites (i.e. leaf nests or dense vegetation) can be compensated by behavioural adaptations such as frequent change of sleeping sites, crypsis and flight responses (Radespiel, 1998; Radespiel et al., 2003a).

3.2 Results

3.2.1 Position of the sleeping sites within the home range

Nests were generally away from the home range edge (Fig. 2.2 – Chapter 2, Section 2.2.2). All or most nests used by AF1, AF2, AF4 and AM2 were more than ten meters away from the MCP edge and all or most of the nests used by AF1, AF2, AF5 and AM5 were more than ten meters away from the kernel edge.

3.2.2 Sleeping site characteristics

In total, nine different tree holes in nine different trees were located (Table 3.1). Only one tree hole was in a partially dead *Uapaca* tree; all the others were in live trees. The live trees used belonged to five different genera: *Eugenia* (n = 3), *Cryptocarya* (n = 2), *Abrahamia* (n = 1), *Ilex* (n = 1) and *Syzygium* (n = 1). The DBH of the nesting trees varied between 26 and 54 cm (median: 31.9 cm). The tree holes were 1.1 to 8.8 m above ground (median: 7.2 m). The smallest tree hole entrance was 4.5 x 3.0 cm and the largest was 22.0 cm high and 7.5 cm wide (median: 7.0 x 3.5 cm).

Table 3.1: Characteristics of the tree holes used by the hairy-eared dwarf lemurs during this study

In total we located 9 different tree holes in separate trees from six different genera. Hairy-eared dwarf lemurs used large live trees at varying heights and with varying tree hole entrance sizes. DBH: diameter at breast height. Nest height: from ground level to base of tree hole. ^a 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.

Nest number	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 ^a	unknown ^a	unknown ^a
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 to 10 ^a	unknown ^a	unknown ^a

3.2.3 Sleeping site use

We located at least one 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 location cases (Table 2.2 – Chapter 2, Section 2.2.1). Nests 2, 3 and 4 were used most often (Table 3.2). Nests 7 and 8 were used to a lesser extent. Nest 1, 5, 6 and 9 were used least often.

Table 3.2: Sleeping site use in number of days of occupation and percentage use

Number of days: total number of days on which a nest was occupied by at least one individual. The percentage use was calculated as the number of days in which a nest was occupied by at least one individual divided by the total number of location days on which at least one individual was located in at least one nest ($n = 159$). Note that Nests 2, 3 and 4 were used most often.

	Nest number								
	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

Each individual used between four and five different sleeping sites but used one or two more than the others (Table 3.3). Female AF1 and males AM2 and AM5 used Nest 1 only shortly at the beginning of the study, before AF2 had been caught. Nests 2 to 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 one occasion and female AF2 slept once with female AF4 in Nest 8.

Table 3.3: Tree hole use per individual in percentage of the total number of locations per individual (n)

The numbers in the table represent the percentage use per nest for each individual and was calculated as the total number of days in which the individual was found in a particular nest divided by the total number of days on which that individual was located in any nest (n in the last column). Note that each individual used between four and five different nests but preferred one or two. AF4 and AF5 were located less often because they were radio-collared later. The smaller number of locations of male AM5 was due to problems with his radio-collar from October onwards.

ID	Nest number									n	
	1	2	3	4	5	6	7	8	9		
AF1	3	27	51	19	0	0	0	0	0	0	149
AF2	0	24	36	39	0	0	1	1	0	0	140
AF4	0	0	0	0	6	11	28	53	2	2	47
AF5	0	0	0	0	21	2	67	5	5	5	42
AM2	4	20	38	38	0	0	1	0	0	0	152
AM5	4	21	34	42	0	0	0	0	0	0	101

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 sleeping site. One individual was observed to use the same cavity for at least eight consecutive days.

Hairy-eared dwarf lemurs lined their tree holes with fresh leaves. On 14 November, we observed nesting behaviour in female AF4. She returned to Nest 8 around 0030 and made five excursions to collect leaves from an adjacent *Erythroxylum* tree and bring them back to her tree hole. The return trips lasted until about 0100. She then stayed in this tree hole until 0145.

3.2.4 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 three 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.

3.2.5 Inter-specific association

We observed seven instances of a sleeping association between hairy-eared dwarf lemurs and white-tailed tree rats (*Brachytarsomys albicauda*, family Nesomyidae). A rat was first observed using the same tree hole as male AM2 (Nest 1) on 30 March. It was sitting at the hole entrance and emitted high pitched alarm calls, while the hairy-eared dwarf lemur was observed with an endoscope, sleeping at the bottom of the cavity (Fig. 3.1). A rat was located together with members of AM2's sleeping group again in the same tree hole on 3 April, 5 April and 6 April. On 6 April, using the endoscope, we were able to observe a rat with one juvenile hairy-eared dwarf lemur on either side of it, curled up together, sleeping. On 5 June, while capturing some members of this same sleeping group to re-fit radio-collars in Nest 3, we found *B. albicauda* again, sleeping together with two adult and two juvenile hairy-eared dwarf lemurs. On 10 June, we observed two rats, one smaller than the other, leaving the same tree hole as members of this sleeping group (Nest 3). We also observed this inter-specific nest association in the other sleeping group. On 7 November, we observed the two 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 two unknown individuals and one juvenile *A. trichotis*.

Fig. 3.1: White-tailed tree rat (*Brachytarsomys albicauda*) occasionally sharing a tree hole with the followed hairy-eared dwarf lemurs

Left picture: at the entrance of a tree hole simultaneously occupied by *A. trichotis* (seen at the bottom of the tree hole using an endoscope (black tube on right-hand side of the picture)). Right picture: at release after capture in the same tree hole as a group of hairy-eared dwarf lemurs.



3.3 Discussion

The aim of this chapter was to describe the characteristics and usage pattern of the sleeping sites in the hairy-eared dwarf lemur. Previous studies found that *A. trichotis* used tree holes in dead trees of at least 30 cm diameter, at heights of 1.4 to 2.2 m; and suggested that hairy-eared dwarf lemurs had high nest fidelity (Goodman and Raselimanana, 2002; Meier and Albignac, 1991; Rakotoarison et al., 1997).

Hairy-eared dwarf lemurs used three or four different tree holes each and shared these with other individuals and occasionally with white-tailed tree rats (*B. albicauda*). Tree holes were in living trees from five different genera with diameters over 26 cm (median 32 cm), at heights of 1-9 m above ground (median 7 m); and were not necessarily located on the edges of the home ranges. Animals lined their tree hole with fresh leaves and had high nest fidelity.

3.3.1 Sleeping site characteristics

Our results extend 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 but 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 to 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 (Deppe et al., 2008; Lahann, 2007a; Wright and Martin, 1995). We also observed leaf nests of *M. lehilahytsara* at approximately two meters 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 varies with the size of the animal. *Cheirogaleus 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 to 15 cm DBH) (Lahann, 2008). There was also a vertical stratification of sleeping sites depending on the species. *Cheirogaleus major* used higher sleeping sites than *M. murinus* and *C. medius* (9.7 m vs. 4.1 and 3.9 m) (Lahann, 2008). On the other hand, Schwab (2000) suggested interspecific resource competition for the 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-tailed 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 gain thermoregulatory or anti-predatory 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 *C. crossleyi*, should also be conducted to clarify the amount of niche separation or competition between the sympatric nocturnal Cheirogaleidae of the Andasibe region.

3.3.2 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). *Cheirogaleus major* and *C. medius* also had high tree hole fidelity (Lahann, 2007a; Müller, 1999b). *Cheirogaleus major* family groups repeatedly used one or two group exclusive tree holes, while *C. medius* family groups re-used their tree holes from one year to the next (Lahann, 2007a; Müller, 1999b). 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 (Lahann, 2008; Radespiel, 1998; Radespiel et al., 2003a). In the dry season however, male *M. murinus* highly increased their sleeping site fidelity (Schmelting, 2000).

Hairy-eared dwarf lemurs used four or five tree holes each. A similar number of sleeping sites was found in *Microcebus ravelobensis* during a study of similar length (eight months) (Radespiel et al., 2003a). In comparison, individual *C. medius* used between four and 15 different sleeping sites within six months (Müller, 1998; Müller, 1999b), *M. murinus* used one to 18 tree holes within eight months (Radespiel et al., 2003a) and *P. pallescens* used between eight and 38 sleeping sites during a two-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 were a limiting resource and that hairy-eared dwarf lemurs were forced to re-use these sites frequently because they were the only available tree holes. This hypothesis remains to be tested.

Most Cheirogaleidae formed sleeping groups of varying composition and stability, except *Mirza coquereli* that tended to sleep solitarily (Braune et al., 2005; Charles-Dominique and Petter, 1980; Dammhahn and Kappeler, 2005; Deppe et al., 2008; Eberle and Kappeler, 2006; Fietz, 1999; Fietz, 2003a; Fietz and Dausmann, 2003; Génin, 2008; Kappeler et al., 2005; Lahann, 2007a; Lahann, 2008; Martin, 1973; Müller, 1998; Müller, 1999b; Radespiel, 1998; Radespiel, 2000; Radespiel et al., 2003a; Rasoazanabary, 2006; Schmelting, 2000; Schülke, 2002; Schülke and Kappeler, 2003; Weidt et al., 2004; Wright and Martin, 1995). We will not discuss the details of sleeping group and social organisation of the Cheirogaleidae in this chapter however, as Chapter Five deals with this point in detail.

3.3.3 Tree hole functions

The choice of a good sleeping site can strongly influence predation pressure (Lahann, 2008; Radespiel et al., 2003a). Although some tree holes used by the hairy-eared dwarf lemur had good anti-predator characteristics (high above ground, small entrances, intact walls), 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*) (Fietz and Dausmann, 2003; Goodman, 2003; Goodman et al., 1993; Wright and Martin, 1995). 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, 1998; Radespiel et al., 2003a). However, escape reactions seem impossible if the tree hole only has one entrance which is blocked by a predator (Schülke and Ostner, 2005). Furthermore, hairy-eared dwarf lemurs had high nest fidelity and preferred to re-use the same tree hole for at least eight consecutive days rather than change sleeping site regularly 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 (Schülke and Ostner, 2001; Schülke and Ostner, 2005). The observation that some individuals changed tree holes after being captured suggests a possible anti-predator strategy by 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 be better insulating than small dead trees (Lahann, 2008; Radespiel, 1998; Schmid, 1998). Although all the study animals were active throughout, even during the colder drier season from May to August, one adult male (AM5) did spend one full night in its tree hole in July, suggesting short periods of torpor could occur. All the other members of his sleeping groups 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 (Müller, 1999b; Perret, 1998; Radespiel et al., 2003a; Vickery and Millar, 1984). Individuals were also observed to return to a tree hole during periods of heavy rain, suggesting that these were also used for protection against adverse weather conditions.

3.3.4 Concluding remarks

Although it seems clear that hairy-eared dwarf lemurs have high nest fidelity, the reasons for this will need further investigation. Additional study on the availability of tree holes, the extent of inter-specific associations and their effects as well as predator pressure should be conducted to detail the factors influencing the choice and extensive use of particular types of nest.

CHAPTER 4:

HABITAT USE

4.1 Introduction

The Cheirogaleidae occupy a large range of microhabitats. Their activity height varies from ground level to over ten meters above ground (Duckworth et al., 1995; Hladik et al., 1980; Lahann, 2007b; Lahann, 2008; Pagès, 1978; Pagès, 1980; Radespiel et al., 2006; Schmelting, 2000). Interspecific difference between sympatric species can be found in their activity- or feeding height (e.g. in Mandena, *C. major* used the upper part of the canopy, *C. medius* used the mid-forest level and *M. murinus* used the lower parts of the trees and the understory (Lahann, 2007b; Lahann, 2008)). Species also differ in their microhabitat use based on their feeding or resting needs (i.e. depending on the distribution of feeding trees or food sources, depending on tree hole availability or depending on the presence of tangles of lianas for nesting) (Charles-Dominique and Petter, 1980; Corbin and Schmid, 1995; Ganzhorn, 1989; Lehman et al., 2006; Martin, 1973; Rendigs et al., 2003; Schwab and Ganzhorn, 2004).

In this chapter, we present results on microhabitat use based on direct observations of radio-collared focal individuals and describe the habitat and microhabitat of the study area. We compare the elements of the habitat used by the hairy-eared dwarf lemur with the overall available habitat.

The hairy-eared dwarf lemur has most often been seen in dense tangles of vegetation, using lianas, bushes or bamboo as supports (Garbutt, 2001; Goodman and Raselimanana, 2002; Rakotoarison et al., 1997). Individuals were most often spotted at two to five meters above ground (Garbutt, 2001; Goodman and Raselimanana, 2002; Rakotoarison et al., 1997).

In Chapter Three, we showed that hairy-eared dwarf lemurs used tree holes in live trees as day sleeping shelters in trees with diameters of 26 to 54 cm from five different genera: *Eugenia* (Myrtaceae), *Cryptocarya* (Lauraceae), *Abrahamia* (Anacardiaceae), *Ilex* (Aquifoliaceae) and *Syzygium* (Myrtaceae). The tree holes were 1.1 to 8.8 m above ground. As hairy-eared dwarf lemurs repeatedly used a limited number of sleeping sites, shared them with conspecifics and occasionally with the white-tailed tree rat (*B. albicauda*), I suggested that tree holes could be a limiting resource.

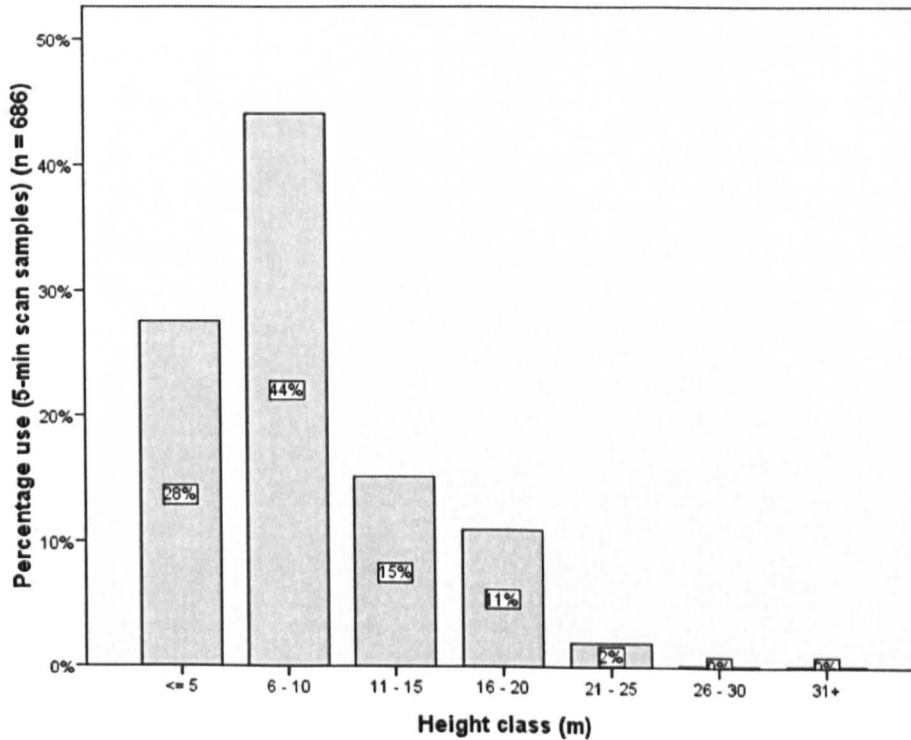
4.2 Results

4.2.1 Microhabitats used during the active period

Hairy-eared dwarf lemurs spent most of their time in trees (91% of five-minute instantaneous scan samples, n = 709). They also used lianas and tangles as supports (5% and 3% of observations respectively). They generally used small supports (76%, n = 659) and only rarely medium and large supports (20% and 5% respectively). These supports were generally oblique (60%, n = 642) and less often vertical or horizontal (23% and 17% respectively). The height at which individuals were observed most often was 6 m (mode, n = 686). Hairy-eared dwarf lemurs were found from ground level up to over 30 m. The mean height was 9 m. When reduced into 5 m interval groups, hairy-eared dwarf lemurs were most often seen at 6-10 m above ground (44%) and under 5 m (28%) (Fig. 4.1). They were also seen at 11-15 m (15%) and at 16-20 m (11%). They were rarely seen above 20 m, most likely because of the dense vegetation. Hairy-eared dwarf lemurs were seen on 31 different tree genera belonging to 24 families. They were most often seen on *Blotia* (Euphorbiaceae, 20% of five-minute instantaneous scan samples, n = 554), *Cryptocarya* (Lauraceae, 12%), *Symphonia* (Clusiaceae, 9%) and *Rhodolaena* (Sarcolanaceae, 9%). The most used families included Euphorbiaceae (21%), Lauraceae (14%) and Clusiaceae (10%).

Fig. 4.1: Forest levels used by the hairy-eared dwarf lemur during their active period in proportion of 5-min scan samples

Note that hairy-eared dwarf lemurs were most often seen at 6-10 m height but used all levels of the forest.

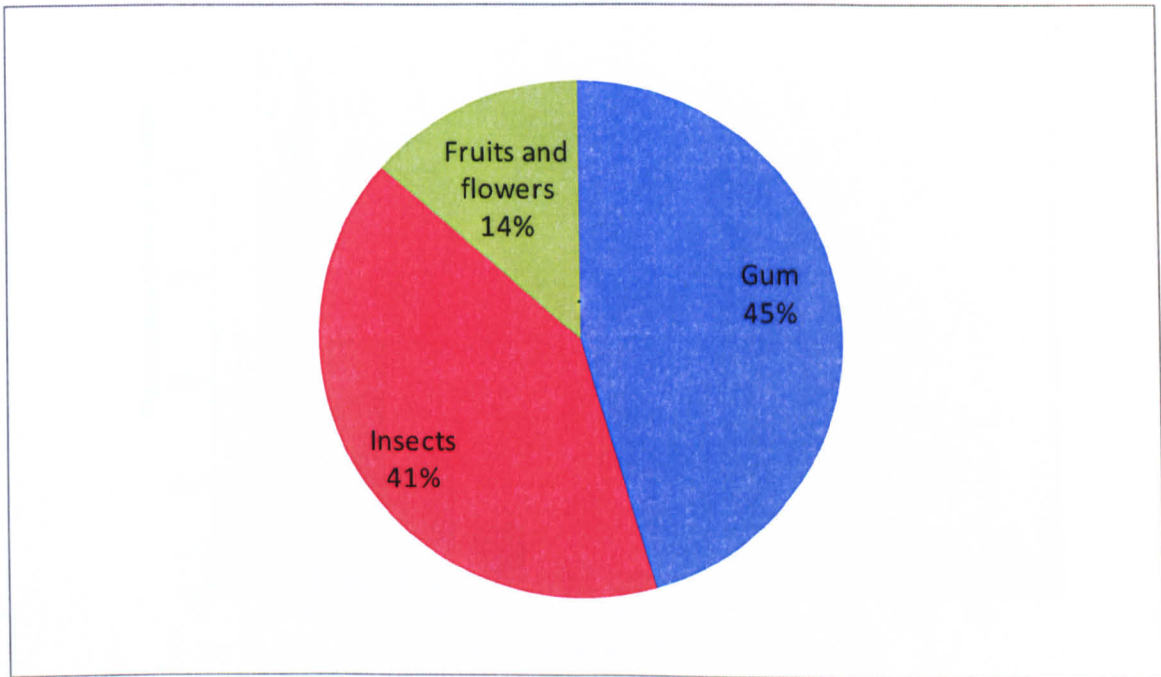


4.2.2 Microhabitats used for feeding and composition of the diet

We observed 24 feeding events in total. Animals were seen feeding between 0.2-15 m above ground (mean, median and mode: 5 m, $n = 21$). Individuals were observed to catch and eat small white moths in nine cases. Prey captures took place high in the dense canopy (mean and median: 8 m, mode: 10 m, range: 3-15 m, $n = 9$). This behaviour was observed in *Cryptocarya* (Lauraceae), *Dichaetanthera* (Melastomataceae), *Weinmannia* (Cunonaceae) and *Dracaena* (Convallariaceae) trees, in the tree crowns as well as in tangles of vegetation and lianas. Individuals were observed to feed on gum in ten cases. Animals generally fed on gum while vertical head down on large tree trunks, at heights of 0.2-6 m above ground (mean: 3 m, median: 2 m, $n = 8$). As scratch marks and up and down head movements were observed, we assume hairy-eared dwarf lemurs used their tooth comb to induce gum flow although this was not clearly observed. Gum feeding trees were most often *Terminalia* (Combretaceae, six observations), but also included *Blotia* (Euphorbiaceae), *Cryptocarya* (Lauraceae), *Symphonia* (Clusiaceae) and *Cleistanthus* (Euphorbiaceae). The feeding height for catching insects and eating gum were significantly different (Mann-Whitney $U = 7$, $n_{\text{insects}} = 9$, $n_{\text{gum}} = 8$, $p < 0.01$). The hairy-eared dwarf lemurs also fed on flowers from *Pittosporum* (Pittosporaceae) and *Leptaulus*

(Icacinaceae) in two cases; on fruits from *Ilex* (Aquifoliaceae) in one observation; and on moss, gum or ants off the trunk of a *Eugenia* tree (Myrtaceae) in two cases. Excluding the last two observations where the food item could not clearly be identified, the diet of the hairy-eared dwarf lemur is mainly gummivore-insectivore with a small portion of fruits and flowers (Fig. 4.2).

Fig. 4.2: Diet of the hairy-eared dwarf lemur in percentage of observed feeding events (n = 24) showing that *A. trichotis* is gummivore-insectivore



4.2.3 Tree composition of the habitat

During point quarter sampling, we measured 1,468 trees with a DBH over ten centimetres, belonging to 114 different genera in 51 families. Tree density was 1,481 trees per hectare. Trees had diameters up to 65 cm with a mean of 17 ± 7 cm ($n = 1,468$). The mode was 11.5 cm. More than half the measured trees had a DBH under 15 cm (Fig. 4.3). The larger the trees, the rarer they were in the environment. The tree-size composition graph (Fig. 4.3) had a typical inverted 'J' shape. The three most common tree genera, in terms of basal area, were: *Cryptocarya* (Lauraceae), *Ocotea* (Lauraceae) and *Eugenia* (Myrtaceae) (Fig. 4.4). The three most common tree families in the habitat were: Lauraceae, Myrtaceae and Clusiaceae (Fig. 4.5).

Fig. 4.3: Size class composition of trees over ten centimetres diameter

The percentage trees for each diameter class was calculated as the number of trees in a diameter class divided by the total number of trees with a DBH (Diameter at Breast Height) over 10 cm ($n = 1,468$) measured during point-quarter sampling in six 1-ha vegetation plots within the home ranges of the followed hairy-eared dwarf lemurs. Note the inversed J shape typical of healthy forests and the limited percentage of large trees.

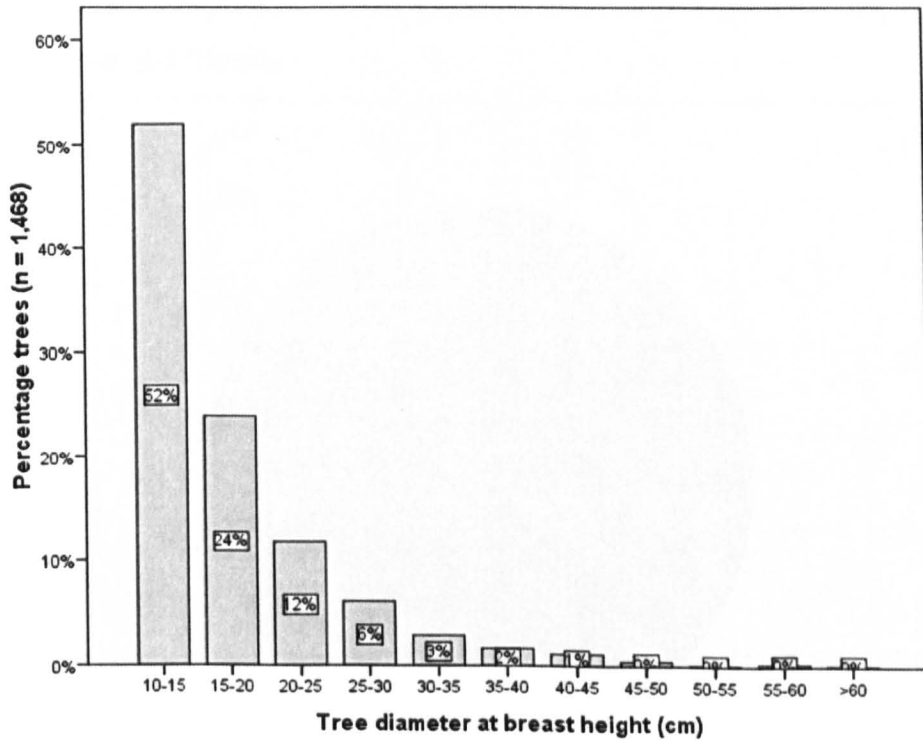


Fig. 4.4: Most dominant tree genera in proportion of total basal area

We calculated the basal area for each genus by adding up the basal area values of individual trees with a DBH over 10 cm, measured during point-quarter sampling in six 1-ha vegetation plots. The proportion of the total basal area was calculated by dividing the total basal area for a genus by the total basal area for all the measured trees (n = 1,468). Although we recorded 114 different genera, the pie-chart only identifies genera which represented at least 2% of the total basal area. Note that the most common tree genera in the habitat are *Cryptocarya*, *Ocotea* and *Eugenia*.

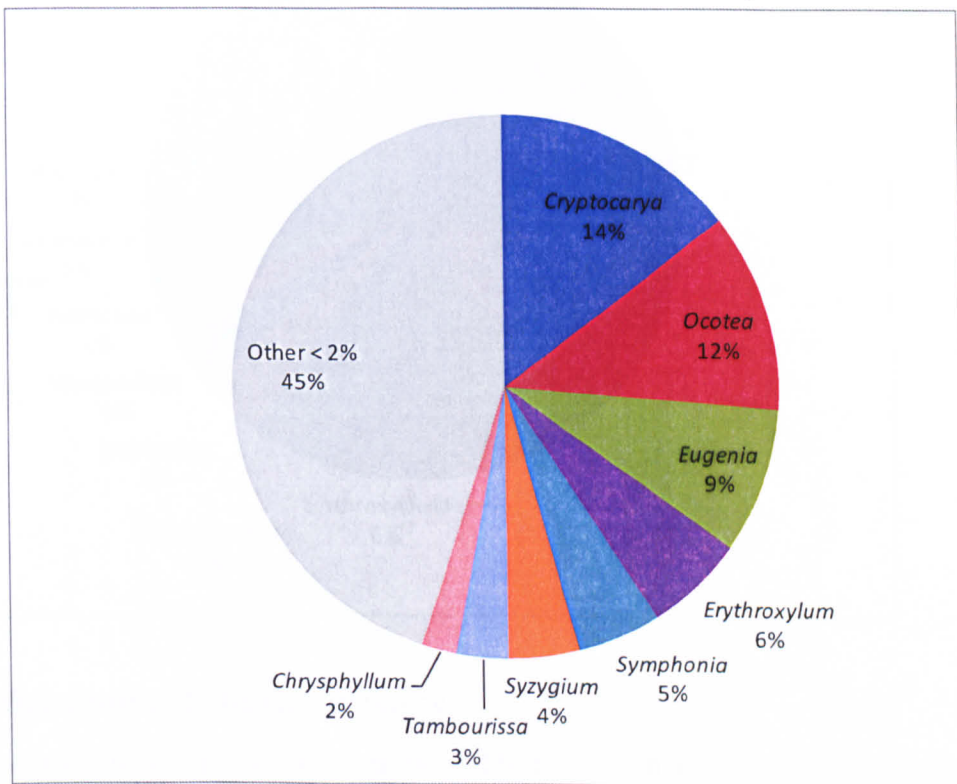
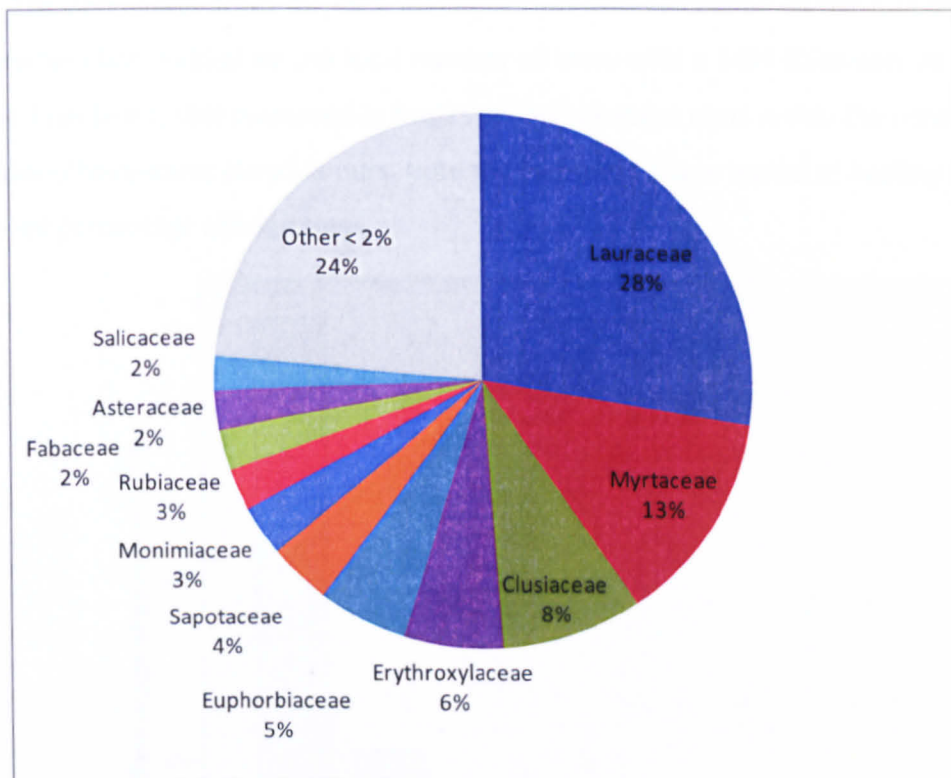


Fig. 4.5: Most dominant tree families in proportion of total basal area

The calculations were conducted in the same way as for Fig. 4.4 but using the family as a unit. We recorded 51 different tree families and represented only the families that represented at least 2% of the total basal area. The most common tree families in the habitat were Lauraceae, Myrtaceae and Clusiaceae.



4.2.4 Microhabitat characteristics

In the microhabitat plots, we measured 1,184 trees with a DBH over one centimetre. The density was 15,787 trees per hectare. Trees varied in diameter from 1.1 cm to 38.4 cm. The average diameter was 4.6 ± 4.7 cm. The mode was 1.4 cm. The thinnest trees are the most common (Fig. 4.6). Trees with a DBH between one and five centimetres represented 69% of the measured trees (Fig. 4.6). The most common tree height classes were 0-5 m (62%) and 5-10 m (29%) (Fig. 4.7). High trees were much rarer than small trees (Fig. 4.6). Lianas were at a density of 1,107 per hectare (I counted 83 lianas in the plots). Most of these were small (63%) or medium (35%) in thickness. Lianas were most common at the 0-5 m level (57%) or at 5-10 m above ground (34%). Large (thick) lianas were much rarer (2%) as well as lianas reaching up to 15 or 20 m above ground (7% and 2% respectively). We recorded 40 tangles in total. The density was 533 tangles per hectare. Most tangles were at heights under 5 m (50%) and under 10 m (38%). Tangles were also found between 10 and 15 m (8%) and between 15 and 20 m (5%). We located 21 arborescent ferns, 62% were less than 5 m tall and 38% were 5 to 10 m high. Ferns were found at densities of 280 per hectare. We counted 25 *Pandanus* shrubs or

trees less than 5 m tall and one *Pandanus* tree 5 to 10 m tall. *Pandanus* (endemic spiky shrub or tree, family Pandanaceae) were at densities of 346 per hectare. The average canopy cover was $87.6 \pm 4.3\%$.

Fig. 4.6: Size class composition of trees over one centimetre diameter

The percentage trees for each diameter class was calculated as the number of trees in a diameter class divided by the total number of trees with a DBH (Diameter at Breast Height) over 1 cm ($n = 1,184$) measured in five 25 m^2 microhabitat plots within the home ranges of the followed hairy-eared dwarf lemurs. Note the inversed J shape typical of healthy forests and the limited percentage of large trees.

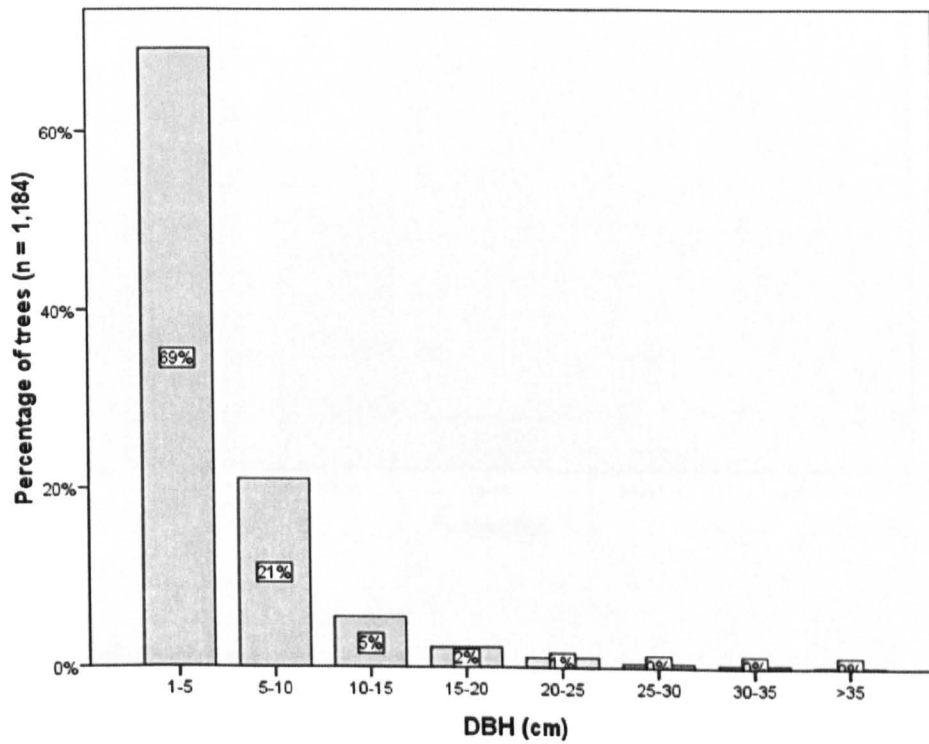
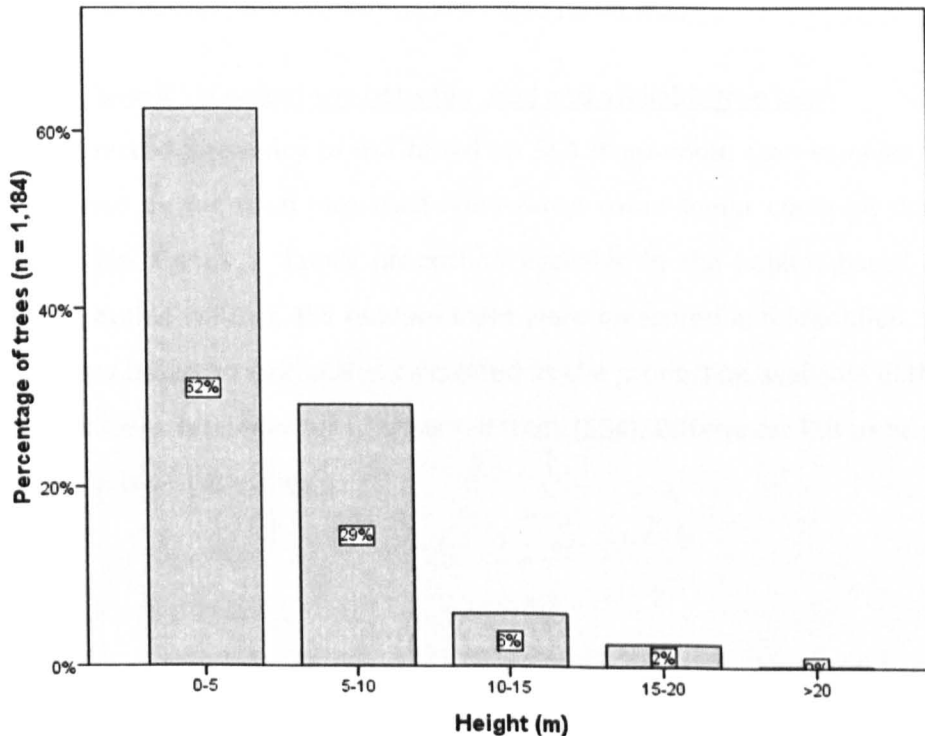


Fig. 4.7: Height class composition of trees over one centimetre diameter

The percentage trees for each height class was calculated as the number of trees in a height class divided by the total number of trees with a DBH (Diameter at Breast Height) over 1 cm ($n = 1,184$) measured in five 25 m² microhabitat plots within the home ranges of the followed hairy-eared dwarf lemurs. Note that low trees are much more common than tall trees.



4.2.5 Other habitat characteristics

In addition to direct observations of gum feeding, my assistants and I located 14 potential gum feeding trees of four different genera within the hairy-eared dwarf lemur's habitat: six *Terminalia* (Combretaceae), five *Garcinia* (Clusiaceae), two *Cleistanthus* (Euphorbiaceae) and one *Dichrostachys* (Fabaceae). Only the *Terminalia* trees were identified to species level. Three were *T. tetrandra* and three were *T. tanalensis*. Areas of the Analamazaotra Special Reserve near the edges of the reserve (especially western edge) were more degraded with many invasive *Camelia* (Theaceae) and guava (*Psidium*, Myrtaceae) trees; *Clidemia hirta* (Melastomataceae) and brambles (*Rubus*, Rosaceae).

4.2.6 Comparison between used and available habitat

We found significant differences between the used and available tree genera: $\chi^2 (27) = 4337.29$, $p < 0.01$; and families: $\chi^2 (22) = 924.74$, $p < 0.01$. Tree genera used more than expected (difference between used and available frequency more than 10 – Table 4.1)

included *Blotia* (Euphorbiaceae), *Rhodolaena* (Sarcolanaceae), *Coffea* (Rubiaceae), *Canarium* (Burseraceae), *Polyscias* (Araliaceae), *Symphonia* (Clusiaceae) and *Dichaetanthera* (Melastomataceae). Tree genera used less than expected (Table 4.1) included *Ocotea* (Lauraceae), *Eugenia* (Myrtaceae), *Syzygium* (Myrtaceae) and *Cryptocarya* (Lauraceae). Families used more than expected included Euphorbiaceae, Sarcolanaceae, Burseraceae, Araliaceae, Melastomataceae, Rubiaceae and Clusiaceae (Table 4.1). Families used less than expected included Lauraceae, Myrtaceae and Fabaceae (Table 4.1).

Table 4.1: Comparison between used and available tree taxa

Observed: Observed frequency of use based on 554 five-minute scan samples for which the tree genus used by the focal individual hairy-eared dwarf lemur could be determined. **Percentage available:** Genus or family proportion available in the habitat based on point-quarter sampling during which 1,468 random trees were measured and identified. **Expected:** Expected frequency based on availability, calculated as the proportion available in the habitat (percentage available) x total number of observed trees (554). **Difference:** Difference between observed and expected frequencies.

Table 4.1: Comparison between used and available tree taxa

Genus	Family	Observed	Percentage available	Expected	Difference	Family	Observed	Percentage available	Expected	Difference
<i>Blotia</i>	Euphorbiaceae	112	0.01	7	105	Euphorbiaceae	117	0.05	29	88
<i>Rhodolaena</i>	Sarcocaulaceae	50	0.01	8	42	Sarcocaulaceae	50	0.02	9	41
<i>Coffea</i>	Rubiaceae	30	0.00	1	29	Burseraceae	36	0.01	8	28
<i>Canarium</i>	Burseraceae	36	0.01	8	28	Araliaceae	24	0.01	4	20
<i>Polyscias</i>	Araliaceae	24	0.00	1	23	Melastomataceae	22	0.01	4	18
<i>Symphonia</i>	Clusiaceae	51	0.05	28	23	Rubiaceae	30	0.03	14	16
<i>Dichaeetanthera</i>	Melastomataceae	22	0.00	1	21	Clusiaceae	58	0.09	47	11
<i>Ilex</i>	Aquifoliaceae	7	0.00	1	6	Aquifoliaceae	7	0.00	1	6
<i>Erythroxylum</i>	Erythroxylaceae	39	0.06	33	6	Erythroxylaceae	39	0.06	33	6
<i>Ouretea</i>	Ochnaceae	5	0.00	1	4	Ochnaceae	5	0.00	1	4
<i>Terminalia</i>	Combretaceae	10	0.01	6	4	Combretaceae	10	0.01	6	4
<i>Pittosporum</i>	Pittosporaceae	4	0.00	1	3	Pittosporaceae	4	0.00	1	3
<i>Capurodendron</i>	Sapotaceae	3	0.00	0	3	Aphloiaceae	3	0.00	2	1
<i>Chrysophyllum</i>	Sapotaceae	14	0.02	12	2	Violaceae	1	0.00	0	1
<i>Cleistanthus</i>	Euphorbiaceae	4	0.00	2	2	Convallariaceae	2	0.00	1	1
<i>Aphloia</i>	Aphloiaceae	3	0.00	2	1	Podocarpaceae	1	0.00	1	0
<i>Dichrostachys</i>	Fabaceae	1	0.00	0	1	Anacardiaceae	9	0.02	9	0
<i>Rinorea</i>	Violaceae	1	0.00	0	1	Cunoniaceae	6	0.01	7	-1
<i>Dracaena</i>	Convallariaceae	2	0.00	1	1	Icacinaceae	1	0.00	2	-1
<i>Leptaulus</i>	Icacinaceae	1	0.00	1	0	Sapotaceae	17	0.04	21	-4
<i>Podocarpus</i>	Podocarpaceae	1	0.00	1	0	Asteraceae	4	0.02	13	-9
<i>Abrahamia</i>	Anacardiaceae	9	0.02	9	0	Fabaceae	2	0.02	13	-11
<i>Croton</i>	Euphorbiaceae	1	0.00	1	0	Myrtaceae	26	0.13	71	-45
<i>Weinmannia</i>	Cunoniaceae	6	0.01	7	-1	Lauraceae	80	0.28	153	-73
<i>Garcinia</i>	Clusiaceae	7	0.02	8	-1					
<i>Albizia</i>	Fabaceae	1	0.01	3	-2					
<i>Brachylaena</i>	Asteraceae	4	0.02	11	-7					
<i>Cryptocarya</i>	Lauraceae	66	0.15	80	-14					
<i>Syzygium</i>	Myrtaceae	7	0.04	23	-16					
<i>Eugenia</i>	Myrtaceae	19	0.09	48	-29					
<i>Ocotea</i>	Lauraceae	14	0.12	65	-51					

Trees with diameters of 26-54 cm used as sleeping sites by the hairy-eared dwarf lemurs represent 11% of trees with diameters over 10 cm ($n = 1,468$) and 0.5% of trees with diameters over one centimetre ($n = 1,184$). There was a significant difference between the used and available tree genera and families (genera: $\chi^2(4) = 76.00$, $p < 0.01$; families: $\chi^2(3) = 75.01$, $p < 0.01$). All five tree genera (*Eugenia* (Myrtaceae), *Cryptocarya* (Lauraceae), *Abrahamia* (Anacardiaceae), *Ilex* (Aquifoliaceae) and *Syzygium* (Myrtaceae)) were used more than expected (difference between observed and expected frequency was 2 for *Eugenia* and 1 for the other genera). Four tree families were used more than expected from availability: Myrtaceae (difference of 3), Aquifoliaceae and Anacardiaceae (both difference of 1). Although attempts were made to detect available tree holes in the microhabitat plots, I only found one tree hole which was a known nest.

There was also a significant difference between the used feeding tree genera and the trees available in the habitat ($\chi^2(11) = 355.93$, $p < 0.01$). Most of the feeding tree genera were used more than expected by availability alone except *Eugenia* (Myrtaceae) and *Symphonia* (Clusiaceae) which were used about as expected and *Cryptocarya* (Lauraceae) which was used less than expected.

4.3 Discussion

The aim of this chapter was to describe habitat use and habitat characteristics and to compare used and available habitat to determine the needs of the hairy-eared dwarf lemur. Focal animals spent most of their time in tree-crowns, on lianas and in tangles of vegetation; using mainly the small branch niche, as was expected from previous observations of hairy-eared dwarf lemurs in dense tangles of vegetation, lianas and bushes; and as is common in other small nocturnal prosimians (Bearder, 1987; Garbutt, 2001; Goodman and Raselimanana, 2002; Harcourt and Thornback, 1990; Martin, 1973; Mittermeier et al., 2006; Nekaris and Bearder, 2007; Rakotoarison et al., 1997). Hairy-eared dwarf lemurs used a large range of forest levels, from ground level to over 30 m above ground; and were most often seen between five and ten meters high; proving that they do not only use the two to five meter height range previously observed (Garbutt, 2001; Goodman and Raselimanana, 2002; Rakotoarison et al., 1997). At this level of the forest, crowns of small trees, lianas and tangles were common. Individuals were most often spotted on *Blotia* (Euphorbiaceae), *Cryptocarya* (Lauraceae), *Symphonia* (Clusiaceae) and *Rhodolaena* (Sarcolanaceae) trees. *Blotia*, *Symphonia* and *Rhodolaena* were used more than expected by availability alone.

The diet of the hairy-eared dwarf lemur was mainly gummivore-insectivore with a small portion of plant material. Animals foraged at different heights and microhabitats depending on

the food type. They used the small branch niche of tree-crowns at median heights of 8 m to catch small moths while they fed on gum on large tree trunks at median heights of 2 m. Slender lorises (*Loris lydekkerianus lydekkerianus*) also used trunks to feed on gum and the terminal branch niche to catch small flying insects, including Lepidoptera (Nekaris, 2005). *Allocebus trichotis* foraged for insects on four different tree genera: *Cryptocarya* (Lauraceae), *Dichaetanthera* (Melastomataceae), *Weinmannia* (Cunonaceae) and *Dracaena* (Convallariaceae). These trees have fleshy fruits (except *Weinmannia*) and flowers that can attract insects (pers. obs.) (Almeda, 2003; Schatz, 2001). Gum feeding trees belonged to five genera from 11 families and included *Cryptocarya* (Lauraceae), *Terminalia* (Combretaceae), *Blotia* (Euphorbiaceae), *Symphonia* (Clusiaceae) and *Cleistanthus* (Euphorbiaceae). *Terminalia* trees are distributed throughout Madagascar and their gum is also eaten by *M. coquereli*, *P. pallescens*, *M. murinus* and *M. ravelobensis* (Birkinshaw and Colquhoun, 2003; Charles-Dominique and Petter, 1980; Pagès, 1980; Radespiel et al., 2006; Schatz, 2001). *Symphonia* trees produce yellow latex (Schatz, 2001). In addition, I located potential gum feeding trees within the hairy-eared dwarf lemur's habitat belonging to the genera *Terminalia* (Combretaceae), *Garcinia* (Clusiaceae), *Cleistanthus* (Euphorbiaceae) and *Dichrostachys* (Fabaceae). Although mouse lemurs also fed on trees of the families Fabaceae, Clusiaceae and Combretaceae (Radespiel et al., 2006); the use of gum from Lauraceae and Euphorbiaceae remains to be confirmed. Fruit and flower feeding trees included *Pittosporum* (Pittosporaceae), *Leptaulus* (Icacinaceae) and *Ilex* (Aquifoliaceae). The small fleshy purple fruits of *Ilex mitis* are also eaten by *M. rufus* (Atsalis, 1998; Schatz, 2001). *Pittosporum* is an aromatic shrub with small to large flowers (Schatz, 2001). *Leptaulus* has small flowers and other lemurs were observed to eat flowers of the family Icacinaceae (Birkinshaw and Colquhoun, 2003; Schatz, 2001). Except for *Symphonia* and *Cryptocarya*, most feeding trees were used more than expected by availability alone.

Chapter Three showed that hairy-eared dwarf lemurs used tree holes as sleeping sites. The used tree sizes were rare in the habitat and all five tree genera where sleeping sites were located were used more than expected by their availability alone. This observation adds strength to our hypothesis that tree holes could be a limiting resource (see Chapter 3, Section 3.3.2).

The height and microhabitat use of the hairy-eared dwarf lemur severely hampered direct behavioural observations because of the dense canopy cover, the small size of the animals and the limited visibility at night. Although hairy-eared dwarf lemurs were followed for almost 633 hours (Table 2.2 – Chapter 2, Section 2.2.1), actual direct observations of focal individuals was only possible 10% of the time (I collected 775 five-minute instantaneous scan samples i.e.

about 65 hours). This problem also explains the small sample size of feeding observations. Insect, fruit and flower consumption, in particular, were most likely highly underestimated because of the lack of visibility. Gum feeding, on the other hand, was more readily observed as animals tended to come lower to the ground and stay on large tree trunks.

Concluding remarks:

Although our results give a first glimpse of the habitat use and feeding ecology of the hairy-eared dwarf lemur, additional research is imperative. As gum is an important part of this species' diet and more easily studied than insect, flower or fruit consumption high in the canopy, we suggest a study focusing on gum-producing trees revealing the exact species, location and seasonal gum-production rates of these trees combined with direct observations of feeding events. This should give us an insight in the distribution and availability of an important food source for the hairy-eared dwarf lemur as well as the potential competitors for this resource. Analyses of the chemical composition of gum collected during this study is currently under way (in collaboration with Dr. Génin and Prof. Ganzhorn); and faecal analysis is being conducted by my Malagasy assistant, Miss Andrianoelina. In addition to the study of important food resources and diet, research should also aim to clarify tree hole availability in the habitat and a simultaneous study of hairy-eared dwarf lemurs and their tree hole 'host', the white-tailed tree rat (*B. albicauda*) (see Chapter 3, Section 3.2.5), should clarify the relationship between these two species.

As mentioned in Chapter Two (Section 2.3.1), specific habitat needs in the hairy-eared dwarf lemur could explain their large home ranges, as is the case in *M. berthae*, and pushing the comparison even further, could also restrict *A. trichotis* to primary and old secondary rainforest and limit its geographical range (Schwab and Ganzhorn, 2004). As studies of habitat use are crucial to inform the conservation needs of a species and could clarify its extent of occurrence; and as competition and/or niche separation can play an important role in the habitat use of a species; further research should aim to study this aspect of the ecology of sympatric cheirogaleids. Horizontal and vertical stratification related to resting and feeding, physical characteristics of the habitat used for a variety of behaviours, and important food and shelter sources should be studied following the example of previous studies (Corbin and Schmid, 1995; Ganzhorn, 1988; Ganzhorn, 1989; Lahann, 2007b; Lahann, 2008).

Few studies focussed on microhabitat use in the Cheirogaleidae, making interspecific comparisons difficult. Furthermore, most of these studies did not use direct observations as I did, but related capture rates to habitat characteristics to determine species' habitat choice

(Rendigs et al., 2003; Schwab and Ganzhorn, 2004). Although these studies showed that vines were also important for *M. berthae* and *M. ravelobensis* and that large trees were also important for *M. murinus*; these habitat characteristics probably relate more to the sleeping site needs of these species than to their habitat requirements during their active period. Moreover, these rare studies only reported the names of foraging trees and not the names of trees used for insect feeding or other behaviours, even though this knowledge would also be useful to determine the habitat needs of a species.

We believe that the full behavioural ecology of the hairy-eared dwarf lemur, as well as many other small bodied nocturnal rainforest species, will only be fully understood once new technologies enabling remote follow and/or observation of these elusive creatures become available. A few of the tools currently in development but too heavy to be used on animals the size of hairy-eared dwarf lemurs include GPS radio-collars (Rodgers, 2001) and 'crittercams' (see <http://www.nationalgeographic.com/crittercam> and <http://news.bbc.co.uk/2/hi/science/nature/3479595.stm>).

CHAPTER 5:

SOCIAL ORGANISATION

5.1 Introduction

In 1978, Charles-Dominique already established the problem of labelling nocturnal prosimians as 'solitary' since they do maintain social networks through vocal and olfactory communication and regularly meet at night even though they do not forage in groups (Charles-Dominique, 1978). Using adult home range overlap patterns and observed sleeping associations, Bearder (1987) proposed five types of social systems within the nocturnal prosimians. He also proposed to use of the term 'dispersed' instead of 'solitary' to define the social organization of solitary foragers which maintain social networks. This was further advocated by Müller and Thalmann (2000) who refined the definitions for nocturnal primate social organisation.

The social organisation of a species can be determined from its component parts: the social system, the mating system and the spacing system (Fuentes, 2007; Müller and Thalmann, 2000). The social system aims to identify the basic social unit of the species, based on inter-individual relationships (interactions through direct contact or vocal and olfactory communication) (Fuentes, 2007; Müller and Thalmann, 2000). This information can be collected through direct observation of nocturnal interactions or by determining day-sleeping group composition (Müller and Thalmann, 2000; Sterling et al., 2000). To define the mating system of a species, direct observations of mating and paternity analysis are necessary although some assumptions can be inferred from sexual dimorphism and relative testes size (Müller and Thalmann, 2000). The spacing system of a species describes the distribution and overlap of individuals in space and time (Müller and Thalmann, 2000). This can easily be deduced from studies of home ranges and inter-individual overlap (Müller and Thalmann, 2000).

In this chapter we present results on home range overlap, sleeping associations and nocturnal inter-individual encounters. We use this information to assess the social, spacing and mating system of the hairy-eared dwarf lemur and discuss the possible social organisation of the species.

We currently have information on the social organisation of only ten Cheirogaleidae (Table 5.1). The most common social system is either a multi-male/multi-female group (*Microcebus*

berthae, *M. ravelobensis*, *M. rufus* and *Mirza zaza*) or a family group composed of an adult pair with or without offspring (*Cheirogaleus spp.* and *P. pallescens*). Male or female uni-sex pairs (*M. griseorufus*), female groups with solitary males (*M. murinus*), or solitary females with offspring and solitary males (*Mirza coquereli*) have also been observed (Table 5.1). The mating system is either promiscuous (polygynandrous) with a varying degree of male competition (*M. berthae*, *M. griseorufus*, *M. murinus*, *M. ravelobensis*, *M. rufus* and *Mirza spp.*) or monogamous but with potential extra-pair mating and young (*Cheirogaleus spp.* and *P. pallescens*) (Table 5.1). The social organisation is therefore either composed of gregarious or dispersed pairs or family groups with monogamous mating (gregarious in *C. major*, dispersed in *C. medius* and *P. pallescens*) or dispersed mixed- or unisex groups of varying composition with different levels of promiscuity (*Microcebus spp.* and *Mirza spp.*) (Table 5.1).

Table 5.1: Summary of previous research on the social organisation of the Cheirogaleidae

For each species we report the source references; the amount of home range overlap, social sleeping and nocturnal social encounters and between which individuals this occurs; whether there were sexual differences in home range size or morphology (sexual dimorphism); whether oestrus synchrony, female philopatry or territoriality have been recorded; whether the testicular volume is high or low compared to similar sizes species; any available information on infant rearing; the mating and social systems; the social organisation; which sexes disperse and between which groups of individuals there is competition. Home range overlap, social encounters: mm: male-male, ff: female-female. Sleeping associations: f : females, m: males. Social organisation: dispersed mm-mf: dispersed multi-male/multi-female. Mating system: EPY: Extra-Pair Young.

Table 5.1: Summary of previous research on the social organisation of the Cheirogaleidae

DWARF LEMURS

Species	<i>Cheirogaleus major</i>	<i>Cheirogaleus medius</i>
References	Lahann (2007a, 2008)	Fietz (1999, 2003a), Fietz and Dausmann (2003), Lahann (2008), Müller (1998, 1999a, b), Schwab and Ganzhorn (2004)
Home range overlap	Family group members (median 77%)	Family group members (median 77%)
Sexual difference in home range size	no	no
Sleeping associations	Family group members (96%)	Family group members (33-85%)
Social encounters	Family group members (49% of sightings, < 10 m, same tree crown)	
Sexual dimorphism	no	no
Oestrus synchrony		no
Testicular volume		low
Rearing pattern		Biparental, obligate paternal care, cooperative breeding (helpers/occasional bigamous groups with two related females)
Mating system	Monogamous	Monogamous but EPY
Social system	Family groups: adult pair with offspring	Family groups: adult pair with offspring, occasional bigamous groups + floater males
Social organisation	Gregarious family groups	Dispersed family groups
Female philopatry		no
Dispersal		both sexes
Competition	Between family groups	Between groups
Territoriality	yes	yes

MOUSE LEMURS

	<i>Microcebus berthae</i>	<i>Microcebus griseorufus</i>	<i>Microcebus murinus</i>
Species			
References	Dammhahn and Kappeler (2005), Schwab (2000), Schwab and Ganzhorn (2004)	Génin (2008)	Andrés et al. (2003), Eberle and Kappeler (2002, 2004a, b, 2006), Fredsted et al. (2005), Kappeler (1990, 1991, 1993), Lahann (2008), Martin (1973), Radespiel (1998, 2000), Radespiel et al. (2002, 2003a, 2003b), Radespiel and Zimmermann (2001a, 2001b), Schmelting (2000), Schmelting et al. (2000), Schmid and Kappeler (1998), Schwab and Ganzhorn (2004), Wimmer et al. (2002)
Home range overlap	Intra- and intersexual overlap (mm more than ff)	Intra- and intersexual overlap	Intra- and intersexual overlap (mm more than ff), more within sleeping groups, seasonal variation mm overlap
Sexual difference in home range size	Male > Female outside mating season	no	Male > Female during mating season
Sleeping associations	Mixed-sex groups (46-48%), female with up to 4 males, high individual variation; some all-male, few all-female	Unisex pairs, f more than m, occasionally fusion of groups -> mixed group	Female groups (2-4 related females), males alone or with related male (at end dry season), few mixed, up to 5 members
Social encounters	Mixed-sex sleeping partners, mm more than ff	Intra- and intersexual encounters	Most intersexual encounters, 5.4% of activity time, ff between sleeping group members
Sexual dimorphism	no	Females > Males	Females > Males
Oestrus synchrony	moderate	no	conflicting reports: moderate or high
Testicular volume	high		high
Rearing pattern	Promiscuous	Possible paternal care (male grooming young)	Female cooperative breeding, no paternal care
Mating system		Between familiar pairs	Promiscuous, breeding neighbourhood smaller than foraging neighbourhood, potential inbreeding, between familiar pairs, mixed paternity, indirect female choice through multiple partners
Social system	Mixed-sex sleeping group	Uni-sex pairs	Related female groups clustered in matrilineal and exchanging males
Social organisation			
Female philopatry	Dispersed mm-mf	Dispersed mm-mf	Dispersed mm-mf, female dominance
Dispersal	yes?	yes	yes
Competition	male	male	male (not obligate)
	Male scramble/sperm competition	Male mate guarding	Male temporary mate guarding (young females), mating plugs, scramble and sperm competition, male hierarchy
Territoriality	no		no

MOUSE LEMURS (cont.)

Species	<i>Microcebus ravelobensis</i>	<i>Microcebus rufus</i>
References	Braune et al. (2005), Radespiel et al. (2003a), Weidt et al. (2004)	Atsalis (2000), Wright and Martin (1995)
Home range overlap	Intra- and intersexual overlap (ff more than mm), more within sleeping group no	Male > Female?
Sexual difference in home range size		
Sleeping associations	Mixed-sex groups (90-98%), 2-6 members, some all-female, rarely all-male	
Social encounters	Intra- and intersexual encounters	Intersexual encounters 1.6% of sightings
Sexual dimorphism	no	no
Oestrus synchrony		
Testicular volume		
Rearing pattern		
Mating system	Promiscuous, between familiar pairs	Promiscuous?
Social system	Mixed-sex sleeping groups	Mixed-sex groups?, mean 8 members?
Social organisation	Dispersed mm-mf	Dispersed mm-mf? yes?
Female philopatry		
Dispersal		
Competition	Male sperm and scramble competition	
Territoriality	no	

GIANT MOUSE LEMURS AND FORK-MARKED LEMURS

	<i>Mirza coquereli</i>	<i>Mirza zaza</i>	<i>Phaner pallescens</i>
Species			
References	Kappeler (1997a, 1997b), Pagès (1980, 1978)	Kappeler et al. (2005)	Charles-Dominique and Petter (1980), Schülke (2002), Schülke and Kappeler (2003), Schülke et al. (2004)
Home range overlap	Intra- and intersexual overlap (ff more than mm, mm only during mating season and then more than ff)		Between pairs (82%), intrasexual with neighbour pair (mm more than ff)
Sexual difference in home range size	conflicting reports: Male > Female, especially in mating season; Female > Male		no
Sleeping associations	Most sleep alone, female with offspring, occasional female groups	Mixed-sex groups, 2-8 members (mean: 0.8 female, 1.1 male, 0.4 juveniles, 1.9 unidentified)	Pairs (36%)
Social encounters	Rare, most intersexual encounters, more affiliative than aggressive, occasional affiliative ff, no direct mm		Most within pair (9% < 15 m, 23% < 25 m), most aggressive, with neighbour: most ff, fm affiliative and aggressive, no affiliative mm; frequent vocal contact
Sexual dimorphism			no
Oestrus synchrony	Males slightly > Females		
Testicular volume	high		
Rearing pattern	no paternal care?		
Mating system	Promiscuous	Promiscuous?	Monogamous but EPY
Social system	Solitary	Mixed-sex sleeping groups?	Pairs, occasional bigamous groups + bachelor males
Social organisation	Solitary or dispersed mm-mf, conflicting reports: no or loose pair bonds	Dispersed mm-mf?	Dispersed pair, female dominance
Female philopatry			
Dispersal			
Competition	Male scramble competition		Male temporary mate guarding, female scent marking, also between groups
Territoriality			yes

The amount of home range overlap, inter-individual nocturnal interactions and sleeping associations are usually used to determine the social and spacing systems of the species. Assumptions are usually made about the mating system but indispensable direct observations of mating and/or paternity analyses have only been conducted in a few species (*C. medius*, *M. griseorufus*, *M. murinus* and *P. pallescens*) (Andrès et al., 2003; Eberle and Kappeler, 2004a; Eberle and Kappeler, 2004b; Fietz, 2003a; Fietz and Dausman, 2003; Génin, 2008; Radespiel et al., 2002; Schülke, 2002; Schülke et al., 2004; Schülke and Ostner, 2005).

5.2 Results

5.2.1 Home range overlap

Male MCP home ranges overlapped with two to four females while the kernel home ranges of males overlapped with two to three females (Table 5.2, Fig. 5.1, Fig. 2.2 – Chapter 2, Section 2.2.2). Female home ranges overlapped with up to two males. Male and female home ranges overlapped with each other. The MCP sociogram (Fig. 5.1.a) shows the high degree of overlap between individuals AF1, AF2, AM2 and AM5 on the one hand and between the females AF4 and AF5 on the other hand. The kernel based sociogram (Fig. 5.2.b) demonstrates the larger amount of overlap between pairs AF1/AM2 and AF2/AM5 as well as the higher degree of overlap between males than between females.

Table 5.2: Home range overlap between individuals

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

Table 5.2.a: Percentage overlap between MCP home ranges

	AF1	AF2	AM2	AM5	AF4	AF5
AF1		88,73	99,93	51,38	6,78	0,00
AF2	28,23		52,51	32,15	18,14	7,55
AM2	46,22	76,33		31,34	28,80	11,98
AM5	48,37	95,16	63,81		0,00	0,00
AF4	5,43	45,68	49,89	0,00		65,91
AF5	0,00	22,38	24,42	0,00	77,57	

Table 5.2.b: Percentage overlap between kernel home ranges

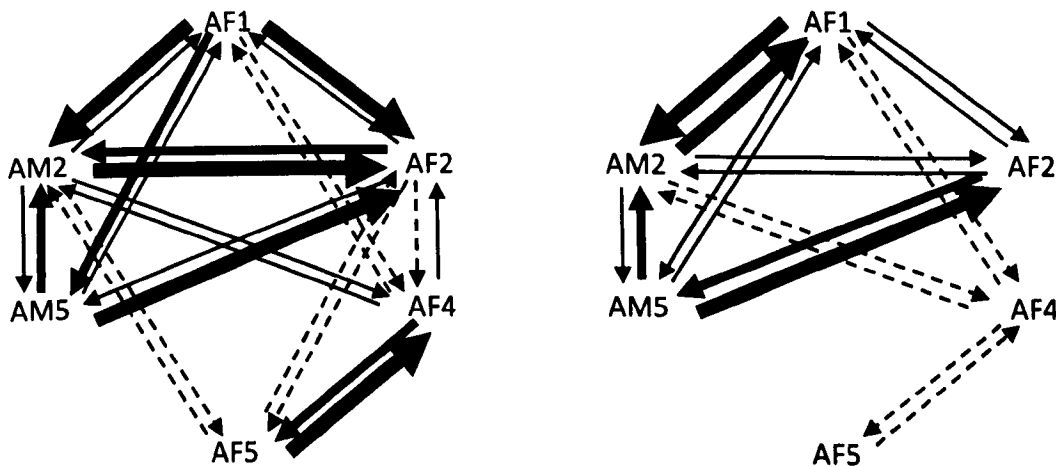
	AF1	AF2	AM2	AM5	AF4	AF5
AF1		19,74	67,82	16,68	1,25	0,00
AF2	14,32		23,99	47,33	0,10	0,00
AM2	61,07	29,78		33,33	1,13	0,00
AM5	16,46	64,38	36,53		0,00	0,00
AF4	1,25	0,14	1,25	0,00		3,31
AF5	0,00	0,00	0,00	0,00	8,54	

Fig. 5.1: 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 overlapped with the home range of AF1 but 75-100% of the home range of AF1 overlapped with the home range of AM2). Note the important amount of MCP home range overlap between AF1, AF2, AM2 and AM5 on the one hand and AF4 and AF5 on the other hand, suggesting two social groups; and the important amount of kernel home range overlap between the pairs AF1/AM2 and AF2/AM5, suggesting within group pair bonding.

a. Based on MCP home range overlap

b. Based on kernel home range overlap



Line thickness represents percentage home range overlap:

	For MCP:	For kernel:
--->	1-25%	1-10%
—>	26-50%	10-25%
—>	51-75%	26-50%
—>	75-100%	51-75%

5.2.2 Sleeping associations

Individuals slept alone in 36% of cases and socially in 64% of cases (n = 294). When sleeping socially, the most common group size was three individuals (42%, n = 187). Hairy-

earred 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 5.3) showed that AF1/AM2, AF1/AF2 and AF2/AM2 shared sleeping sites in at least three out of four 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 only associated with AF5 on one occasion and AF2 and AF4 also slept together once.

Table 5.3: Results of Cole's index of association for each pair of individuals sleeping together

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 its tree hole, and B = number of days individual B was located in its tree hole. The closer the index is to 1, the more the two individuals slept together. High associations between adults suggest two sleeping groups.

		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

Juveniles were found in adult sleeping holes on 29 days. In 11 cases, one or two juveniles were found to sleep with individuals AF1, AF2, AM2 and AM5. In five cases, one or two juveniles slept with AF1 and AM2. In four cases, one or two juveniles slept with AF4 and AF5. In three cases, one or two juveniles slept with AF1, AF2 and AM2. In two cases, two juveniles slept with AF1, AM2 and AM5. In one instance each, at least one juvenile slept with AM2 and AM5 and at least one juvenile slept with AF1, AF4 or AF5.

In six cases, unknown adult individuals were seen sharing radio-collared individuals' sleeping sites. One and on another day two adults shared a nest with AF5. One and on another day two 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 one juvenile.

The percentage use of each tree hole per individual (Table 5.4) showed that Nest 1 was only used by AF1, AM2 and AM5 shortly at the beginning of the study, before AF2 had been captured. Nests 2 to 4 were used exclusively by AF1, AF2, AM2 and AM5. Nests 5, 6 and 9 were

used exclusively by AF4 and AF5. Male AM2 and female AF2 slept together with female AF5 in Nest 7 on one occasion and female AF2 slept once with female AF4 in Nest 8.

Table 5.4: Tree hole use per individual showing group exclusive sleeping site use

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). Note that Nest 1 was only used by AF1, AM2 and AM5 at the beginning of the study, before AF2 had been captured. Nests 2 to 4 are used exclusively by Group 1 (AF1, AF2, AM2 and AM5), while Nests 5 to 9 are almost exclusively used by Group 2 (AF4 and AF5), with the exception of Nests 7 and 8 which were shared between AM2, AF2 and AF5 once (Nest 7) and between AF2 and AF4 once (Nest 8).

ID	Nest number									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

5.2.3 Nocturnal encounters

The pair AM2/AF1 met most often (72 observed interactions throughout the study period). Female AF2 met males AM2 and AM5 a roughly equal amount of times (8 and 9 respectively) and female AF1 rarely met male AM5 (3 sightings). Males met more often at night than females (14 vs. 2 sightings). Juveniles were seen with adult individuals on 20 occasions. One juvenile was seen with AF1 in six cases, with AM2 or AF4 in four cases each, with AM2 or AM5 accompanied by unidentified adults in one and three cases each, with AF1 and AM2 in one case and with AF5 in one case. An unidentified adult individual was also seen within the home ranges of AF1 and AM2. The first captured male, AM1 (Table 1.2 - Chapter 1, Section 1.2.2), was caught within the home ranges of AF1, AF2, AM2 and AM5 and its radio-collars was discovered 244 m South of its capture locations, within the home ranges of AF2 and AM5.

Congregating individuals were observed sitting close together or moving around in the same tree crown, moving around in adjacent trees less than 10 m away, walking one after another on a liana or to return or enter their sleeping site, allogrooming, playing and chasing each other in a tree crown. Different types of calls, which were assumed to be emitted by the hairy-eared dwarf lemurs but could not be confirmed by direct observation, were heard. Calls were most often heard when individuals were alone but also occurred when they were with other adult or juvenile individuals. Vocalizations occurred at all times of the night, before and after dispersal and reunion in or near the sleeping site.

5.3 Discussion

The aim of this chapter was to describe the spacing, social and mating systems of the study individuals to determine the social organisation of the hairy-eared dwarf lemur. We used home range overlap between individuals, day-sleeping associations and nocturnal encounters to clarify inter-individual relationships.

5.3.1 Social system

Cole's index of association based on sleeping group composition (Table 5.3) and the sociogram based on the overlap of MCP home ranges (Fig. 5.1.a) revealed two potential groups: Group 1 composed of two females (AF1 and AF2) and two males (AM2 and AM5); and Group 2 composed of two females (AF4 and AF5). As in previous research, there was a high degree of home range overlap within groups and only limited overlap between groups; group members usually slept together in group-exclusive sleeping sites; and group members were observed to meet at night (Charles-Dominique and Petter, 1980; Fietz, 1999; Fietz, 2003a;

Génin, 2008; Lahann, 2007a; Lahann, 2008; Martin, 1973; Müller, 1998; Müller, 1999a; Müller, 1999b; Radespiel, 1998; Radespiel, 2000; Schülke, 2002; Schülke and Kappeler, 2003; Weidt et al., 2004).

Three members of Group 1 (AF1, AF2 and AM2) shared a tree hole about 75% of the time. The lower association index of male AM5 could be due to the problems I encountered with this individual's radio-collar during the last two months of the study, which made it impossible to locate its sleeping site although he might have been associating with the other members of his group. Both this male and female AF1 slept away from the other adult individuals of the group most often however, confirming the lower association of male AM5 to the group.

The overlap of kernel home ranges, sleeping association and amount of nocturnal interactions clearly showed a stronger bond between AF1 and AM2. These two individuals had the highest amount of kernel home range overlap, the highest sleeping association index and met most often at night. Female AF2's relationship with both males was not so clear. Although there was a higher percentage overlap between AF2/AM5 than between AF2/AM2, this situation was reversed for sleeping associations (higher for AF2/AM2 than for AF2/AM5) and female AF2 met both males about as often at night. When looking at the most likely male-female associations when the group split up to sleep in pairs, we found that on ten days, the pairs sleeping together were AF1/AM2 and AF2/AM5 while the opposite association (AF1/AM5 and AF2/AM2) only happened once. We therefore conclude that there were indeed stronger bonds within the pairs of Group 1. Furthermore, up to two juveniles regularly associated with members of Group 1. As these juveniles most often slept and met with AF1 and/or AM2, we conclude that the two young are probably this pair's offspring. In other Cheirogaleidae, adult and juveniles sharing home ranges, frequently sleeping together and meeting or allogrooming at night, were also assumed to be parent and offspring (Fietz, 1999; Fietz, 2003a; Génin, 2008; Kappeler, 1997b; Kappeler et al., 2005; Lahann, 2007a; Lahann, 2008; Müller, 1998; Müller, 1999a; Müller, 1999b; Pagès, 1978; Wright and Martin, 1995).

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 testicles; contradicting the hypothesis of a family group social system as both males were sexually active and inbreeding would occur. In *C. medius*, *C. major* and *P. pallescens*, where a family group social system is present, the group is usually composed of one reproducing pair or of one male and two females (Charles-Dominique and Petter, 1980;

Fietz, 1999; Fietz, 2003a; Lahann, 2008; Müller, 1998; Müller, 1999a; Müller, 1999b; Schülke, 2002; Schülke and Kappeler, 2003; Schwab, 2000).

The intra-sexual relationships within Group 1 suggest potential stronger bonds between the two males than between the two females. Males shared a higher proportion of their kernel home range compared to females and met much more often at night. However, females slept together more often than males did and the group split to sleep in uni-sex pairs (AM2/AM5 and AF1/AF2) on 6 days but on at least two days where the two females slept together, the males slept separately; suggesting the female sleeping association is stronger. As for most other cheirogaleids, the intra-sexual relationships therefore remain to be resolved. Matriarchies have been confirmed in *M. murinus*, *M. berthae* and *M. griseorufus* (Dammhahn and Kappeler, 2005; Eberle and Kappeler, 2002; Eberle and Kappeler, 2006; Fredsted et al., 2005; Génin, 2008; Lahann, 2008; Martin, 1973; Radespiel, 1998; Radespiel, 2000; Radespiel et al., 2003a; Radespiel et al., 2003b; Wimmer et al., 2002); while both sexes disperse in *C. medius* (Müller, 1999a; Müller, 1999b)

In addition to the radio-collared individuals, I also captured an adult male (AM1 – Chapter 1, Table 1.2, Section 1.2.2) within Group 1's home range and observed an unknown adult individual sleeping with members of this group once. Because this individual's radio-collar was found 244 m South of where it was captured, within the home ranges of AF2 and AM5, and because it only slept with member of this group once, we suspect he is part of another unidentified neighbouring group living further South than Group 1. He could also be a 'floater male' (Charles-Dominique and Petter, 1980; Fietz, 2003a; Müller, 1998; Müller, 1999a; Müller, 1999b).

The two females of Group 2 slept together about every third day and so seemed less socially cohesive than members of Group 1. However, two unknown adults were observed to sleep with these two females once and their sociality could therefore be underestimated if these two individuals were also part of their social group. Up to two juveniles also associated with the two females of Group 2. When the females slept apart, only one juvenile was found with each female; suggesting they both had one offspring (see previous comment about how this has been assumed in other cheirogaleids). It is therefore possible that Group 2 actually had a similar composition to Group 1, with two adult males, two adult females and two juveniles however this remains to be confirmed and in either case, it was clear that these two females slept together much less often than those of Group 1 and that they most likely both reproduced.

Inter-group sleeping associations were rare and only occurred once between AF2, AF5 and AM2 and once between the females AF2 and AF4. As mentioned before, the adult male sleeping with members of Group 1 could also have been from a different group. There were also inter-individual variations in inter-group overlap. Although AM2, AF1 and, to a more limited extent, AF2 from Group 1 interacted with AF4 from Group 2; AF5 from Group 2 only had very limited home range overlap with AM2 and AF2 from Group 1; and AM5 from Group 1 had no inter-group overlap at all. There therefore seemed to be inter-individual variations in inter-group interactions with occasional visits of certain individuals to neighbouring groups. Although group-exclusive sleeping sites were used in *M. ravelobensis*, *C. medius*, *C. major* and *P. pallescens*, inter-group sleeping was never observed (Braune et al., 2005; Fietz, 1999; Lahann, 2007a; Müller, 1999a; Müller, 1999b; Schülke, 2002; Schülke and Kappeler, 2003). This means that either I was lucky to observe a rare event or that inter-group sleeping is more common in the hairy-eared dwarf lemur.

5.3.2 Spacing system

There were large amounts of inter- and intra-sexual home range overlap (Fig. 2.2 - Chapter 2, Section 2.2.2). Based on MCP home range overlap, each male had access to at least two females and one other male; and each female had access to at least one male and two other females. As only six individuals of the population were radio-collared; one male was captured within the home range of Group 1; at least one unknown adult associated with Group 1; and two unknown adults slept with Group 2; these numbers are most likely underestimated. It is more likely that each male had access to at least two females and two males; while each female had access to at least two males and two females. Although home ranges overlapped most between group members, occasional visits from neighbouring groups were possible. These values are much lower than for the promiscuous *M. murinus* where males overlapped with 2-19 other males, and 3-21 females while females overlapped with 1-18 males and 1-15 females (Eberle and Kappeler, 2002; Radespiel, 2000). In less promiscuous species, where mating probably takes place between familiar pairs, the spacing system resembles that of the hairy-eared dwarf lemurs more closely: in *M. griseorufus*, females overlapped with on average 2.8 males and males overlapped with on average 4.7 females (Génin, 2008); and in *M. ravelobensis*, males overlapped with 2 males and 2-3 females while females overlapped with 1.5-2.5 males and 2.5-3 females (Weidt et al., 2004).

5.3.3 Mating system

The lack of intersexual difference in home range size, as was the case for the hairy-eared dwarf lemur (Chapter 2, Section 2.3.2), does not necessarily imply a monogamous mating

system but could indicate preferential mating between a male and a female within the population. *Microcebus griseorufus* and *M. ravelobensis* had no significant sexual dimorphism and male home ranges were not significantly larger than the females, nor did they increase particularly during the mating season (Table 5.1). Although their mating system is labelled as promiscuous, because several males probably mate with several females and vice-versa, Génin (2008) highlighted the low promiscuity in *M. griseorufus* with familiar pairs mating and successful male mate guarding; and Weidt et al. (2004) suggested that the mixed-sex sleeping groups in *M. ravelobensis* could be a way for males to localise oestrus females and it is also possible that mating occurred between familiar pairs in this species. On the other hand, larger home ranges in males compared to females, especially during the mating season; a high testicular volume relative to body mass; and moderate to high female oestrus synchrony invariably predict high male scramble and sperm competition in a promiscuous mating system (e.g. *M. berthae*, *M. murinus* and *Mirza coquereli*) (Table 5.1).

As we were only able to follow six individuals from one complete- and one most likely partial social group, could not observe any sexual behaviour, and did not conduct analyses of paternity, we can only hypothesise on the potential mating system of the species. As has been shown previously, it was likely that stronger bonds existed between a particular male and female in hairy-eared dwarf lemur groups and this could explain the lack of inter-sexual home range size differences. However, inter-group interactions also occurred and males and females were therefore not limited to mating with their familiar partners. On the other hand, the close association of male AM2 with juveniles, suggested the presence of paternal care, which has so far only been proven in monogamous mating systems (e.g. *C. medius*) but could also be present in species where mating takes place between a familiar pair (e.g. *M. griseorufus*) (Fietz and Dausmann, 2003; Génin, 2008).

5.3.4 Social organisation

Based on our results, I hypothesise the following social organisation: the hairy-eared dwarf lemur most likely lived in dispersed multi-male/multi-female or multi-pair groups. We introduce the term 'multi-pair' based on the definition of 'multiple pairs' by van Schaik and Kappeler (1993) in which: "a group consists of multiple adults of both sexes that show a tendency towards pair-wise social bonds in addition to various intrasexual bonds; these pairs may also be preferential mates'. The basic social unit was the sleeping group, composed of one or two males, one or two females and their offspring. It is not yet clear whether these were male or female philopatric, although female philopatry seems more likely with a mother-daughter or sister pair and unrelated sexually mature males. Although these sleeping groups

shared large portions of their home ranges, regularly slept together and met at night and had a stable composition over time; they did not seem territorial. Inter-group interactions occurred, including affiliative sleeping associations, and no fighting wounds were observed. It is however possible that *A. trichotis*, like *C. medius*, defends small patches rather than whole home ranges and uses calls and/or scent marking to protect these (Müller, 1999a; Müller, 1999b). We suggest that the mating system of the species could be monogamous or slightly promiscuous; with mating usually between familiar pairs with long term bonds, but occasionally with other partners from neighbouring groups.

The social organisation of the hairy-eared dwarf lemur therefore resembles most closely that of *M. ravelobensis* where the social system is also a multi-male/multi-female group with two to five members (one to three males and one to three females) which regularly sleep together during the day in group exclusive sites but forage alone at night and coordinate their dispersal and reunion at the sleeping site (Braune et al., 2005; Radespiel et al., 2003a; Weidt et al., 2004). The spacing system is composed of inter- and intra-sexual overlapping home ranges where males have access to 2-3 females and 2 other males and females have access to 2-3 males and 2-3 females (Weidt et al., 2004). As mentioned before, the mating system can be labelled as promiscuous but mating most likely occurs between familiar pairs (Weidt et al., 2004).

5.3.5 Concluding remarks

More research is needed to clarify the social organisation of the species. A much larger sample size, additional home range studies, focused attempts to observe mating and genetic analyses to determine offspring parents and group member relatedness are needed. Long term studies of known individuals (e.g. using subcutaneous transponders) would be very useful to clarify inter-individual and inter-group relationships as well as dispersal patterns.

CHAPTER 6:

ACTIVITY AND SEASONALITY

6.1 Introduction

The Cheirogaleidae are exceptional among primates for their physiological response to periods of food scarcity during the colder drier season in Madagascar (Hemingway and Bynum, 2005; Wright and Martin, 1995). *Cheirogaleus spp.* in particular are extreme in their response and enter a six- to eight-month hibernation period after a severe fattening phase (Dausmann et al., 2004; Dausmann et al., 2005; Fietz and Ganzhorn, 1999; Hladik et al., 1980; Lahann, 2007a; Müller, 1999b; Wright and Martin, 1995). *Microcebus murinus* and *M. rufus*, on the other hand, are less extreme in their response and although a portion of the population can enter longer periods of torpor after fattening, some individuals remain active all year (Atsalis, 1998; Atsalis, 1999b; Fietz, 1998; Hladik et al., 1980; Randrianambinina et al., 2003; Rasoazanabary, 2006; Schmid, 1999). Which animals enter torpor or not and the timing and duration of lethargic phases can vary according to individual body mass and/or sex and according to annual climatic conditions (Atsalis, 1998; Atsalis, 1999b; Fietz, 1998; Randrianambinina et al., 2003; Rasoazanabary, 2006; Schmid, 1998; Schmid, 1999). Other mouse lemurs only use short periods of daily torpor (*M. griseorufus* and *M. ravelobensis*) (Génin, 2008; Randrianambinina et al., 2003). Torpor and hibernation enable important energy savings during periods of food scarcity (Schmid, 2000; Wright and Martin, 1995). Interspecific variations could be related to animal size, local differences in climate and/or food availability (Randrianambinina et al., 2003; Wright and Martin, 1995). *Mirza coquereli* and *P. pallescens* do not enter periods of torpor but switch their diet, focussing on insect secretions and tree exudates respectively, a more common response to periods of food scarcity in other primates as well (Hemingway and Bynum, 2005; Hladik et al., 1980).

All the Cheirogaleidae have a seasonal reproduction starting after the dry season with birth timed so that offspring start feeding when food availability is highest (Atsalis, 1998). In general, male body mass and testes size increase just before the onset of the reproductive season and males range further during the mating season (Atsalis, 1998; Fietz, 1998; Fietz and Dausmann, 2003; Kappeler, 1997b; Schmelting, 2000; Schmelting et al., 2000; Schmid and Kappeler, 1998). The cost of reproduction is obvious in *M. murinus* males and in both sexes of *C. medius* which lose weight during the mating season (Eberle and Kappeler, 2002; Eberle and Kappeler, 2004; Fietz and Dausmann, 2003; Schmelting, 2000). This is not the case for *M.*

murinus females which can continue to gain weight during the same period (Eberle and Kappeler, 2002). In species using hibernation or long periods of torpor during the dry season, males tend to emerge earlier than the females, most likely in preparation of the mating season (e.g. re-establish territories or male hierarchy) (Atsalis, 1999b; Müller, 1999b; Schmid, 1999). Polyestry, where a second mating phase can occur for at least some individuals of the population, could be the norm in mouse lemurs but has so far only been observed in two species: *M. murinus* and *M. rufus* (Blanco, 2008; Schmelting, 2000; Schmelting et al., 2000).

In this chapter we first present results on the climate of Andasibe during the study period. There is currently no long term weather data available for the region (Dolch, pers. comm.). We then present results from radio-tracking and direct observations to reveal the overall nocturnal activity (dispersal and reunion times, activity duration, and activity budget) and the seasonal variations in nocturnal activity and monthly home range size. Finally, we present results from captures to describe the seasonal variations in weight and the reproductive cycle. We discuss the seasonal activity and reproductive cycle of the hairy-eared dwarf lemur compared to other Cheirogaleidae, suggest how the species responds to the colder drier season, and propose timing for the main parts of the reproductive cycle.

6.2 Results

6.2.1 Climate

Our records show that the rainy season in 2007 lasted from January to March (Fig. 6.1). This was also the cyclone season and cyclone Indlala in particular reached Andasibe on 15-16 March 2007 and brought constant heavy rains (at some point around 25 mm/hr) and very strong winds. It caused heavy floods in the village and the forest and broke a main-access bridge in the Analamazoatra Special Reserve. The local ANGAP office closed the Special Reserve and National Park for several days because of the risk of falling tree or branches and to assess damage and start repairs. Temperatures during these three months varied between 18°C minimum and 30°C maximum (Fig. 6.2). April and May were intermediate months with 86 mm and 67 mm of rainfall respectively and temperatures ranging from 15°C to 28°C. June and July were the coldest and driest months with temperatures as low as 11°C and up to 24°C, and 18 mm and 15 mm of rain respectively. August and September remained cold and dry (temperatures: minimum 10°C, maximum: 26°C, monthly rainfall: 24 mm and 26 mm respectively). Although the weather became warmer again in October and November (the minimum temperature recorded early October was 11.5°C but 14°C later in October and 17°C in November; the maximum was 27°C in October and 30°C in November), it remained

relatively dry in October (monthly rainfall: 34 mm) and it was exceptionally dry in November (5.5 mm) although the rainy season usually started mid-November. Although no longer recorded, the weather remained hot and dry in December 2007 and the heavy rains only started end of December 2007, after we had completed our fieldwork.

Fig. 6.1: Variations in monthly rainfall in 2007

Data collected between January and November 2007 using a 50 mm rain-gauge. Although efforts were made to record the total amount of rainfall per month, this was not always possible because of heavy rainfall during the night, especially in February and March, when the rain-gauge could not be emptied on time and was overflowing. The true total rainfall for these months is therefore higher than presented. This is also the case for January because the records only started mid-January. Total rainfall amounts per months are accurate for all the other months. Note that the wet season lasted from January to March; that April and May were intermediate months; and that the weather was dry from June onwards (months considered 'dry' when monthly rainfall was under 50 mm). Although the wet season usually starts mid-November, November 2007 was an unusually dry month.

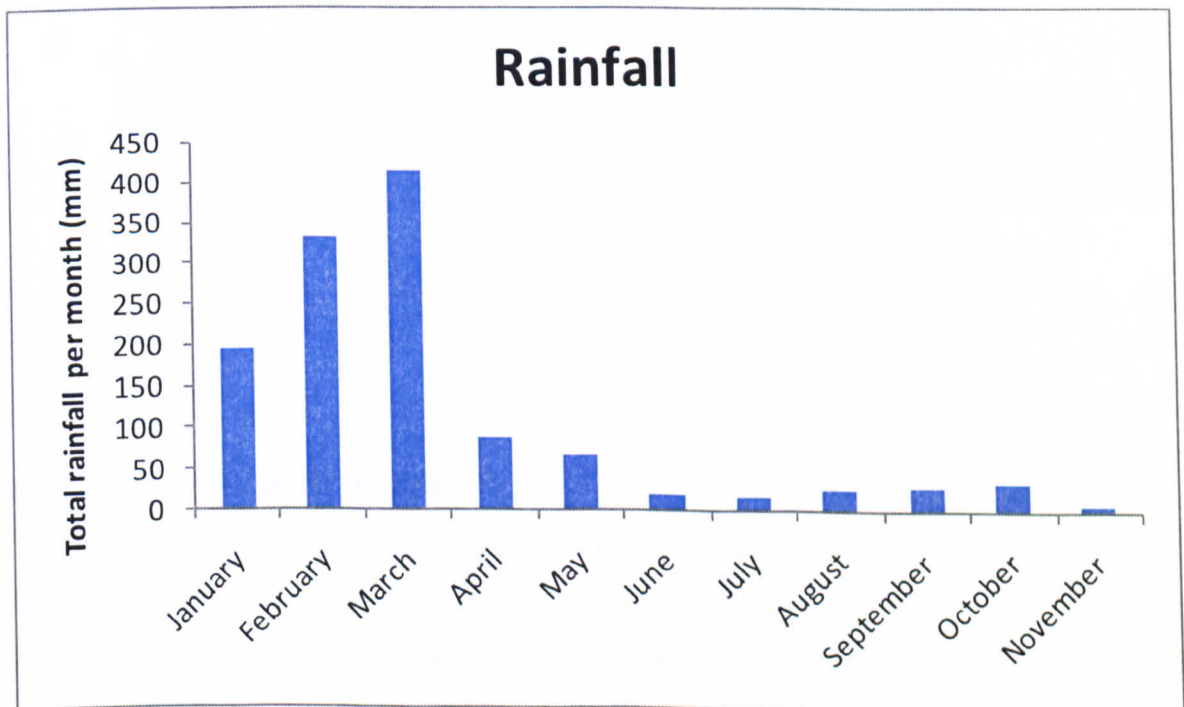
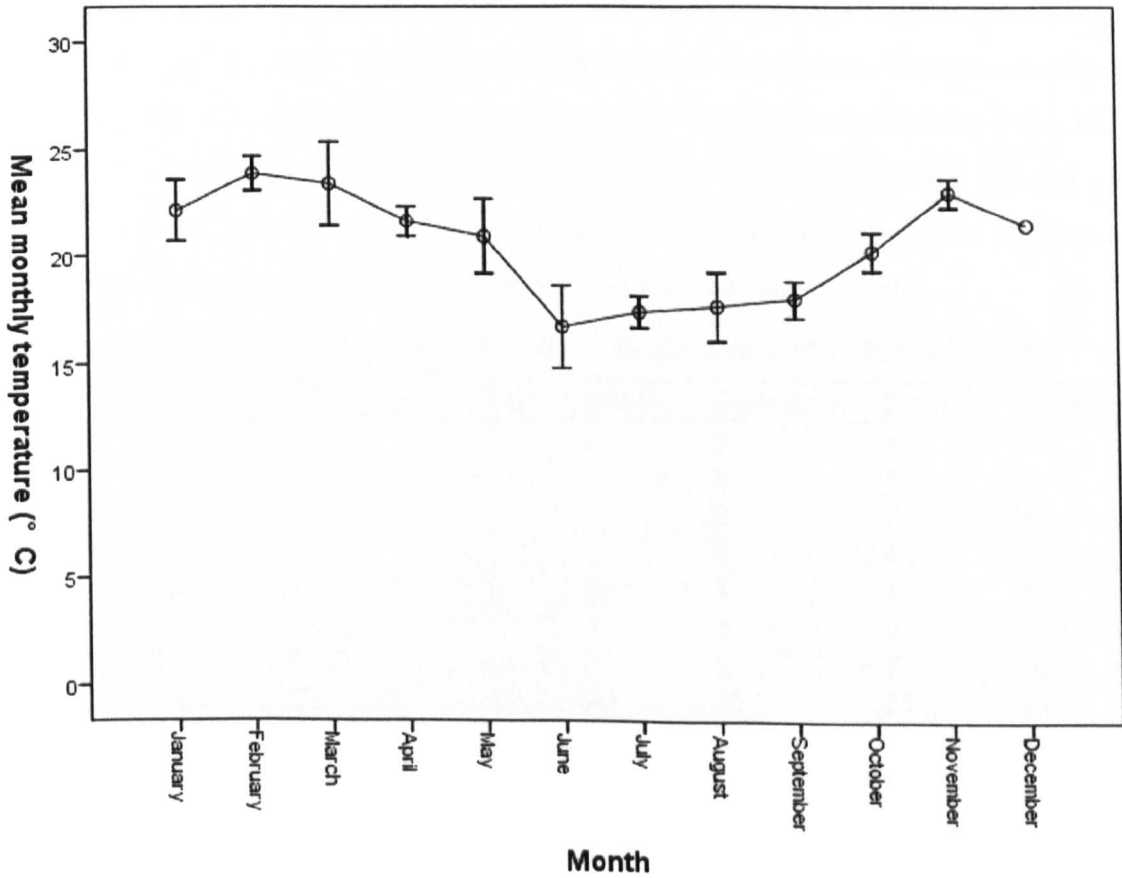


Fig. 6.2: Variations in monthly temperatures in 2007

The figure shows mean monthly temperature \pm standard deviation recorded for each month. Note that the mean temperature remains under 20°C between June and September and is above 20°C in other months. The hot season therefore lasted from January to May, the cold season from June to September, and the second warm season started in October.



6.2.2 Nocturnal activity period

We observed individuals leaving their nest on 186 occasions and entering their nest on 62 occasions (for detail of data collected see Table 6.1). Overall, animals left their nests between 2 min and 2 hr 22 min after sunset (mean: 44 min, median: 39 min, $n = 186$) and returned between 16 min and 3 hr 05 min before sunrise (mean: 1 hr 28 min, median: 1 hr 23 min, $n = 62$). Their total activity time was on average 10 hrs per night (mean: 9 hr 56 min, median: 10 hr 03 min).

Table 6.1: Details of the number of observations used to determine the nocturnal activity period of the followed hairy-eared dwarf lemurs

The tables show the number of observations of animals leaving (Table 6.1.a) or entering (Table 6.1.b) their nest per individual and per month. Unidentified individuals were either radio-collared adults whose identity could not be confirmed, non-radio-collared individuals, or juveniles. We were not able to observe animals leaving their nest in June. The lower number of observations in some months is mainly due to the lack of visibility for certain tree holes. More observation of animals leaving were recorded because we usually stayed near the nest until the focal animal left and were able to record other animals dispersing from the sleeping site while records of animals entering the nest was mainly the focal animal itself.

Table 6.1.a: Number of observations of animals leaving their tree hole at dusk.

ID	April	May	June	July	August	September	October	November
AF1	4	3		2	6	0	3	3
AF2	2	1		3	3	2	3	4
AF4						0	7	2
AF5						3	4	1
AM2	2	1		5	5	1	1	3
AM5	4	2		1	1	3	0	1
Unidentified	33	14		13	7	6	7	20
TOTAL	45	21	0	24	22	15	25	34

Table 6.1.b: Number of observations of animals entering their nest at dawn.

ID	April	May	June	July	August	September	October	November
AF1	0	3	2	4	5	1	0	2
AF2	0	2	1	1	2	1	2	2
AF4						1	2	3
AF5						1	2	1
AM2	0	1	2	2	4	1	0	2
AM5	0	1	0	0	4	0	1	0
Unidentified	1	2	0	1	1	0	0	1
TOTAL	1	9	5	8	16	5	7	11

Individuals left their sleeping sites on average earlier and earlier from April to October, from about one hour after sunset to less than 30 minutes after sunset (Fig. 6.3). They only left on average more than 30 minutes after sunset again in November. The range of dispersal times varied greatly. It decreased from April/May, reached a minimum in August, and then increased again until November. The earliest time animals left their nest remained under 30 minutes after sunset and only decreased slightly from May onwards to reach a minimum in October. The latest time individuals left their sleeping site was much more variable however. In April/May and again in November, animals left as late as 2 hours after sunset. However, in

August, most animals left their nest at the latest about 45 minutes after sunset. Exceptional cases where individuals had not left their sleeping site more than four hours after sunset were considered to be potential temporary torpor cases and are discussed below. Animals entered their sleeping site sooner from April onwards (Fig. 6.4). Between June and September, animals entered the soonest, between 1.75 and 2.25 hours before sunrise. Individuals then started to enter later again from September onwards. The nocturnal activity period decreased from April/May to October/November (Fig. 6.5). It was at a maximum in May (over 11 hours) and at its minimum in September (9.5 hours).

Fig. 6.3: Variation in the time after sunset at which individuals left their sleeping site

The minimum, maximum and medium times after sunset at which individuals left their nest was based on all the available data for all the followed animals (see Table 6.1.a for sample sizes). Note that no observations were made in June, explaining why this month is missing in the figure. Hairy-eared dwarf lemurs left their tree holes on average earlier from April to October. The range (difference between minimum and maximum) was much lower in the colder season, from July to October.

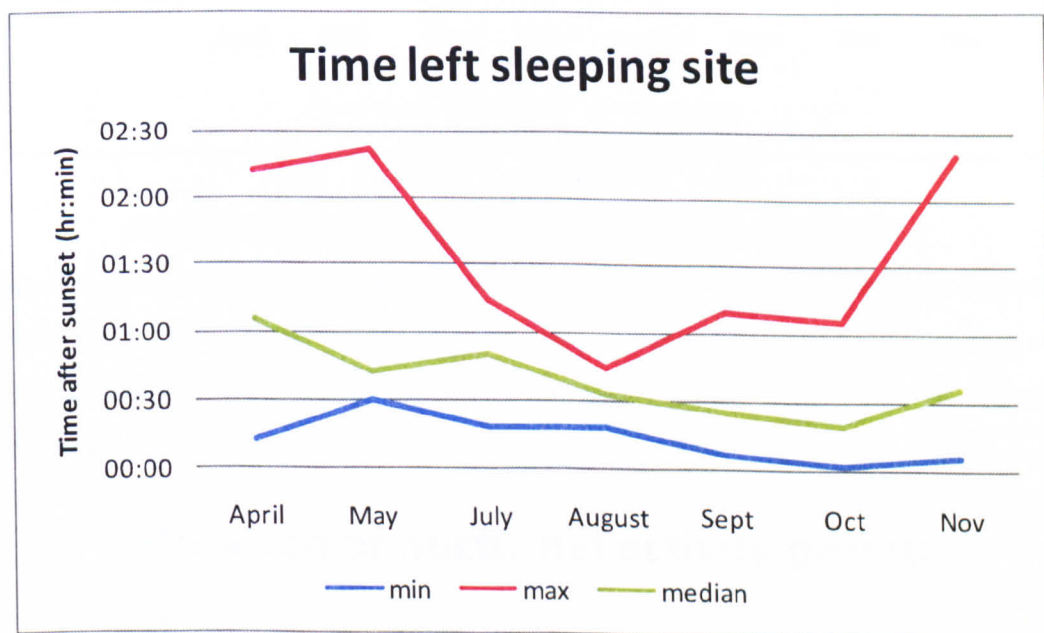


Fig. 6.4: Variation in the time before sunrise at which individuals entered their sleeping site

The minimum, maximum and medium times before sunset at which individuals entered their nest was based on all the available data for all the followed animals (see Table 6.1.b for sample sizes). Hairy-eared dwarf lemurs entered their tree holes on average sooner in the colder season, from June to September.

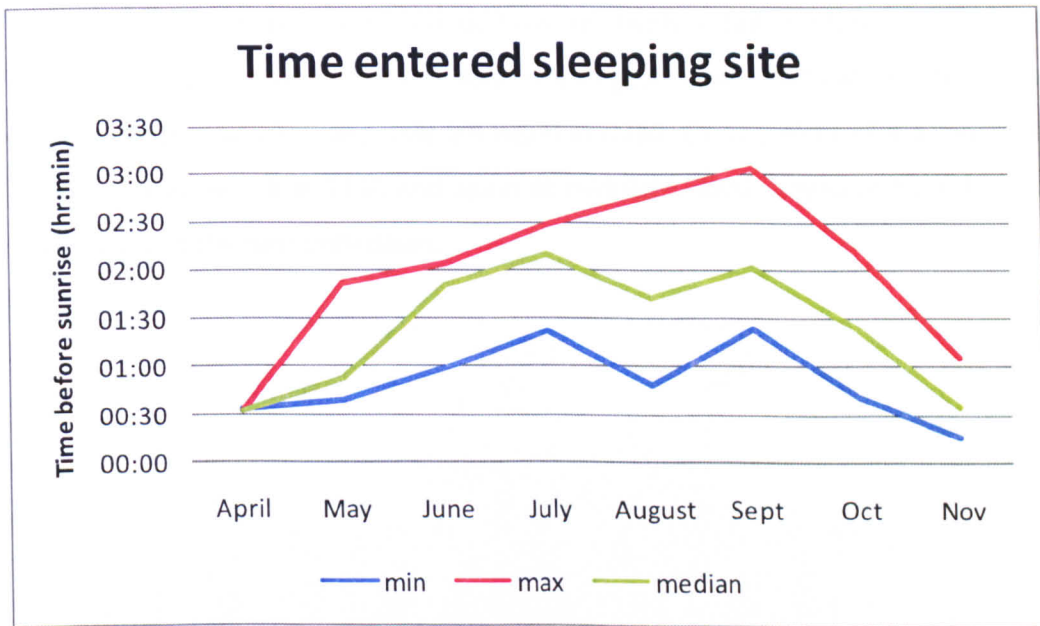
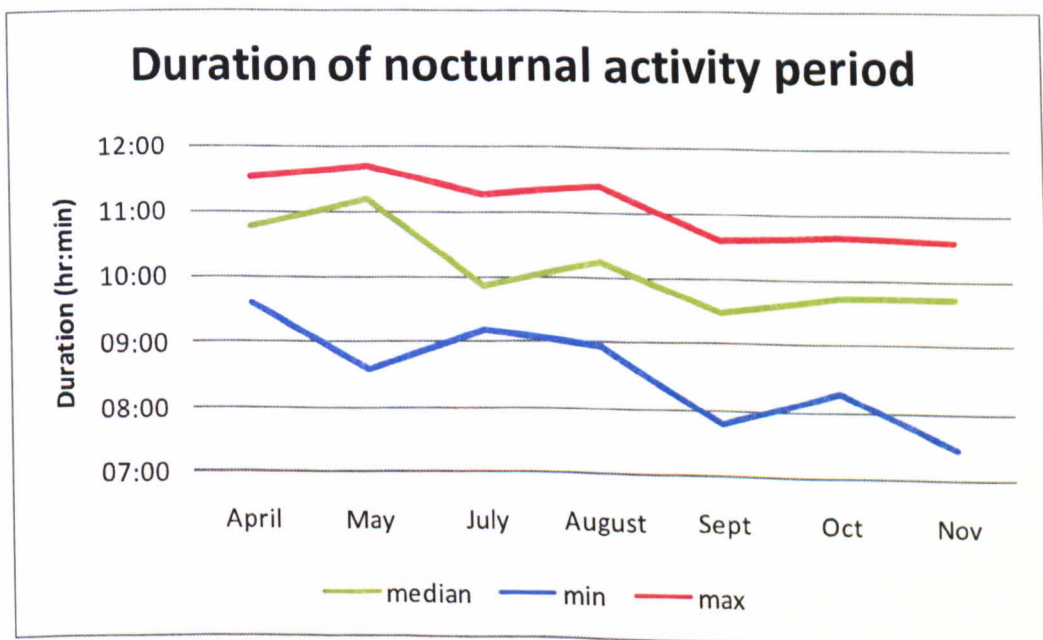


Fig. 6.5: Variation in the duration of the nocturnal activity period

The duration of the nocturnal activity period was calculated as the difference between the minimum, maximum or median times at which animals left and entered their nest each month, regardless of the animal's identity. The hairy-eared dwarf lemurs' activity time decreased from April to November.



Individuals returned to their sleeping site during the night throughout the study period but most often in July (Table 6.2). Although this behaviour was sometimes related to heavy rain, this was not always the case. We sometimes stayed near the sleeping site to see if the animal would come out. Animals did not leave their sleeping site in the 20 minute to four hour period during which we observed the nest. As we tended to follow other focal individuals to continue collecting data on their home range, it was not clear in most cases exactly how long individuals stayed in their nests and whether they had actually not left it at all or stayed in it until dawn from the moment they were located. We do have relatively detailed information however for two nights in July. On the night from 31 July to 1 August, male AM2 entered Nest 4, where AM5 was also staying, at 2210 and only left again at 0230. On the night of 3-4 July, AM2 and AM5 were found in Nest 4 at 2150 and again at midnight. AM2 stayed in Nest 4 until 0038 while AM5 stayed in the nest until dawn.

Table 6.2: Potential torpor periods

The table shows the number of times individuals returned to their tree hole during the night. Hairy-eared dwarf lemurs returned to their tree hole during the night most often in July.

	April	May	June	July	August	September	October	November
AF1		1		4		2	1	1
AF2			1	2	1		1	
AF4							1	2
AF5			2			1	1	1
AM2			3	4		1	4	
AM5	1			5	3			
TOTAL	1	1	6	15	4	4	8	4

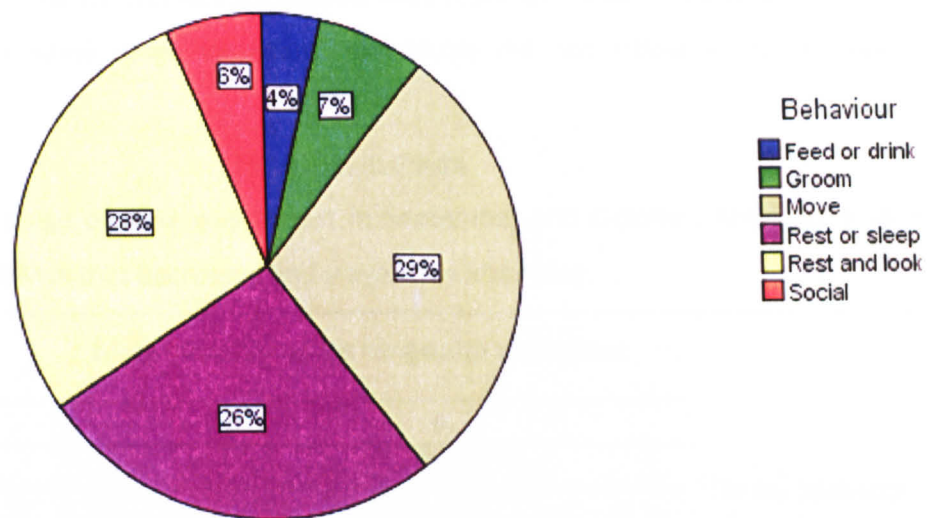
We used a stepwise multivariate linear regression including monthly means of nocturnal activity duration, start and end of activity in hours before and after sunset, nightlength, rainfall and temperature to identify correlations between night length, weather variables and activity. Mean monthly nocturnal activity duration was significantly correlated with monthly rainfall ($r^2 = 0.67$, $p = 0.025$, regression equation: $y = 0.018 x + 9.5$). There were no significant correlations between the start of activity and the chosen variables. The multivariate regression showed a significant correlation between the end of the activity period in time before sunrise and the mean monthly nightlength and temperature ($r^2 = 0.98$, $p < 0.01$, resulting regression equation: $y = -0.315 x - 0.247 z + 10.568$; x is nightlength and z is temperature). This means that animals increase the duration of their nocturnal activity in months with more rainfall and that they return to their nest sooner in months where nights are longer and temperatures are lower. We found no significant effect of any of the variables on the total number of monthly potential torpor periods.

6.2.3 Activity budget

Hairy-eared dwarf lemurs spend most of their activity time moving or resting while looking around or sleeping ($n = 800$ five-minute instantaneous scan samples)(Fig. 6.6). Other observed behaviours included feeding or drinking, grooming or social behaviours (i.e. allogrooming, playing or chasing).

Fig. 6.6: Activity budget

The percentage for each behaviour was calculated as the proportion of 5-min instantaneous scan samples for which each behaviour was observed, combined for all individuals. Feed or drink included observations where the animal was seen feeding or drinking. Grooming is self-grooming. Move can also include periods of foraging where an animal moved around high in the canopy and could have been hunting for flying insects or eating small fruits. Rest or sleep occurred when an animal was immobile and not looking around. Rest and look included frequent looking around and was most likely related to foraging or hunting. Social behaviours included allo-grooming, playing and chasing.



Moon phase did not influence behaviour. We used a chi-square test to evaluate the effect of moon phase (full, quarter or new) on behaviour (active or inactive – active including feed or drink, groom, move, rest and look and social; inactive including rest or sleep). We found no significant correlations.

6.2.4 Monthly home range

The mean monthly home range was 5.2 ± 3.0 ha for MCP (range: 0.2 to 12.9 ha) and 2.2 ± 1.6 ha (range: 0.2 to 6.6 ha) for kernel. Visual inspection of home range maps showed monthly home range shifts. Inter-individual variation in monthly home range size was large. Males AM2 and AM5 did not follow similar fluctuation patterns (Fig. 6.7.a). The home range of AM2 peaked in September-October. He made two excursions in late August and early September, to an area 400 to 500 meters North of his normal area of activity. Male AM5, on the other hand, had no such peak in home range size. His home range was largest in April-May, dropped until July, and then remained small (under 2 ha for MCP). Female home range sizes also followed different fluctuation patterns (Fig. 6.7.b). The home range of female AF1 was largest in April. It decreased in May and only increased slightly during the colder season (May to August). Her range decreased again in September and increased gradually until November. Female AF2

followed a different pattern. She often made excursions to an area 600 to 700 m Southeast from her closest sleeping hole, especially in May to August, which explains her larger overall home range compared to AF1 (see Chapter 2, Section 2.2.2). Her home range peaked in May and then again in September-October. It decreased gradually during the colder season, from May to August.

Fig. 6.7: Individual monthly home range size variations

Monthly home ranges were estimated as for the overall individual home ranges, using 100% MCP (Minimum Convex Polygon) and 95% kernel, using monthly locations (see Materials and methods, Section M.7.1 and M.7.8). Striped lines represent MCP home range variations; dotted lines kernel home range variations. Individuals did not follow similar fluctuation patterns.

Fig. 6.7.a: In males

The home range of AM2 was largest in September and October. AM5 had a larger home range in April-May that decreased and stayed low after May.

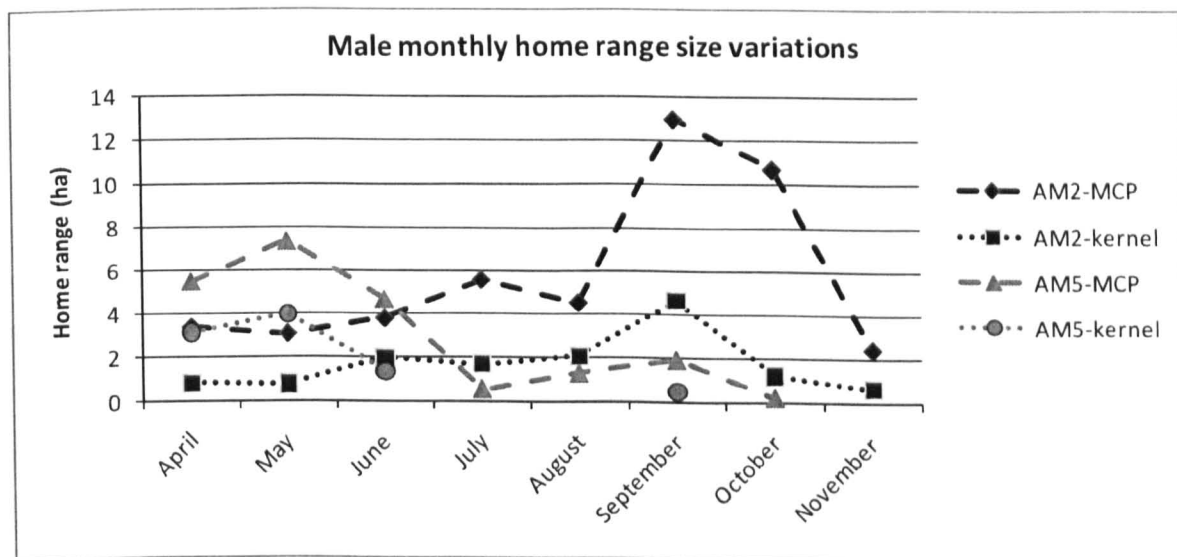
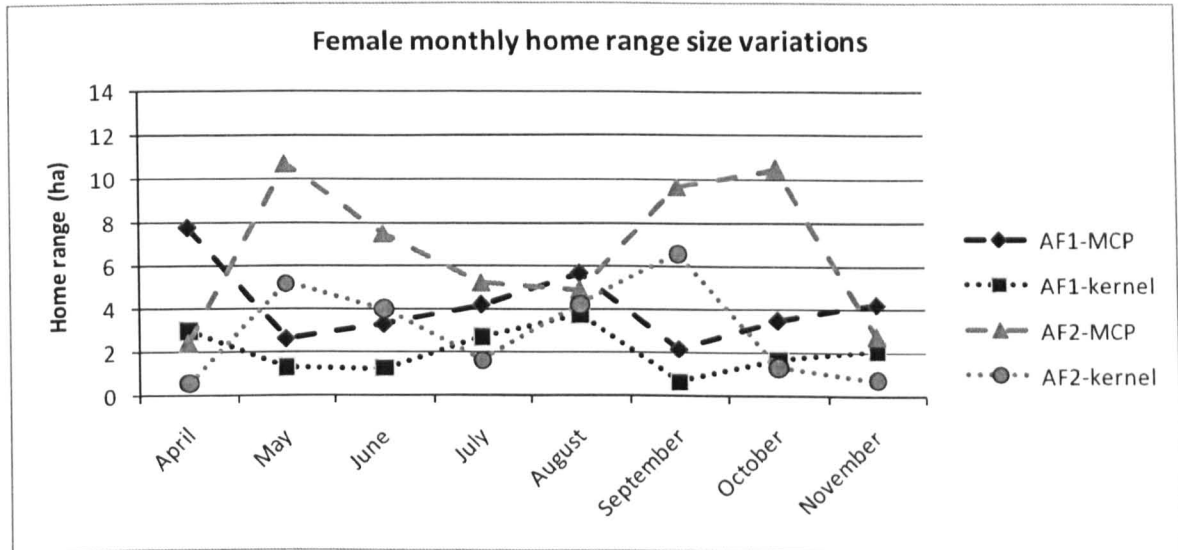


Fig. 6.7.b: In females

The home range of AF1 was largest in April, decreased in May and increased slowly during the colder season (May to August) before shrinking again in September and rising afterwards. 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.



6.2.5 Seasonal weight variations

Female AF1 was pregnant and heaviest in December. She lost 5 g (about 6% of her body mass) at the beginning of the dry season (weight in April: 87 g; in June and August: 82 g – Table 6.3). Female AF2 was also heaviest in April but lost about 16% of her body weight during the colder season, almost three times more than AF1 (weight in April: 82 g; in August: 69 g; a 13 g loss – Table 6.3). She also gained weight afterwards but was not pregnant in December (weight in December: 79 g, a 10 g gain, about 14% of her body mass – Table 6.3). Females AF4 and AF5 were caught for the first time in September and their weight did not vary much until their recapture and release late November or in December (Table 6.3).

Table 6.3: Weight variations in individual hairy-eared dwarf lemurs

Weights of all the captures are shown per individual. Females tended to lose weight in the colder drier season (between April and August, see AF1 and AF2) while male weights tended to increase in the same period (see AM2 and AM5). The high weight of female AF1 in December is related to her pregnancy. Females AF4 and AF5 were only captured in September.

ID	Weight (g)											
	March	April	May	June	July	August	September	October	November	December		
AF1		87		82		82						95
AF2		82				69						79
AF4							69					67
AF5							67		70			
AM2	74	82	76	74		81						78
AM5		82	80			82						91

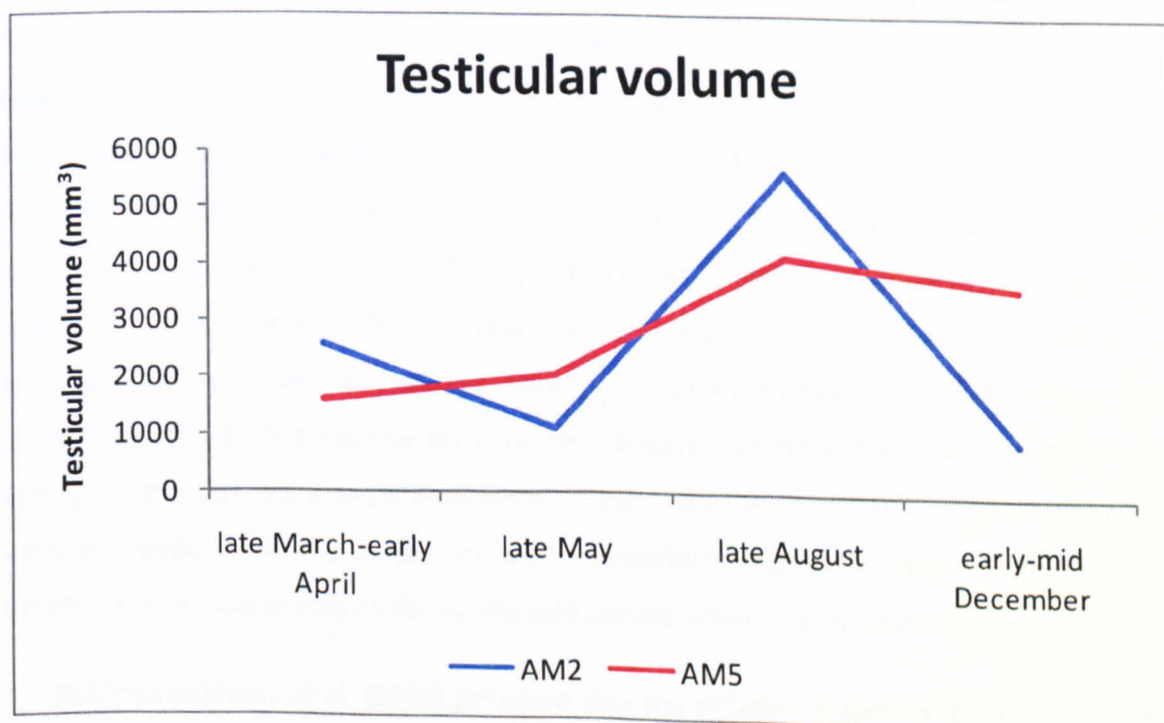
Male AM2 was heaviest in April and in August (82 g and 81 g respectively – Table 6.3). He was lightest in March and June (74 g). His weight varied most between March and April, between April and June, and between June and August (Table 6.3). He gained 11% of body mass between March and April (8 g), lost 10% between April and June (8g) and gained 10% again between June and August (7 g) (Table 6.3). Male AM5 was heaviest in December (91 g) and lightest in May (80 g) (Table 6.3). His weight stayed relatively stable between April and August but he gained 11% of his body mass between August and December (9g) (Table 6.3).

6.2.6 Reproductive cycle

Female AF1 was the only pregnant female in December. She was still lactating in April (I observed swollen nipples) but no longer in June. Male testicular volumes were highest for both males late August (Fig. 6.8). Large fluctuations were observed in male AM2. Between late March and late May, this individual's testicles regressed by 56%. They then increased five-fold to reach a peak in August and regressed again by 83% until mid-December (Fig. 6.8). The fluctuations in male AM5 were less pronounced. This male's testicles first increased by 29% between early April and late May; they then doubled to reach their largest volume late August and remained high until early December (only a small reduction of 12%) (Fig. 6.8).

Fig. 6.8: Seasonal variations in hairy-eared dwarf lemur male testicular volume

Testicular volume was calculated using the formula for the volume of an ellipsoid using the testicle breadth and width measurements taken for each capture (see Materials and methods, Section M.3 and M.7.8). Both males reached a maximum testicular volume in August.



6.3 Discussion

In 2007, the climate was hot and humid from January to March. The cold dry season lasted from June to September. April and May were intermediate months and October and November were warm but unusually dry. Usually, the rainy season lasts from mid-November to March (ANGAP, 2002). April and May are intermediate months with intermittent rainfall and frequent fog (ANGAP, 2002). June, July and August are the coldest months with frequent drizzle and the weather is mainly dry afterwards until mid-November (ANGAP, 2002).

In general, hairy-eared dwarf lemurs left within 45 minutes after sunset but returned 1.5 hours before sunrise. They spent most of their activity time either moving around or resting. During the drier colder season, hairy-eared dwarf lemurs continued to leave their sleeping sites soon after sunset but the range of the time of dispersal was much smaller and they tended to return to their sleeping sites much sooner. The duration of their nocturnal activity period thereby decreased from 11 hours in May to 9.5 hours in September. Although individuals did not enter hibernation like *C. medius* and *C. major* nor long bouts of torpor like *M. murinus* and *M. rufus*, they often returned to their sleeping sites during the night in the colder drier season and could therefore have been entering periods of daily torpor similar to *M. griseorufus* and *M. ravelobensis* (Atsalis, 1998; Dausmann et al., 2005; Fietz and Dausmann, 2003; Génin, 2008; Hladik et al., 1980; Lahann, 2007a; Müller, 1999b; Randrianambinina et al., 2003; Rasoazanabary, 2006; Schmid, 1999; Schmid and Kappeler, 1998; Wright and Martin, 1995). In some individuals, these lethargic phases could have lasted more than 24 hours (male AM5 could have spent one whole night and one whole day in its tree hole). The heavier males and females (with weights over 80 g in August) most likely used torpor more often and for longer periods. Inter-individual differences, where heavier individuals used longer periods of torpor, were also found in *M. murinus* and *M. rufus* (Atsalis, 1999b; Randrianambinina et al., 2003; Schmid, 2000). Although monthly home range size tended to decrease in the dry cold season, this was not the case for all hairy-eared dwarf lemurs as some increased their home range. *Microcebus berthae* females also remained active throughout the dry season and increased their locomotor and feeding activity, although their home ranges did not increase (Dammhahn, 2008). The monthly home range size increased in most individuals in September but again, this was not a unanimous trend. These trends were not related to weight nor to whether animals entered torpor or not. I therefore suggest additional inter-individual variations in survival strategies during the cold season, which remain to be identified.

Randrianambinina et al. (2003) proposed that the different responses to the colder drier season in different Cheirogaleidae could be related to species-specific adaptations adjusted to

the environmental conditions. They hypothesized that mouse lemurs of western and eastern Madagascar would undergo long periods of torpor because of lower minimum temperatures compared to north-western Madagascar, where mouse lemurs only use short bouts of daily torpor. The results of our study challenge this view. Although the sympatric *M. rufus* and *C. major* most likely enter longer periods of torpor, this does not seem to be the case in the hairy-eared dwarf lemur (Atsalis, 1998; Atsalis, 1999b; Lahann, 2007a; Randrianambinina et al., 2003; Wright and Martin, 1995). This difference could be related to diet. Torpor has been linked to fruit scarcity which is an important part of the diet of the first two species but not of the hairy-eared dwarf lemur, which could rely on its diet high in insects and tree exudates to survive the drier colder season (see Chapter 4) (Atsalis, 1998; Atsalis, 1999a; Ganzhorn, 1988; Lahann, 2007b; Wright and Martin, 1995). Additional research on seasonality in cheirogaleids of the East coast of Madagascar should enable more accurate comparisons and a better hypothesis on the source of these inter-specific variations.

As most other Cheirogaleidae, hairy-eared dwarf lemurs fattened-up before the colder drier season to reach a peak in April (Atsalis, 1998; Atsalis, 1999b; Fietz and Ganzhorn, 1999; Génin, 2008; Hladik et al., 1980; Müller, 1999b; Radespiel et al., 2006; Randrianambinina et al., 2003; Schmid, 1999; Schmid and Kappeler, 1998; Wright and Martin, 1995). This seasonal fattening was not as spectacular as in *C. medius* however (gain 88% of their body mass between December and April) as hairy-eared dwarf lemurs only gained up to 11% of their body mass in one month (e.g. AM2 from March to April) (Fietz and Ganzhorn, 1999). Females lost up to 16% of their body mass over the dry season (e.g. AF2) but this was not a general trend as AF1 only lost 6% of her body mass, and was much less pronounced than for other mouse lemurs (*M. murinus* females lost more than 30% of their body mass over the dry season; *M. berthae* females lost on average 23% of their body mass - (Dammhahn, 2008; Dammhahn and Kappeler, 2008a; Rasoazanabary, 2006; Schmid, 1999)). In *M. murinus*, females also lost weight during the dry season while males tended to gain weight or have no significant weight variations (Fietz, 1998; Rasoazanabary, 2006; Schmid, 1999; Schmid and Kappeler, 1998).

The increase in male weight (peak in August for AM2 and in December for AM5) and testicular volume (peak in August for both males, remaining high until December in male AM5); the larger monthly home ranges in most individuals in September; and the pregnancy of female AF1 in December; all point to the onset of the reproductive period in September. As male AM5's testes remained large until December and previous research suggested that male testes volume reached its highest two to four weeks before females start their reproductive cycle, I propose that the mating season lasted from October to December (Wrogemann et al., 2001). If gestation length is similar than in other Cheirogaleidae (52 to 62 days) I suggest that

the birthing season could have been between December and February (Atsalis, 1998; Génin, 2008; Gould and Sauther, 2007; Wrogemann et al., 2001). These periods fit with those proposed by Meier and Albignac (1991).

Concluding remarks:

Although it is clear that hairy-eared dwarf lemurs reduce their activity in the colder drier months, when nights are shorter and temperatures are lower; and increase activity during the rainy season; much work remains to be done on the activity cycle of the hairy-eared dwarf lemur. Further investigation and comparison of behaviour, activity and diet between the cold – dry and hot-wet seasons should be conducted. More detailed study of what triggers a return to the nest or a torpor phase on a night by night scale would also be interesting. Finally, physiological measurements as well as data on the temporal environment within nest would clarify whether animals really enter periods of torpor.

SUMMARY AND CONCLUSIONS

S.1 Summary

For this research project, we followed the hairy-eared dwarf lemur (*Allocebus trichotis*), a small nocturnal Data Deficient strepsirrhine primate (IUCN, 2008), using radio-tracking during a one-year study. Originally known from only five museum specimens, later believed to have a very restricted and patchy distribution, and currently proven to have a much wider distribution range, the hairy-eared dwarf lemur remains elusive and still very little is known about its behaviour in the wild (Garbutt, 2001; Goodman and Raselimanana, 2002; Meier and Albignac, 1989; Meier and Albignac, 1991; Mittermeier et al., 1994; Petter et al., 1977; Rakotoarison, 1998; Rakotoarison et al., 1997; Schütz and Goodman, 1998; Tattersall, 1982). From January to May 2006, we organised a pilot study aiming to locate a viable population of the species in Andasibe-Mantadia and Marojejy National Park. As we found individuals in the Analamazaotra Special Reserve and subsequently in the neighbouring Analamazaotra Forest Station, these forests became the focus of my one-year PhD project.

The main aim of this study was to clarify the behavioural ecology of the hairy-eared dwarf lemur to inform conservation needs. In particular, our objectives were to determine habitat use, social organisation and seasonal activity cycle.

We conducted field work between January and December 2007 in the Analamazaotra Special Reserve of Andasibe. The difficulty in capturing a first individual delayed the start of the radio-tracking phase until April 2007. We used bamboo-nose poles to capture a first individual and nets surrounding tree holes to capture sleeping groups. Captured individuals were sexed, weighed, measured, photographed and marked by tail-fur cuts. Adult animals were radio-collared and re-captured every two to three months. We used partial nocturnal focal individual follows covering all-times of the night to determine animal locations and behaviour; estimate MCP and kernel home range sizes and inter-individual percentages of overlap; describe home range use; calculate activity budget, timing and duration; and establish seasonal changes in activity and home range. We located radio-collared individuals in their tree hole during the day to determine sleeping site characteristics and use and sleeping group composition. We set up vegetation plots to estimate tree density, diameter- and genus composition, using point-quarter sampling; and microhabitat plots to describe habitat characteristics. We compared used and available trees. We collected monthly weather data

(minimum and maximum temperature and total rainfall). We assessed seasonal variations in individual body weight and reproductive cycle.

In total my team and I captured 11 individuals: three adult males, four adult females and four juveniles. Their overall appearance matched the description by Meier and Albignac (1991). Adult individuals weighed on average 77 g and measured 13 to 14 cm (head and body). Tails were 12 to 15 cm. Juveniles were smaller and lighter than the adults. There was no sexual dimorphism. We found that individual from the southern part of the species range (this study) tended to be lighter with a shorter tail than those from the northern part of the species range (Mananara and Marojejy: Meier and Albignac, 1991, Goodman and Raselimanana, 2002).

Based on inferences from previous studies (Table 2.1 – Chapter 2), we expected hairy-eared dwarf lemurs to have home ranges of 0.5 ha to 2.8 ha if their home ranges were related to their size and weight; to be over 1.5 ha if they had a diet high in invertebrates; and to be the same for males and females if they had a monogamous mating system. We followed four adults (two males and two females) for eight months, between April and November; and two females for three months, between September and November. Contrary to our expectations, individuals had much larger home ranges than other Cheirogaleidae. Our estimates were on average 15 ha for MCP and 5 ha for kernel. We found no differences between males and females. Individuals used shared feeding areas. Most social encounters and calls took place in areas of overlap. We propose that a highly insectivorous diet or the use of very patchily distributed gum-producing trees could be the cause of the large home ranges.

We located nine different tree holes in nine separate trees that were used as sleeping sites by the hairy-eared dwarf lemurs. Nests were generally away from the home range edge. Each focal animal used four or five different sleeping sites and shared these with conspecifics and occasionally with white-tailed tree rats (*Brachytarsomys albicauda*). Tree holes were in living trees from five different genera with diameters at breast height of on average 32 cm, at heights of on average 7 m, with hole entrances of on average 7 x 4 cm. It is not yet clear whether niche separation or competition is present between sympatric cheirogaleids of Andasibe but the inter-specific association between *A. trichotis* and *B. albicauda* seemed neutral or affiliative. The high nest fidelity and limited number of sleeping sites used could be a sign that tree holes are a limiting resource in the habitat. Tree holes could have anti-predator and thermoregulatory functions.

Hairy-eared dwarf lemurs spent most of their activity time in tree-crowns, on lianas and in tangles of vegetation; using mainly the small branch niche. They used a large range of forest

levels but were most often seen at five to ten meters height. Several tree genera used during nocturnal activity were used more than expected from their availability in the habitat (*Blotia*, *Symphonia* and *Rhodolaena*). *Allocebus trichotis* was gummivore-insectivore and tended to use the small branch niche of tree-crowns at median heights of 8 m to catch small moths and feed on gum on large tree trunks at median heights of 2 m. Trees were individuals foraged for insects included *Cryptocarya*, *Dichaetanthera*, *Weinmannia* and *Dracaena*. Gum feeding occurred on *Cryptocarya*, *Terminalia*, *Blotia*, *Symphonia* and *Cleistanthus*. Other gum producing trees in the habitat included the genera *Terminalia*, *Garcinia*, *Cleistanthus* and *Dichrostachys*. Most feeding trees, except *Symphonia* and *Cryptocarya*, were used more than expected from their availability in the habitat. The sizes of trees used for sleeping holes were rare in the habitat and all five genera were used more than expected from their availability alone. This strengthens our hypothesis that tree holes could be a limiting resource. The following tree families were used more than expected by their availability alone for at least two types of use: Euphorbiaceae (microhabitat and feeding), Melastomataceae (microhabitat and feeding) and Aquifoliaceae (nesting and feeding); and could be important resources for the hairy-eared dwarf lemur.

Based on home range overlap, sleeping associations and nocturnal encounters, we propose that the sleeping group is the basic social unit of the species. We suggest a dispersed multi-male/multi-female or multi-pair social system. The spacing system confirmed this grouping pattern but showed that inter-group interactions occurred, including affiliative sleeping associations, suggesting hairy-eared dwarf lemurs were non-territorial. Although much more research is needed, we hypothesise a monogamous or slightly promiscuous mating system, with familiar pairs with long term bonds mating most often and potential extra-pair copulations and young.

In 2007, the weather was hot and humid from January to March and the cold dry season lasted from June to September. Hairy-eared dwarf lemurs usually left their sleeping site within 45 minutes after sunset and returned 1.5 hours before sunrise. They spent most of their activity period moving and resting. During the colder drier season, they continued to leave their sleeping sites soon after sunset but the range of time of dispersal was much smaller. They tended to return to their sleeping site sooner. The duration of the nocturnal activity period decreased from 11 hours in May to 9.5 hours in September. Individuals often returned to their sleeping site during the night in the colder drier season and probably entered periods of daily torpor. Heavier individuals might have used torpor more than smaller individuals. General trends in monthly home range size variations were difficult to establish. Some individuals decreased their range in the colder drier season while others increased it. Most home ranges

were larger in September but again this was not a unanimous trend. We therefore suggest inter-individual differences in strategies related to survival during the cold season. Weight variations also were not universal. Most individuals fattened up before the colder drier season and reached a peak in April. Females tended to lose weight during the dry season while males gained weight and increased testicular volume, most likely in preparation for the reproductive season in September. Based on monthly variations in home range size, individual weights, male testicular volumes, and female pregnancy; we propose that the mating season lasted from October to December with births between December and February.

S.2 Recommendations for conservation

Our results clearly show that hairy-eared dwarf lemurs need a much larger home range than other cheirogaleids do (Chapter 2), and this should be taken into account in conservation management. To estimate the minimum number of individuals potentially living in the Analamazaotra Special Reserve, we used the group home range estimate because there is a large amount of overlap between individuals of Group 1. We 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. We estimated 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, we used the smallest available home range value, which is the mean individual kernel home range estimate (5.4 ha). In this case, we expect a maximum of 150 adult individuals ($810 \div 5.4 = 150$). 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 about 100 individuals and explains why *A. trichotis* is so much harder to find than *Microcebus* spp. or *Cheirogaleus* spp. because it has much lower population densities (about 11-19 individuals/km²). In comparison, densities of the sympatric *C. major* and *M. rufus* have been estimated at 75-110/km² and 110/km² respectively (Fietz, 2003b; Kappeler and Rasoloarison, 2003).

As our results suggest that specific habitat needs could be the cause of large home ranges, in particular the use of patchily distributed feeding trees or a limited number of suitable nesting trees, conservation management strategies should ensure the maintenance of large trees used for nesting and feeding, in particular belonging to the families Euphobiaceae, Melastomataceae and Aquifoliaceae. 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. Potential important feeding resources, like gum feeding trees, should also be maintained and additional research should focus on the dietary needs of the hairy-eared dwarf lemur and aim to identify potential keystone resources used especially during the drier colder season. Finally, studies comparing diet, behaviour, activity and habitat use between the dry and wet season should be conducted to inform the survival strategies of this species during periods of food scarcity and low temperatures.

As the hairy-eared dwarf lemur has recently been re-classified as Data Deficient (IUCN, 2008), it is crucial to continue efforts to assess its conservation status. Surveys should aim to locate the species and determine its density and distribution range. Only once this has been accomplished, will it be possible to conduct behavioural ecology studies in other sites and compare between populations.

S.3 Conclusions and further research

Although this study presents crucial data on a rare nocturnal species, the overall small sample sizes limit the assurance of its conclusions. Results were based on only one probably complete and one partial sleeping group, totalling only six individuals. This is mainly due to the difficulty in finding and capturing hairy-eared dwarf lemurs and could be due to their low population density (about 11-19 individuals/km², see above). Only four individuals were followed for a long period. Direct behavioural observations were very difficult due to the dense canopy cover, the small size of the animals and their nocturnal habits, resulting in small sample sizes, in particular on feeding events. It is therefore clear that much more research is needed to clarify the population structure, habitat needs, social organisation, behaviour and seasonality of the hairy-eared dwarf lemur.

Although we have shown that hairy-eared dwarf lemurs need large home ranges, the reasons for this are not yet clear. Further research should investigate further investigate the effect of diet and weather variables. These large home ranges could be due to specific habitat needs, e.g. diet, nests. We have shown that the species is mainly gummivore-insectivore and that they only use a limited number of sleeping sites. Furthermore, they occasionally share these sites with other species. This has led us to suggest that nesting trees could be limited in the environment. A better understanding of the reasons for using tree holes with specific characteristics would also help in understanding the needs of the species. It is however clear that hairy-eared dwarf lemurs live in family groups and that nest are an important meeting point. Further studies on the behaviour in the nest using infrared camera's for example, could clarify the social structure as well as the reproductive activity of the species. We only found

one pregnant female in December and notices seasonal variations in male testes size but could not determine the exact mating season. A longer study, especially covering more of the rainy season, would be invaluable for comparison with this study where observations mainly took place over the dry season and only the beginning of the wet season.

Because this species is very difficult to locate and capture, we 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. The hairy-eared dwarf lemur is also known to occur in other forest of the area (Mantadia National Park, Analamazoatra Forest Station and Maromiza forest) (pers. obs.; N. Garbutt pers. comm., K. Marquart 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 intra-group interactions.

Although most studies have focused on Cheirogaleidae of the West coast of Madagascar, this study and others (Atsalis, 1998; Blanco, 2008; Deppe et al., 2008; Louis et al., 2006a; Randrianambinina et al., 2003) have proven that it is possible to study small nocturnal strepsirrhine primates in the eastern rainforests of Madagascar. Continuing discoveries of new mouse and dwarf lemur species will continue to increase the number of Data Deficient species which might be in dire need of conservation (e.g. *Microcebus margotmarshae* and *M. arnoldhi*: two recent additions to the long list of new species: Louis et al., 2008). It is no longer acceptable to focus on describing new species without initiating thorough behavioural ecology studies. Indeed, what is the point of naming a species if it is about to disappear due to lack of knowledge of its specific habitat- and conservation needs?

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