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“Eco-ethology of the red collared brown lemur (*Eulemur collaris*): comparison between groups living in well preserved and degraded littoral forest fragments, in South-eastern Madagascar”

Relatori:

Prof.ssa Silvana Borgognini

Prof. Giuseppe Donati

Candidato:

Marco Campera

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ABSTRACT

The red collared brown lemur, *Eulemur collaris*, is a cathemeral lemur with an extraordinary ecological flexibility that allows this lemur to live in almost every forest type in Madagascar. The littoral forests of southeastern Madagascar are among the most endangered habitats in the world, and *Eulemur collaris* is well adapted to live in these forests. The red collared brown lemur is mostly frugivorous, and it is an important seed disperser for a large number of plant species.

Our goal was to study ecological and behavioral differences between groups of collared brown lemurs living in a more intact and in a more degraded forest fragment. For this, two groups in Mandena (a more degraded fragment) and two groups in Sainte Luce (a more intact fragment) were studied for 7 months. Each month, we collected data during 4 days per group and 1 night per site, from 06:00 to 18:00 for diurnal and from 18:00 to 06:00 for nocturnal sessions. We collected data on habitat use, activity patterns, feeding behavior, behavioral thermoregulation and social structure.

Overall, lemurs at Mandena had a lower group size, had greater home ranges, spent more time resting and used more energy-saving behaviors compared to lemurs at Sainte Luce.

CHAPTER 1

GENERAL INTRODUCTION

1.1. The red collared brown lemur, *Eulemur collaris*.

The red collared brown lemur, *Eulemur collaris* GEOFFROY 1817, is a strepsirrhine primate, belonging to the family Lemuridae. It was previously classified as one of the six subspecies of *Eulemur fulvus*. Subsequently, Groves (2001) elevated all former *E. fulvus* subspecies (*albifrons*, *albocollaris* (now *cinereiceps*), *collaris*, *fulvus*, *rufus* and *sanfordi*) to full species.

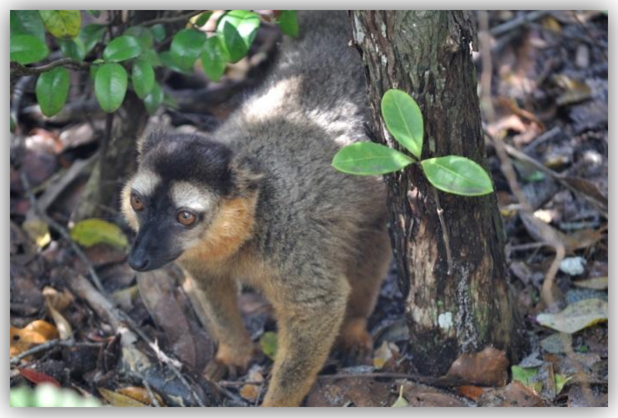


Fig 1.1: Male red collared brown lemur (*Eulemur collaris*), Sainte Luce.
Photo by Marco Campera.

Eulemur collaris is a medium-sizes lemur with a head-body length of 39-40 cm, a tail length of 50-55 cm, an overall length of 89-95 cm, and a body weight of 2.25-2.5 kg (Tattersall, 1982). This species is sexually dichromatic. In males the dorsal coat is brownish-gray, the tail is darker, and there is also a dark stripe along the spine. The ventral coat is a paler gray. The muzzle, face and crown are dark gray to black. The creamy to rufous-brown cheeks and beard are thick and bushy, while the creamy to gray-colored eyebrow patches vary in their prominence. In females, the dorsal coat is browner or more rufous than that of the male. The ventral coat is a pale creamy-gray. The face and head are gray. The cheeks are rufous-brown, but less prominent than in males. Both sexes have orange-red eyes (Mittermeier *et al.*, 2010).

Fig 1.2: Female red-collared brown lemur (*Eulemur collaris*), Mandena. Photo by Marco Campera**.** We can see the gray face and head, and the cheeks less prominent than in males.

The color pattern of the red-collared brown lemur is similar to that of *Eulemur cinereiceps* (present valid name of *E. albocollaris*, Johnson *et al.*, 2008). Male *E. collaris* can be distinguished from male *E. cinereiceps* by their beards, those of the former being cream-colored or rufous while those of the latter are white. Female *E. collaris* are virtually indistinguishable from female *E.*

cinereiceps. Recent genetic analyses support full species status for both taxa (Djletati *et al*., 1997; Wyner *et al*., 1999).

This lemur is found in tropical moist lowland and montane forests in southeastern Madagascar , from Tolagnaro (Fort Dauphin) north to the Mananara River (Fig. 1.3). The western limits of this range are the forests of the Kalambatritra region, including the Kalambatritra Special Reserve. The Mananara River serves as a boundary between the ranges of *E. collaris* and those of *E. cinereiceps*, except for an isolated population at Midongy du Sud National Park (Irwin *et al*., 2005) and another at Vohipaho, near Vangaindrano (Mittermeier *et al*., 2010). Even if the typical habitat of this lemur is the mountain rain forest, they can also inhabit the humid littoral forests. In fact, we can find this lemur in the Mandena Conservation Zone and in the Sainte Luce Private Reserve.

Fig. 1.3: Distribution of Eulemur collaris (in red).

The red collared brown lemur is the largest lemur species of the humid littoral forests of South-Eastern Madagascar (Donati *et al*., 2007a), where it can be considered as the main seed disperser for many plant species (Bollen and Donati, 2006). Indeed, this lemur is the only frugivore in this forests able to shallow and thus to disperse large seeds, up to 16.5 mm (Ganzhorn *et al.*, 1999; Bollen *et al.*, 2004).

The littoral forests around Tolagnaro are under substantial pressure to meet the daily needs of the local human population (Bollen and Donati, 2006). Hunting also threatens the survival of *Eulemur collaris*, and can lead to a local extinction without appropriate conservation measures. This could entail the eventual loss of plant species that are dependent on this lemur for seed dispersal.

This species is mainly frugivorous but it shows a great dietary flexibility, feeding also on leaves, flowers, mushrooms, petioles, roots, gums and invertebrates in variable proportions depending on forest phenology and food availability (Donati *et al*, 2007a; Donati *et al*, 2011). The species is cathemeral (active both day and night throughout the year), a trait seen in other members of the genus (Curtis and Rasmussen, 2002; Kappeler and Erkert, 2003; Schwitzer *et al.*, 2007a). Multimale–multifemale groups of *E. collaris* have been observed in the wild (Donati, 2002; Donati and Borgognini-Tarli, 2006; Donati *et al.*, 2007a; Donati *et al.*, 2010; Donati *et al.*, 2011), but social structure is still poorly understood and the literature available only concerns other species of the genus *Eulemur* (Sussman, 1974; Overdorff, 1998; Pereira and McGlynn, 1997; Wimmer and Kappeler, 2002; Ostner and Kappeler,2004; Marolf *et al.*, 2007). Females give birth to one or two offspring between September and October. The 2008 IUCN Red List assessment classified *E. collaris* as *Vulnerable* (VU A2cd). The principal threats are habitat loss due to slash-and-burn agriculture and charcoal production, hunting for food, and capture to supply local pet trades (Raharivololona and Ranaivosoa, 2000).

1.2. The littoral forests of south-eastern Madagascar.

Madagascar is considered an important global conservation priority because of the high endemicity of its flora and fauna (Mittermeier *et al.*, 1999) and the severe threats to the island's environment. In 1985, 3.8 million hectares of rain forests remained, representing only 50 percent of the 7.6 million hectares existing in 1950, and 34 percent of the estimated original extent (11.2 million hectares). Between 1950 and 1985, the rate of deforestation averaged 111 000 hectares per year (Green and Sussman, 1990) (Fig 1.4).

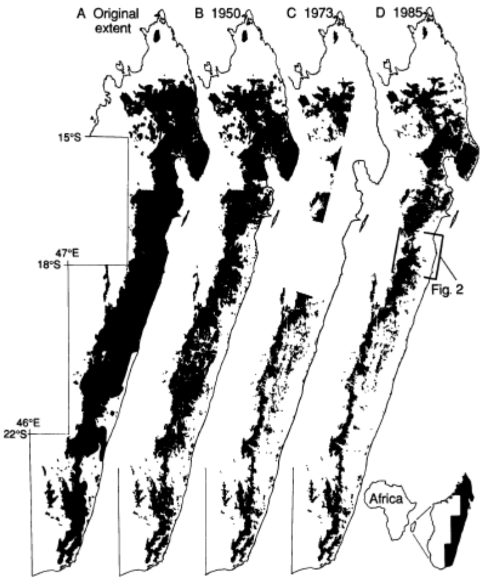


Fig 1.4: Maps of distribution of rain forest in eastern Madagascar through time (Green and Sussman, 1990)**.**

Prior to human occupation, humid and sub-humid littoral forest covered approximately 461 000 ha (0.8 percent of the total land surface of Madagascar), of which only about 47 900 ha remain today, with a habitat loss of 89.7 % (Consiglio *et al.*, 2006). Thus, from the original littoral forest, only 10.3 % remains in the form of little forest fragments, and only 1.5 % of these are included within the existing protected areas network (Vincelette *et al.*, 2007c). In particular, the littoral forest on sandy soil of south-eastern Madagascar is one of the most threatened ecosystems on this island. By 2005, the Tolagnaro region (Fig 1.5) littoral forests were heavily fragmented and covered only 3128 ha, distributed in 289 blocks varying in size from 0.06 ha to 252.4 ha (Vincelette *et al.*, 2007c). In the Fort Dauphin (Tolagnaro) area the remaining littoral forests on sandy soil form three groups of fragments: Petriky, Mandena and Sainte Luce.

Fig.1.5. Anosy region (in red) and Tolagnaro.

The littoral forest ecosystem is restricted to unconsolidated sand in a narrow coastal band, extending along Madagascar’s east coast from north of Vohimarina to just southwest of Tolagnaro (Consiglio *et al.*, 2006). This forest has aseasonal rainfall and strongly seasonal patterns in flushing, flowering, and ripe fruiting. Intra-annual differences occur in phenophases leading to periods of abundance and scarcity (Bollen and Donati, 2005).

1.3 The role of QMM

QIT Madagascar Minerals (QMM) is a company jointly owned by Rio Tinto (80%) and the Malagasy State (20%) represented by the *Office des Mines Nationales et des Industries Stratégiques de Madagascar* (OMNIS).

QMM is an ilmenite mining project. Ilmenite contains titanium dioxide, used principally as a raw material in the manufacture of white pigment. From 1985, QMM began an extensive exploration program along the eastern coast of Madagascar to locate deposits of heavy mineral sands containing titanium dioxide. Major mineral sediments were found in Mandena, Petriky and Sainte Luce, underneath southeastern Madagascar's largest remaining stands of littoral forest (Lowry *et al.*, 2008). As the mining project was developed, a series of studies commissioned by QMM demonstrated the importance of the region's biodiversity (e.g. Ganzhorn *et al.*, 2007), that cannot be lost and require appropriate conservation plans.

Mining at the first of the three sites (Mandena) started in 2009; the lifetime of the project is expected to be around 40-50 years.

"The region in which QMM works is recognized and valued globally for its rich and unique biodiversity. As a member of the Rio Tinto group, QMM has made a commitment to have a Net Positive Impact on biodiversity." (Biodiversity Action Plan 2010-Rio Tinto QMM).

To achieve a Net Positive Impact on biodiversity, the goal of QMM is to minimize the mine's negative impacts on biodiversity and create a model project for investment compatible with biodiversity conservation. The aim of Rio Tinto is to avoid harm to biodiversity where possible, mitigate impacts, restore and rehabilitate areas that have been affected by mining, and offset residual negative impacts on biodiversity by protecting species and reducing rates of habitat loss in areas outside the mining zone.

Avoiding impacts is the priority of QMM Biodiversity Action Plan. An avoidance area where no mining will take place has been legally designated and agreed with local communities and the Malagasy government for all three prospective mining sites as part of the EMP (Environmental Management Plan, 2002). These are currently managed to protect habitats, species and biodiversity-based livelihoods. This avoidance areas is called "Conservation Zones", and Rio Tinto established three zones (Fig 1.6):

- The Mandena Conservation Zone (230 ha), established in 2000, that represents the last remaining significant tract of littoral forest in this area, the rest having been lost or heavily degraded by subsistence charcoal makers over the past 20 years. In Mandena an ecological center and a tree plantation nursery are present.
- The Sainte Luce Conservation Zone (274 ha), established in 2005, set up with local communities *dinas*.
- The Petriky Conservation Zone (120 ha), established in 2008.

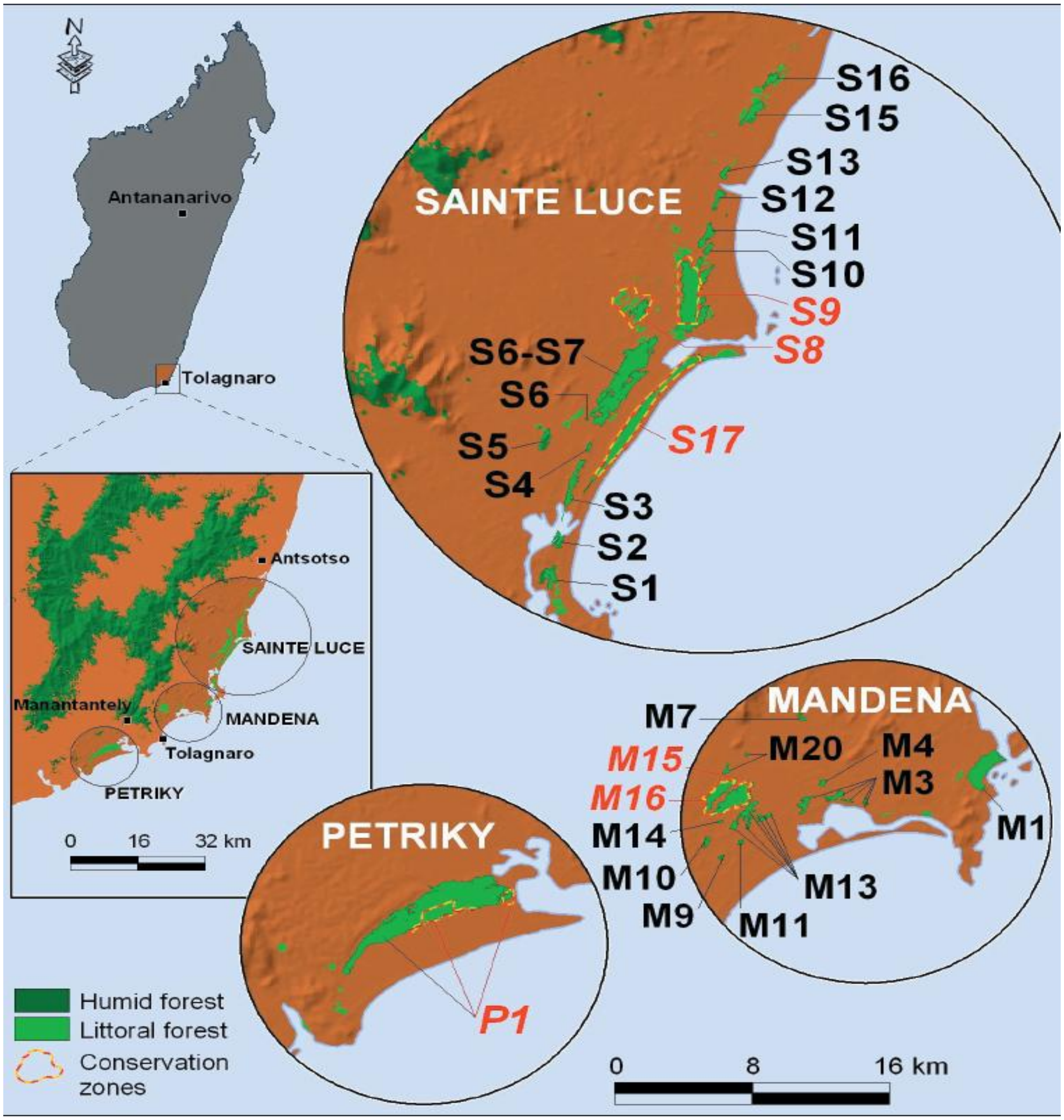


Fig. 1.6: Conservation zones. Maps of the Sainte Luce, Mandena and Petriky areas in south-eastern Madagascar, indicating the location of major littoral forest parcels (light green), including those that comprise the established conservation zones at the two sites (dashed red and yellow lines), (Lowry *et al*., 2008).

CHAPTER 2

THE AIM OF THE STUDY

One of the imperative goals of conservation biology is to determine how animals react to the increasing rate of habitat degradation. Response to degradation seems to be highly variable depending on primate species and habitat type, so that no clear generalization seems to be possible (Cowlishaw and Dunbar, 2000; Onderdonk and Chapman, 2000). As a general rule, folivorous primates seem to cope better with habitat degradation since secondary growth may produce higher food quality, i.e. higher protein and lower fiber content, than mature forest (Ganzhorn, 1995; Plumptre and Reynolds, 1994; Chapman *et al.*, 2002). By contrast, frugivorous primates may find more problems due to the fluctuating spatial and temporal food distribution, the need to obtain proteins and minerals from alternative food and their higher home range requirements (Estrada and Coates-Estrada, 1996; Lovejoy *et al.*, 1986; Rode *et al.*, 2006). However, plant-frugivore interactions are important components of the complex forest communities, and seed dispersion by vertebrates is a key process in vegetation dynamics and recovery (Wallace and Painter, 2002). Frugivores play a vital role in the maintenance of biodiversity in tropical forests, where they constitute a large proportion of the vertebrate biomass (Fleming *et al.*, 1987), and zoochorous tree species make up the bulk of tropical plant species (Howe and Smallwood, 1982). Loss of fruit-frugivore interactions can thus have profound consequences (Corlett, 1998).

In Madagascar, lemurs have been shown to be important seed dispersers (Birkinshaw *et al.*, 2002; Dew and Wright, 1998; Ganzhorn *et al.*, 1999; Overdorff and Strait, 1998; Ralisoamalala, 1996; Scharfe and Schlund, 1996), in particular since the guild of frugivorous birds and bats is poor in this island as compared to other continents (Fleming *et al.*, 1987; Ganzhorn *et al.*, 1999). *Eulemur collaris* is particularly important for the dispersal of the seeds of numerous plant species in the littoral forests of South-eastern Madagascar (Bollen *et al.*, 2004). It is probably the last of the remaining large-bodied frugivores in these littoral forests that is capable of ingesting large-sized seeds, thus matching the situation of brown lemurs in some malagasy dry deciduous forests (Ganzhorn *et al.*, 1999).

In a co-evolutionary perspective, there are five species of plants that apparently are dispersed exclusively by *Eulemur collaris*, namely *Canarium boivinii*, *Diospyros sp.*, *Eugenium sp.*, *Hyperacanthus mandenensis*, *Cinnamosma madagascariensis var. namoronensis* (Bollen *et al.*, 2004). Their fruits are significantly heavier and longer (up to 30 mm seed length) than the fruits of other plant species living in the same forests. Even though red-collared brown lemurs often drop the seeds under the parent plant, occasionally seeds are swallowed and defecated or dropped some distance away from the parent plant. Thus, in terms of conservation, these relationships are of crucial importance to preserve the integrity of the littoral forest.

Figure 2.1: Bibi, a juvenile male of group B at Sainte Luce. Photo by Marco Campera

As Malagasy forests become more fragmented the remaining patches become increasingly isolated and inaccessible to arboreal lemur species (Ganzhorn *et al.*, 2001). Large frugivores are often the most vulnerable to habitat fragmentation (Kannan and James, 1999) and this is the case for *E. collaris* in Sainte Luce, where the species is only present in the largest fragments, S9 (377 ha) and S17 (237 ha), two of the last remaining areas of littoral forest in Southeastern Madagascar. This species is also present in the Conservation Zone of Mandena, a series of littoral forest fragments located about 50 km South-West from the Sainte Luce area (Fig. 2.2). Floristic and structural characteristics of the Mandena forest show a fragmented and seriously compromised habitat (Vincelette *et al.*, 2007c; Donati *et al.*, 2007b). Nevertheless, the degradation of the Mandena forest provides a model to study and to understand ecological and behavioral mechanisms used by animals to cope with such degraded habitat. Previous studies in degraded and/or fragmented areas have underlined the influence of habitat modification on primate ecology and behavior (Ganzhorn *et al.*, 2007).

The most significant changes concern time budget, feeding choices, social interactions, group size and structure, and habitat use (Donati, 2002; Bollen *et al.*, 2005; Bollen and Donati, 2005; Ganzhorn *et al.*, 2007; Donati *et al.*, 2007a; Donati *et al.* 2010, Donati *et al.*, 2011). However, what is not yet clear is how the above behavioral and ecological flexibility may affect animal stress levels. Therefore, one part of our project concerned the study of stress by measuring fecal glucocorticoids levels. However, the aim of this piece of research is to understand whether the population of red collared brown lemurs in Mandena uses different ecological and social strategies as compared to the population living in the well preserved forest of the Sainte Luce area. In particular we investigated whether or not, in the more degraded forests of Mandena, lemurs use more energy-saving behaviors to compensate a lower quality diet.

To answer these questions our work was structured in several different levels of investigation: habitat use, activity patterns, feeding ecology, behavioral thermoregulation, and sociality. These eco-ethological aspects were studied at both sites of Mandena and Sainte Luce. The data collected allowed us to integrate knowledge on *Eulemur collaris*, that in some aspects were scarce, especially as concerns social structure.

The comparison of the data obtained from groups living in well preserved and in degraded habitats allowed us to recognize ecological and social strategies/behaviors used by *Eulemur collaris* to survive in a secondary forest. This knowledge is essential for proper wildlife management which leads to preservation of the species and of the ecosystem. In fact, to protect *Eulemur collaris* means to protect the littoral forest and its biodiversity.

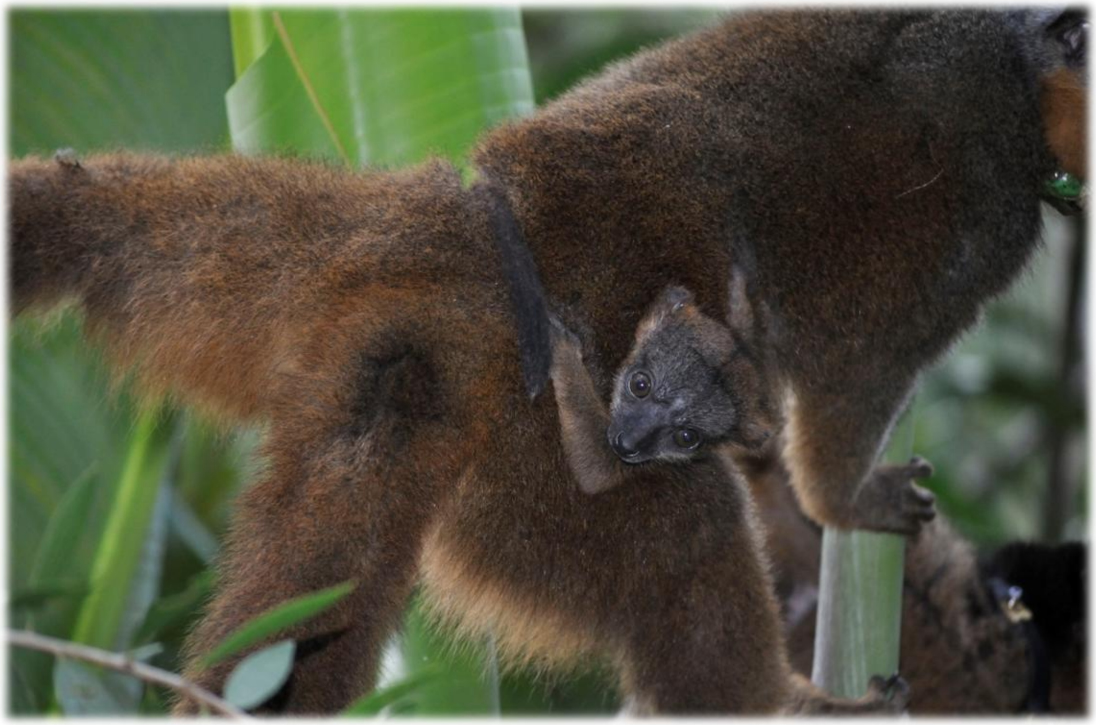


Figure 2.2: Olivia, infant of group C at Mandena, aged 1 month. Olivia was born on October 4th 2011, and this photo was taken on November 4th 2011. Olivia in this photo was still young to move and feed alone, and her mother, Mamiska, cared about her. Photo by Marco Campera.

CHAPTER 3

MATERIALS AND METHODS

3.1 Study site and species

This comparative study was conducted in the littoral forest fragments of Mandena (MAN) and Sainte Luce (STL) near Fort Dauphin in south-eastern Madagascar (Fig 3.1).

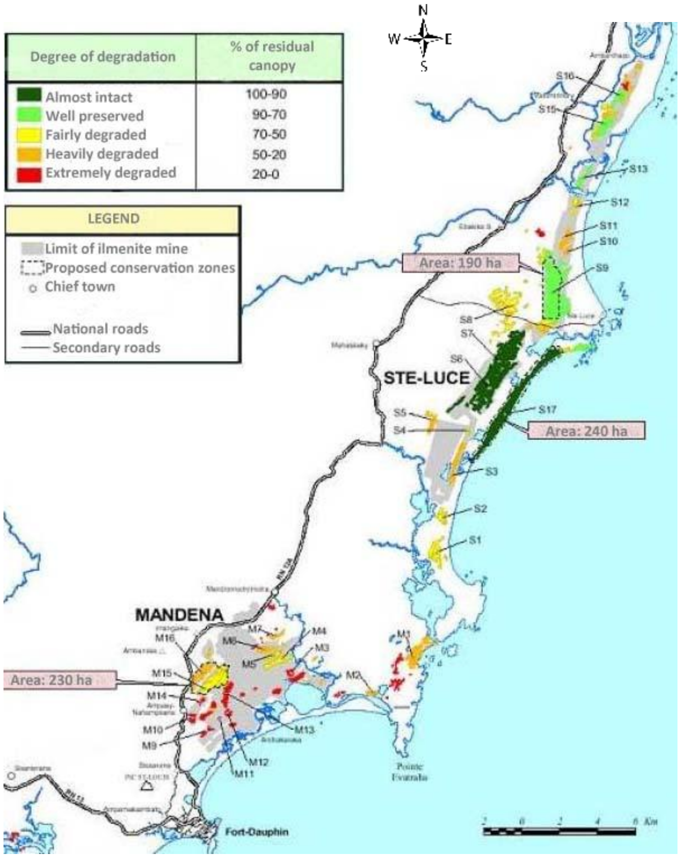


Fig. 3.1: Study sites and forest conservation status. Map of littoral forest fragments remaining in 2000 at Sainte Luce and Mandena. Study sites in Mandena (M15 and M16) are more degraded than the study site in Sainte Luce (S9), that is well preserved. Map by QMM, modified.

The Conservation Zone of Mandena (24°57' S, 47°0' E), 11 km North-West of Fort Dauphin, is located on sandy soils at an altitude 0–20 m above sea level. Our study was conducted in M15 and M16 fragments (about 148 ha of ‘fairly degraded’ littoral forest), included in the Conservation zone. The two fragments are surrounded by a swamp (approximately 82 ha), that collared lemurs use for daily activities such as travelling, resting and feeding, but also for drinking during hottest periods. Thus, we considered the two fragments (M15 and M16) and the swamp as a single area of about 240 ha, included in the Conservation zone. The average canopy height in M15 and M16 is 8.9 ± 4.4 m (Rabenantoandro *et al.*, 2007). In addition, some groups of *Eulemur collaris* use to live in another smaller fragment not included in the Conservation Zone: M20, that is approximately 6 ha of “heavily degraded” forest, and is located North-East of the other two fragments (see Ganzhorn *et al.*, 2007 for fragment areas). Collared lemurs use especially the swamp that links M20 to other fragments. This swamp (about 40 ha) is called by local people *analamafotra* (*ala* = forest) from the vernacular name of the tree (*mafotra*) that characterize this swamp (“the forest of *mafotra*”). This swamp is out of the Conservation Zone and local people use it to pick up fruits, gather dead woods and cut trees. In addition to *Eulemur collaris*, four nocturnal (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*, *Avahi meridionalis*), and one cathemeral lemur species (*Hapalemur meridionalis*) are found in this area.

The second study site, the littoral forest of Sainte Luce (24°46’S, 47°10’E), about 30 km North of Fort Dauphin, is among the most intact littoral ecosystems in Madagascar and possesses a very high vegetation diversity (Bollen and Donati, 2006). Our study fragment was S9, about 252 ha of ‘well preserved’ littoral forest and swamp, 190 of which are included in the Conservation Zone. *Eulemur collaris* still occurs in S17, an ‘almost intact’ fragment of 237 ha, all included in the Conservation Zone. We studied only groups in S9 because in S17 there are no tracks and there is not a biological station as in S9. The average canopy height in S9 is 14.7 ± 4.3 m (Rabenantoandro *et al.*, 2007). In addition to *Eulemur collaris*, four nocturnal (*Microcebus murinus, Cheirogaleus medius, Cheirogaleus major, Avahi meridionalis*), are present in S9. *Hapalemur meridionalis* is not present at Sainte Luce because the swamp, that is vital for this critical species, is smaller than the one present at Mandena.

Floristically Mandena and Sainte Luce littoral forests are very similar, suggesting that these two areas were once connected. However, structural differences indicate that at the time of our study, the Mandena forest represents a degraded form of the vegetation type present at Sainte Luce. This hypothesis is also suggested by the absence of some tree families known to be logged in Mandena but not in Sainte Luce (Rabenantoandro *et al.*, 2007).

Individuals of red collared brown lemurs presently living in the Mandena forest fragments have been translocated in M15 and M16 between 2000 and 2001 (Donati *et al.*, 2007b) from other littoral forest fragments (M3 and M4), threatened by charcoal makers (Fig.

3.2). M15 and M16 in the meantime became an effective protected area.

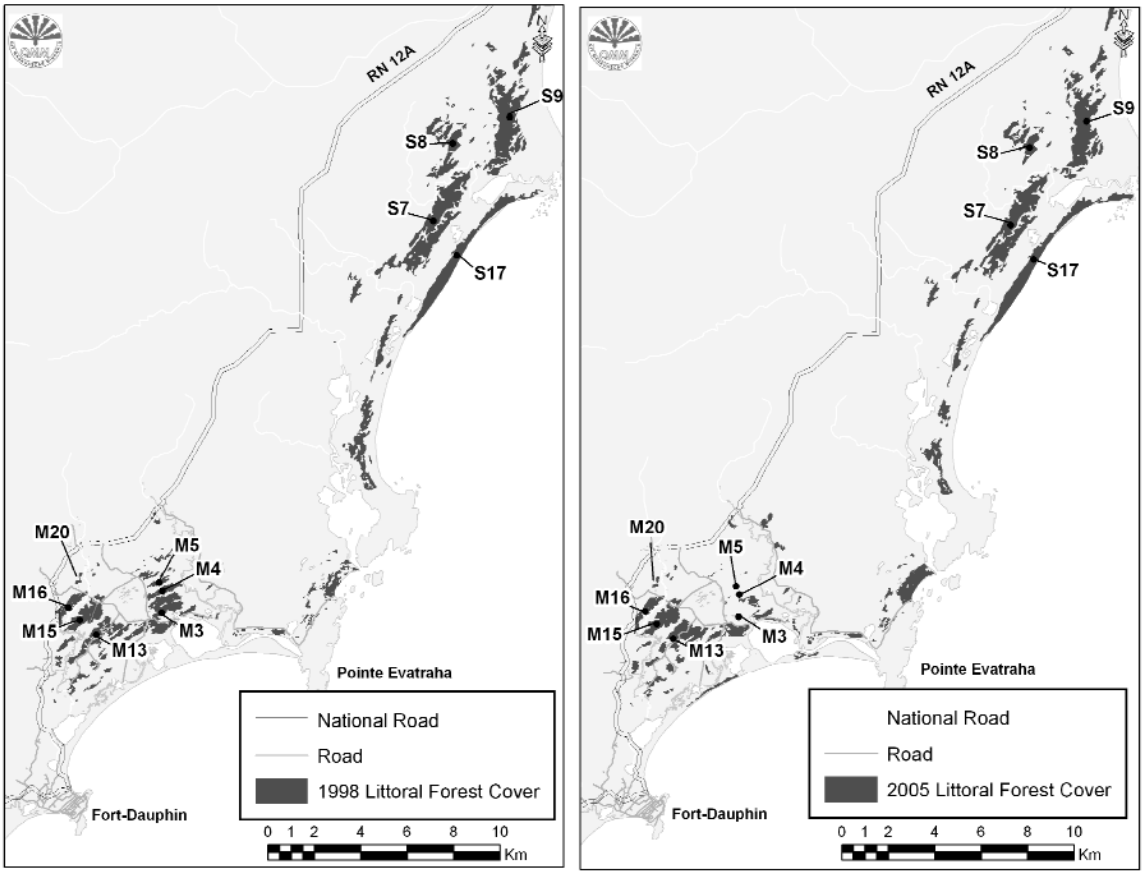


Fig. 3.2: Forest fragments in Mandena and Sainte Luce and and extent of littoral forest reduction between 1998 and 2005 (Donati *et al*., 2007b**).**

Translocation is rare in lemurs, and it is a risky option, but in this case it was the only opportunity to avoid the extinction of the species at Mandena (now M3 and M4 are ‘extremely degraded’ forest fragments). At the moment of translocation the animals were 28, resulting in a density of 12 individuals per km^2 (Donati *et al*, 2007b). Then, after a slight reduction, they were 36 in 2003, suggesting a good response to translocation and a good adaptation to the new environment (Donati *et al.*, 2007b). Unfortunately, in 2004 animals decreased to 25 due to predation by two immigrated subjects of *Cryptoprocta ferox*, that, subsequently, have been captured and then transferred to the Antananarivo Botanical and Zoological Park of Tsimbazaza.

During our study period the population of red collared brown lemurs in Mandena was about 17 animals. The cause of this reduction of population density is still unknown. It may be due to predation, scarcity of food resources, hunting for food by local people or to animal migration towards other forest fragments out of the Conservation Zone. So, during our observation period, the density of *E. collaris* in Mandena was about 7 individuals per km^2. This is well below the density of 38 ind/ km^2 found in Sainte Luce in 2002 (Donati, 2002), which probably increased until 2011 due to cessation of human hunting. However, this remains an unproved hypothesis since we were not able to make a census.

3.2 Behavioral data

Data were collected from July 2011 to January 2012, as a second part of an one year project (from February 2011 to July 2011 data were collected by Marta Barresi and Valentina Serra). I collected data with Michela Balestri, and on July 2011 data was collected by the two team pairs to evaluate inter-observer differences.

We collected data on four groups of *Eulemur collaris* (see chapter 1 for further information on the species): two groups at Mandena (group AB and group C), and two groups at Sainte Luce (group A and group B). Group composition is shown in table 3.1.

	STE LUCE		**MANDENA**	
	Group A	**Group B**	**Group AB**	**Group C**
Adult males	4	3-4	2	2-3
Adult females	3	3-4	1	1-2
Juveniles	1	2	0	1
Infants	5	3	1	1
Total	**13**	**11-13**	**4**	**5-7**

Table 3.1: Composition of the four study groups during the study period.

Every lemur of each group under study at Sainte Luce received a malagasy name given by the first two students (Marta and Valentina), while the QMM biodiversity staff gave names inspired on a Brazilian soap called *Cor do Pecado* to the animals of Mandena groups. Me and Michela gave Malagasy names to the infants born in the second study period at both study sites. Group composition changed over time: in group B one adult male (called Fotsy that means white) and one adult female (called Rano that means water) left the group in September, probably due to overcrowding, hopefully not to hunting or predation. Also in group C one sub-adult female (Tina) left the group in September. In this case we are sure that Tina is still alive because she is collared and we saw her with a male. Probably, it is not by chance that she left the group a short time before the birth season and after the mating season. Strangely, one male (Eddy) chased away from group AB on June (after a battle with the dominant male of the group, Abelardo), joined group C in September after a period apent living alone. Infants were born between the end of September and the beginning of October. Every adult female in our group gave birth to at least one infant, and two females (called Volana and Ala that mean moon and forest) in group A gave birth to two twins (Volana one male and one female, Ala two females). (see chapter 9 for further information on social structure)

To ensure a continuous observation, four animals (one for each group) were captured in order to install radio-tracking collars, to be monitored by the use of a SIKA receiver (Biotrack). The adult individuals were captured by caging them, using banana slices as a bait, and rapidly anesthetized with Zoletil 100 (5 mg/kg of tiletamine hydrochloride) to prevent trauma. Morphometric measurements were taken (appendix IV) and then thermo-sensitive collars TW-3 (medium mammal tag) were fixed. All animals recovered from anesthesia within 1.5 hours and were not moved from the capture area nor kept in a cage, but were followed until regaining full mobility. There were no injuries as a consequence of the captures.

Every group was followed four days per month and one group per site was followed one night per month. Overall, 556 diurnal observation hours in Mandena (296 h 25’ in group AB, 259 h 35’ in group C) were compared with 564 hours in Sainte Luce (282 h 55’ in group A, 282 h 25’ in group B), while the amount of nocturnal observations was 152 hours, 76 h 20’ in Mandena and 75 h 40’ in Sainte Luce. Diurnal observation hours were distributed as shown in Figure 3.3.

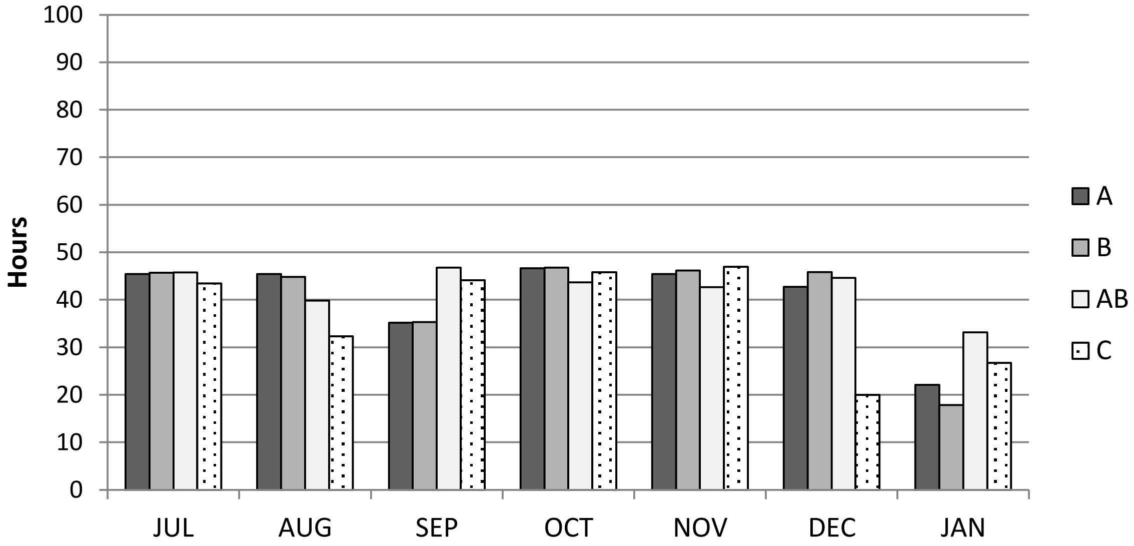


Fig. 3.3: Monthly amount of observation hours at Sainte Luce (group A and group B) **and at Mandena** (group AB and group C).

The lower amount of observation hours for group C is mainly due to the impossibility to follow this group into the swamp during wet periods, when the water level of the marsh made observations impossible. Moreover, on January a cyclone passed near our region and caused a lot of precipitation that covered the unmade roads. Thus, we stopped our work in Sainte Luce, due to the impossibility to come back in Fort Dauphin to take the flight back for Italy if the precipitation had gone on.

The groups were followed from 6:00 to 18:00 during each observation day and from 18:00 to 6:00 during each observation night. A focal animal was chosen among the adult individuals, trying to balance the time spent observing males and females. The focal animal was followed as long as possible, and substituted with the first visible animal of the same sex when it was lost. Individual recognition was possible observing radio-collars and some characteristics of the animals such as age, sex, size, canine length, tail shape, fur color, and distinctive traits. We collected ethological data using the instantaneous sampling method, with records every five minutes, the all occurrences method and the *ad libitum* method (Altmann, 1974). Behavioral data concerned animal activity: resting, moving, feeding, social interactions and anti-predator strategies, recorded by the use of a specific ethogram, shown in Appendix I (Donati, 2002, modified in this study). We also recorded resting/huddling postures, position in the tree crown (height, distance from the trunk), proximity, food items, and tree species.

During nocturnal observations it was often impossible to recognize a specific animal, we therefore followed the general activity of the group. We used a very basic ethogram, with the only voices of resting, moving and feeding, but we could often only assess if animals were active or not (see chapter 5). Trees were marked after three instantaneous of focal animal resting or during one instantaneous of feeding with a flag signed by a specific code (group name-activity-progressive number), and the diameter at breast height (DBH) was measured. Then the field assistant provided the vernacular name of the species and a small branch sample for identification. By these data a botanist of QMM was able to identify the scientific names of the plants. List of species used as feeding plants from July 2011 to January 2012 by *E. collaris* is shown in Appendix II. Every half hour the position of the animals was recorded by GPS (Garmin eTrex Legend HCx).

3.3 Statistical analysis

We mostly used non parametric statistical analyses (Mann-Whitney test, Kruskal-Wallis test, Spearman correlation index) because the sample size was often small, and the Kolmogorov-Smirnov test indicated significant deviations from normality. Specific statistical analysis are described in each chapter.

We performed all tests with STATISTICA for Windows, version 8.0 and we considered $p<0.05$ as the significant level.

CHAPTER 4

HABITAT USE

4.1 Introduction

Ecological factors such as forest structure, resource availability and predation, are critical in determining the spatial distribution of primates (Boyle *et al.*, 2009a). Home range is defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt, 1943). Because most habitats are heterogeneous, the animal will likely not use the whole home range in equal proportion. Home range size can vary according to the body weight, diet, sex, and age, and according to season, population density, and climate (Burt, 1943; Clutton-Brock and Harvey, 1979). A uniform distribution of food resources allows animals to minimize their movements to fulfil energy needs, while a habitat where resources are more scattered, often requires more travelling. So, the conservation status of the habitat plays a fundamental role in shaping home range dimension, in relation to resource distribution and availability (Merker *et al.*, 2005; Schwitzer *et al.*, 2007b).

Home range also varies in relation to social systems and activity cycles. The home range of the smallest lemur, the nocturnal and solitary *Microcebus murinus* is 0.6-4.8 ha, depending on sex and reproductive cycle (Radespiel, 2000), while the ranging area of one of the largest lemurs, the diurnal and group living *Propithecus diadema* is 25-100 ha (Wright, 1995). However, ranging patterns in the family Lemuridae appear to be mostly influenced by forest type than by group size (Sussman, 1974; Curtis and Zaramody, 1998): groups of *Lemur catta* and *Eulemur rufus*, which inhabit forests of different type, have different home range areas in spite of similar group sizes (Sussman, 1974; Overdorff, 1996).

The well preserved forest fragment at Sainte Luce and the degraded fragments at Mandena provide ideal observational conditions to make comparisons between strategies used by groups of *Eulemur collaris* living in different habitats in the wild. In this chapter we will analyze differences in overall (from July 2011 to January 2012), monthly and daily home ranges among the four groups and between the two sites. Additionally, we will evaluate the number and the size of feeding trees used by lemurs during our study period. In Mandena we expect to find significant differences as compared to Sainte Luce, such as increase in ranging areas and in the number of feeding trees used daily, as already shown by Donati *et al*., 2011.

4.2 Materials and methods

We collected behavioral data using the instantaneous sampling method, with records every five minutes, the all occurrences method and the *ad libitum* method (Altmann, 1974). Trees were marked after three instantaneous of focal animal resting or during one instantaneous of feeding with a flag and a specific code (group name-activity-progressive number, e.g. ABR1 is the first resting tree of group AB, and AB1 is the first feeding tree of group AB). Tree height was estimated at 1-m intervals and the diameter at breast height (DBH) was measured. The field assistant provided the vernacular name of the species and collected a small branch sample for identification. By these data a botanist of QMM was able to identify the scientific names.

We recorded animal location every 30 minutes by GPS (Garmin eTrex Legend HCx) during diurnal and nocturnal observations. We conducted analyses of home range size and location via Ranges 7 (Anatrack Ltd.). We estimated the monthly and the overall home ranges per group via 100% minimum convex polygons (MCP) with harmonic means centers using all the location points. The method creates a polygon including all the locations where an individual was observed (Mohr, 1947). Although it is a quick and easy method, it is also well known to overestimate home range size (Barg *et al.*, 2005; Burgman and Fox, 2003; Mohr, 1947; Pimley *et al.*, 2005). We therefore also used 95% and 50% adaptive core weighted Kernel analyses with contours fitted to locations and fixed multiplier. This method is based on the actual amount of use of different areas by a given individual (the utilization distribution) and therefore produces much more accurate home range estimates, excluding the outliers (Barg *et al.*, 2005; Pimley *et al.*, 2005). We calculated day range (ha) and area used per hour (ha/h) for each day in each study site to evaluate the lemurs’ use of the forest. The primary purpose for calculating day range was to determine whether the lemurs in the fragments were maximizing the entire forest fragment daily. We determined an hourly average in addition to a total daily area because contact hours with the lemurs varied daily and between groups. Additionally, we calculated the daily distance traveled (km) and the distance traveled per hour (km/h) for each day. Graphic representations of home ranges were performed with Map Source (version 6.13.7, Garmin Software), and with Range 7 (95% Kernel method), using all waypoints per group and the site pathways tracked by GPS.

Statistical comparisons between sites or groups were made by the non parametric Mann-Whitney U test and Kruskal-Wallis H test for independent data. T-test for independent data was performed in the case of normal distributions. Normal distribution was tested via Kolmogorov-Smirnov and Lilliefors test for normality. We performed all tests with STATISTICA for Windows, version 8.0 and we considered $p<0.05$ as the significant level.

4.3 Results

Overall home ranges of *Eulemur collaris* at Sainte Luce (groups A and B) and Mandena (groups AB and C), calculated via 100% minimum convex polygon method (MCP), were on average ($\bar{x}$±SD) 18.81±1.82 ha and 83.61±41.28 ha respectively; using the 95% Kernel method they were 14.82±0.69 ha in Sainte Luce and 49.82±28.55 ha in Mandena. Average core areas calculated via 50% Kernel method were ($\bar{x}$±SD) 4.13±0.13 ha at Sainte Luce and 8.44±5.11 ha at Mandena (Table 4.1).

Table 4.1: Overall home range values of the four study groups during the study period. MCP: Minimum convex polygon.

	Overall home range area (ha)		
	100 % MCP	**95% Kernel**	**50% Kernel**
Group A	20.09	15.31	4.04
Group B	17.53	14.33	4.22
Group AB	54.42	29.63	4.82
Group C	112.80	70.00	12.05

As regards monthly home ranges (Table 4.2), comparisons between the four groups gave significant differences ($H (3, N=27) = 16.91$, $p<0.001$) using the MCP only. The Kruskal-Wallis test gave no statistically significant differences using the 95% Kernel method ($H (3, N=27) = 2.876$, $p=0.411$) and the 50% Kernel method ($H (3, N=27) = 4.171$, $p=0.244$). The Mann-Whitney U test between sites gave significant differences ($U_{14,13}=7$, $p<0.001$) using the MCP only.

Table 4.2: Monthly home ranges values (mean and standard deviation) of the four groups. MCP: Minimum convex polygon.

	Monthly home ranges (ha)		
	100 % MCP	**95% Kernel**	**50% Kernel**
Group A	9.48±2.99	11.97±4.70	3.91±0.93
Group B	10.34±3.27	9.51±3.22	2.73±1.15
Tot STL	**9.91±3.04**	**10.74±4.08**	**3.32±1.18**
Group AB	21.02±10.59	13.13±7.09	3.76±1.74
Group C	28.56±19.84	19.43±14.25	4.35±2.78
Tot MDN	**24.79±15.77**	**16.28±11.29**	**4.06±2.25**

Significant differences between group A and group B at Sainte Luce were found using the 50% Kernel method only ($U_{7,7}=7$, $p=0.025$). On the other hand, there were no statistically significant differences between group AB and group C using the three methods. Details on monthly home ranges per group are shown in figure 4.1.

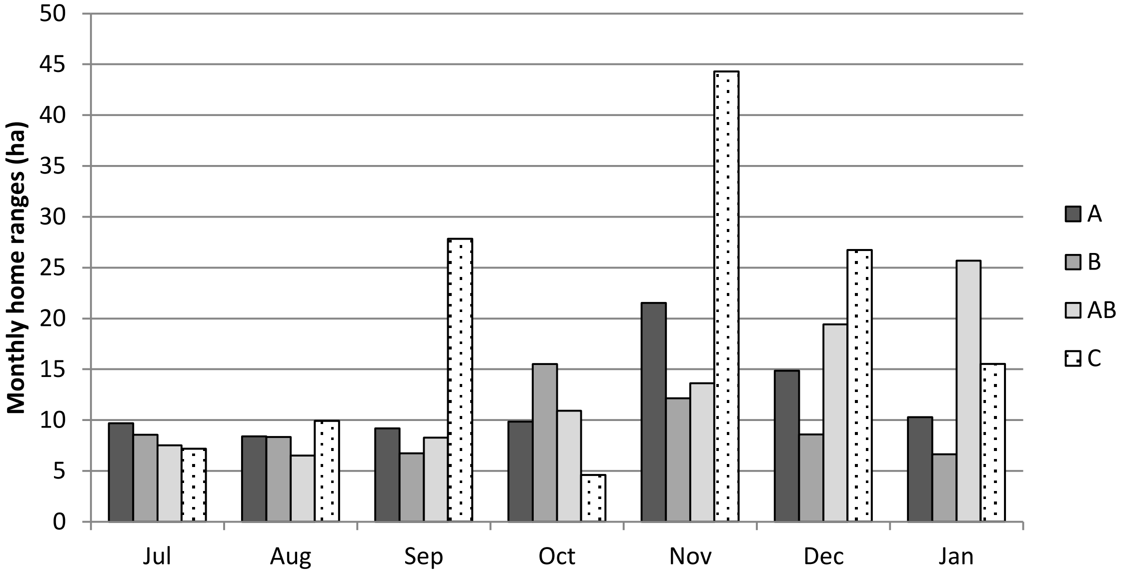


Fig. 4.1: Monthly home ranges (ha) at Sainte Luce (group A and group B) **and at Mandena** (group AB and group C). Values obtained via Kernel 95% method analysis (Range 7).

Overall home ranges of the four study groups are represented in figure 4.2, 4.3 and 4.4. As regards daily home ranges we found significant differences between Mandena and Sainte Luce with both methods (Table 4.3). In fact, daily home ranges of lemurs at Sainte Luce were higher than those at Mandena. Considering the different contact hours with the lemurs, the area used per hour remained significantly higher at Sainte Luce (tendency using the MCP). We found differences between lemurs at Sainte Luce (group B had daily home ranges and area used per hour significantly higher as compared to group A using MCP: $U_{23,24}$=125, p=0.001, $U_{23,24}$=130, p=0.002 respectively). No significant differences were found between group AB and group C.

Table 4.3: Daily home ranges and area used per hour of the four groups. Values are in medians (in bold) and quartiles. MCP: Minimum convex polygon. Bottom: results of Mann-Whitney test between daily ranges and area used per hour at Sainte Luce and Mandena. *p<0.05 **p<0.01

		Daily home ranges (ha)			**Area used per hour (ha/h)**		
	N	**100 % MCP**	**95% Kernel**	**50% Kernel**	**100 % MCP**	**95% Kernel**	**50% Kernel**
Group A	**24**	**3.11**	**4.98**	**1.97**	**0.27**	**0.47**	**0.17**
		2.08-4.16	3.32-8.26	1.07-2.90	0.19-0.36	0.29-0.73	0.09-0.25
Group B	**23**	**5.00**	**6.56**	**1.99**	**0.45**	**0.59**	**0.17**
		3.84-5.95	4.43-7.47	1.28-2.63	0.37-0.52	0.37-0.69	0.11-0.23
STL	**47**	**4.08**	**6.25**	**1.98**	**0.37**	**0.54**	**0.17**
		2.84-5.31	3.47-7.53	1.18-2.63	0.24-0.48	0.30-0.69	0.11-0.23
Group AB	**25**	**2.82**	**4.28**	**1.01**	**0.32**	**0.45**	**0.12**
		1.75-4.70	1.60-8.25	0.40-1.95	0.15-0.47	0.14-0.79	0.04-0.18
Group C	**24**	**2.83**	**3.30**	**0.75**	**0.25**	**0.33**	**0.07**
		1.54-4.60	1.67-6.48	0.35-1.38	0.16-0.42	0.16-0.59	0.03-0.12
MDN	**49**	**2.82**	**4.20**	**0.97**	**0.26**	**0.38**	**0.08**
		1.58-4.70	1.66-7.02	0.37-1.59	0.16-0.44	0.14-0.65	0.03-0.15
U		829*	827*	602**	904	873*	634**
p-level		0.018	0.017	<0.001	0.070	0.041	<0.001

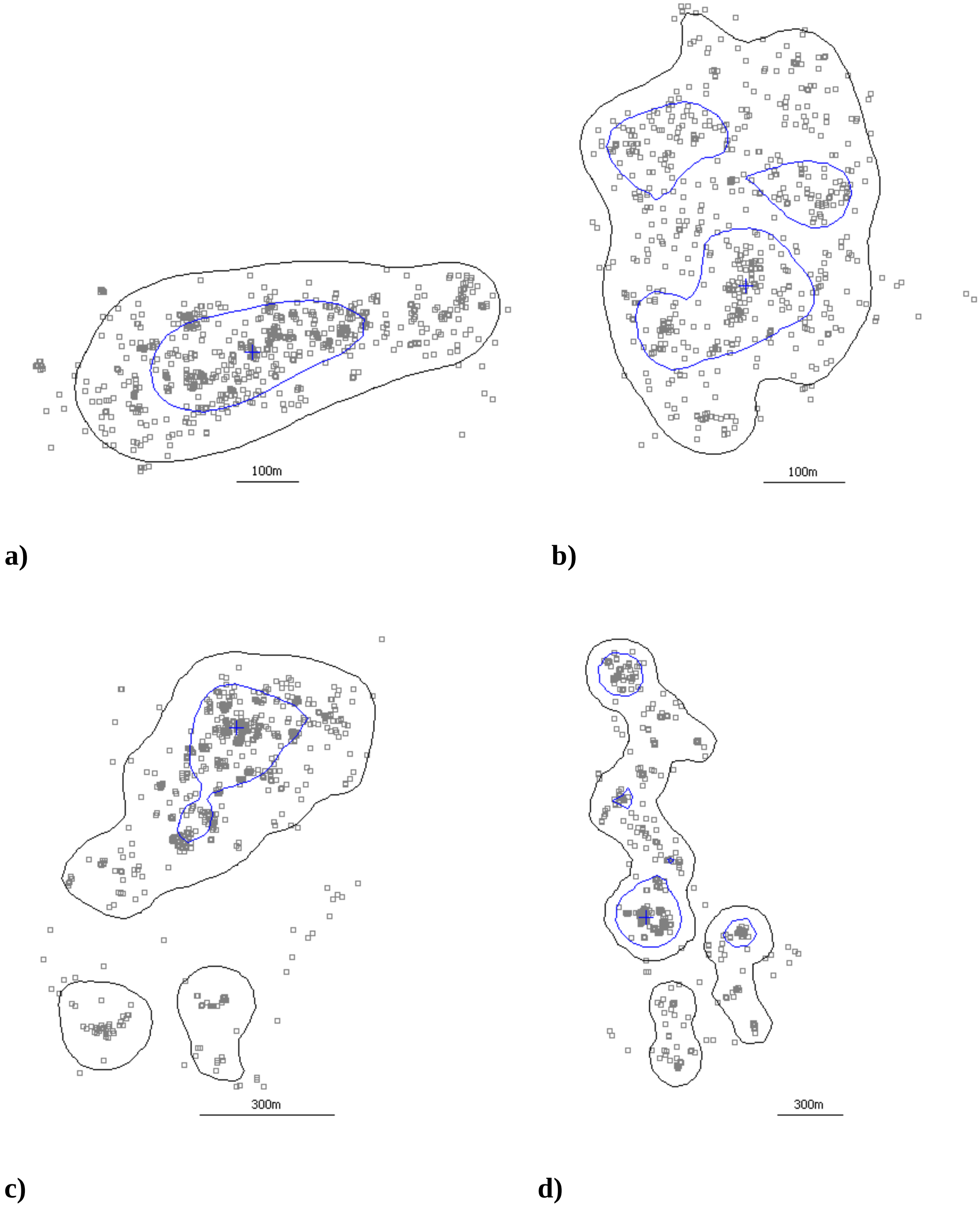


Fig. 4.2. Overall home ranges of the four study groups.

Graphs obtained via 95% and 50% Kernel method analysis. White squares represent group waypoints (Range 7). Note the different scale.

a) Sainte Luce, home range of group A (July-January); b) Sainte Luce, home range of group B (July-January); c) Mandena, home range of group AB (July-January); d) Mandena, home range of group C (July-January).

Fig 4.3: Overall home ranges of group AB (above) and group C (below) at Mandena. White squares represent group waypoints between July 2011 and January 2012; gray lines are the forest pathways at Mandena, tracked via GPS (black points are waypoints of pathways). Graphs performed with Map Source.

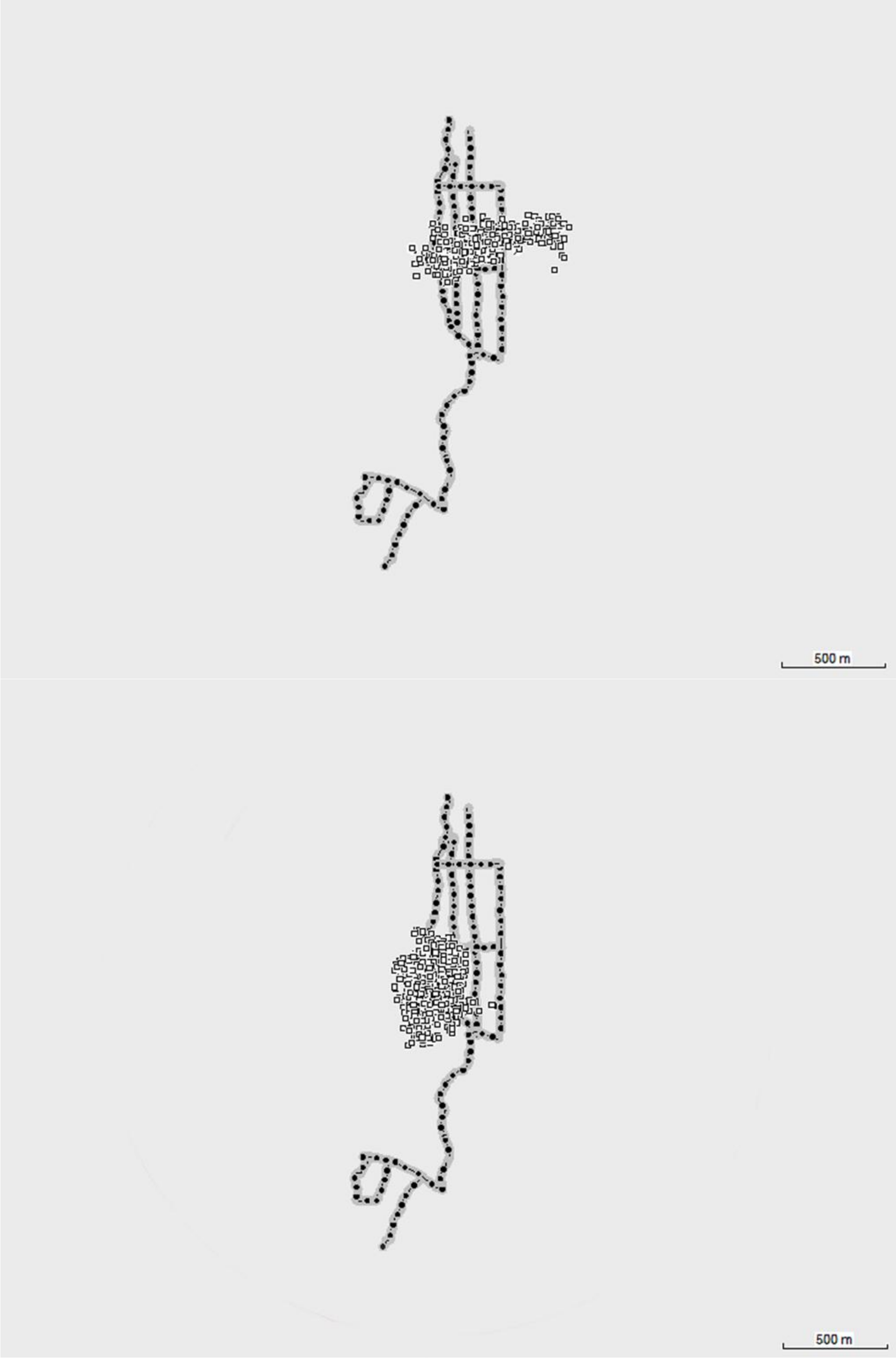


Fig 4.4: Overall home ranges of group A (above) and group B (below) at Sainte Luce. White squares represent group waypoints between July 2011 and January 2012; gray lines are the forest pathways at Sainte Luce, tracked via GPS (black points are waypoints of pathways). Graphs performed with Map Source.

Daily distance traveled by lemurs were significantly higher at Sainte Luce as compared to Mandena (Table 4.4). Considering the different contact hours with the lemurs, the distance traveled per hour remained significantly higher at Sainte Luce. Group B had significantly higher distance traveled per day ($U_{23,24}$=144, p=0.005) and per hour ($U_{23,24}$=144, p=0.005) as compared to group A. In Mandena we found no significant differences between group AB and group C.

		Daily distance (m)	Distance per hour (m/h)
Group A	**24**	**898.1**	**78.4**
		427.0-1430.5	36.9-121.7
Group B	**23**	**1092.0**	**100.0**
		605.0-1965.1	51.9-172.2
STL	**47**	**1057.5**	**93.0**
		427.0-1965.1	36.9-172.2
Group AB	**25**	**765.1**	**73.1**
		312.9-1555.7	29.8-158.8
Group C	**24**	**759.0**	**64.3**
		331.4-1397.7	35.4-135.4
MDN	**49**	**765.1**	**70.9**
		312.9-1555.7	19.8-158.8
U		634**	748**
p-level		<0.001	0.003

Table 4.4: Daily distance traveled and distance traveled per hour of the four groups. Values are in medians (in bold) and range (min-max). Bottom: results of Mann-Whitney test between daily distance and distance per hour at Sainte Luce and Mandena. *p<0.05 **p<0.01

The proportion of home range locations that fall within the home ranges of the other group living in the same site, calculated via Kernel 95% and minimum complex polygon are shown in Table 4.5.

	AB (on C hr)	C (on AB hr)	A (on B hr)	B (on A hr)
Kernel 95%	9%	2%	6%	5%
MCP 100%	15%	17%	13%	8%

Table 4.5: Overlap of range locations on home ranges (hr) of groups at Mandena and Sainte Luce. Proportion of locations of group AB that fall within the home range of group C and *vice versa*. Proportion of locations of group A that fall within the home range of group B and *vice versa*. Home ranges calculated via Kernel 95% or Minimum Convex Polygon (MCP) 100% methods.

Lemurs at Sainte Luce used a higher number of feeding plants per day than those living in Mandena (Table 4.6). However, considering the different time spent by lemurs feeding each day, the number of feeding plants used per hour of daily feeding was significantly higher in Mandena as compared to Sainte Luce. No significant differences were present between groups living in the same sites.

	N	n° of feeding plants/day	n° of feeding plants/h
Group A	**24**	**21.0**	**6.4**
		15.0-26.5	5.4-7.4
Group B	**24**	**21.0**	**6.9**
		17.5-27.0	5.4-8.0
STL	**48**	**21.0**	**6.6**
		15.5-26.5	5.4-7.9
Group AB	**24**	**9.0**	**8.5**
		8.0-11.0	6.2-9.6
Group C	**22**	**10.0**	**8.2**
		8.0-12.0	6.8-9.6
MDN	**46**	**9.5**	**8.2**
		8.0-12.0	6.7-9.6
U		199**	608**
p-level		<0.001	<0.001

Table 4.6: Daily number of feeding plants used by lemurs and number of feeding plants used by lemurs per hour of feeding in the four groups. Values are in medians (in bold) and quartiles. Bottom: results of Mann-Whitney test between daily number of feeding plants and number of feeding plants used per hour of feeding at Sainte Luce and Mandena. *p<0.05 **p<0.01

A total of 748 (363 for group A, 385 for group B) feeding plants used by lemur groups in Sainte Luce and 461 (247 for group AB, 214 for group C) in Mandena were marked and measured. The analysis of the size of feeding trees showed that Mandena groups fed on smaller plants, in term of height and DBH, than those used by Sainte Luce groups. The mean DBH and height of the feeding trees used by lemurs are shown in Table 4.7. Frequency classes of height and DBH of feeding trees and normality tests are shown in Figure 4.5 and 4.6.

Table 4.7: Dimensions of feeding trees (DBH and height) in Mandena and Sainte Luce. Values are in means and standard deviations. Bottom: results of T-test between dimensions of feeding trees used at Sainte Luce and Mandena. *p<0.05 **p<0.01

	N	DBH of feeding trees (cm)	Height of feeding trees (m)
Group A	350	20.82±10.79	9.37±2.89
Group B	270	22.82±13.81	8.64±2.57
Tot STL	**620**	**21.69±12.23**	**9.05±2.78**
Group AB	212	13.88±10.62	6.12±1.90
Group C	206	13.29±8.13	5.46±1.50
Tot MDN	**418**	**13.59±9.47**	**5.79±1.74**
T		11.44**	21.29**
p-level		<0.001	<0.001

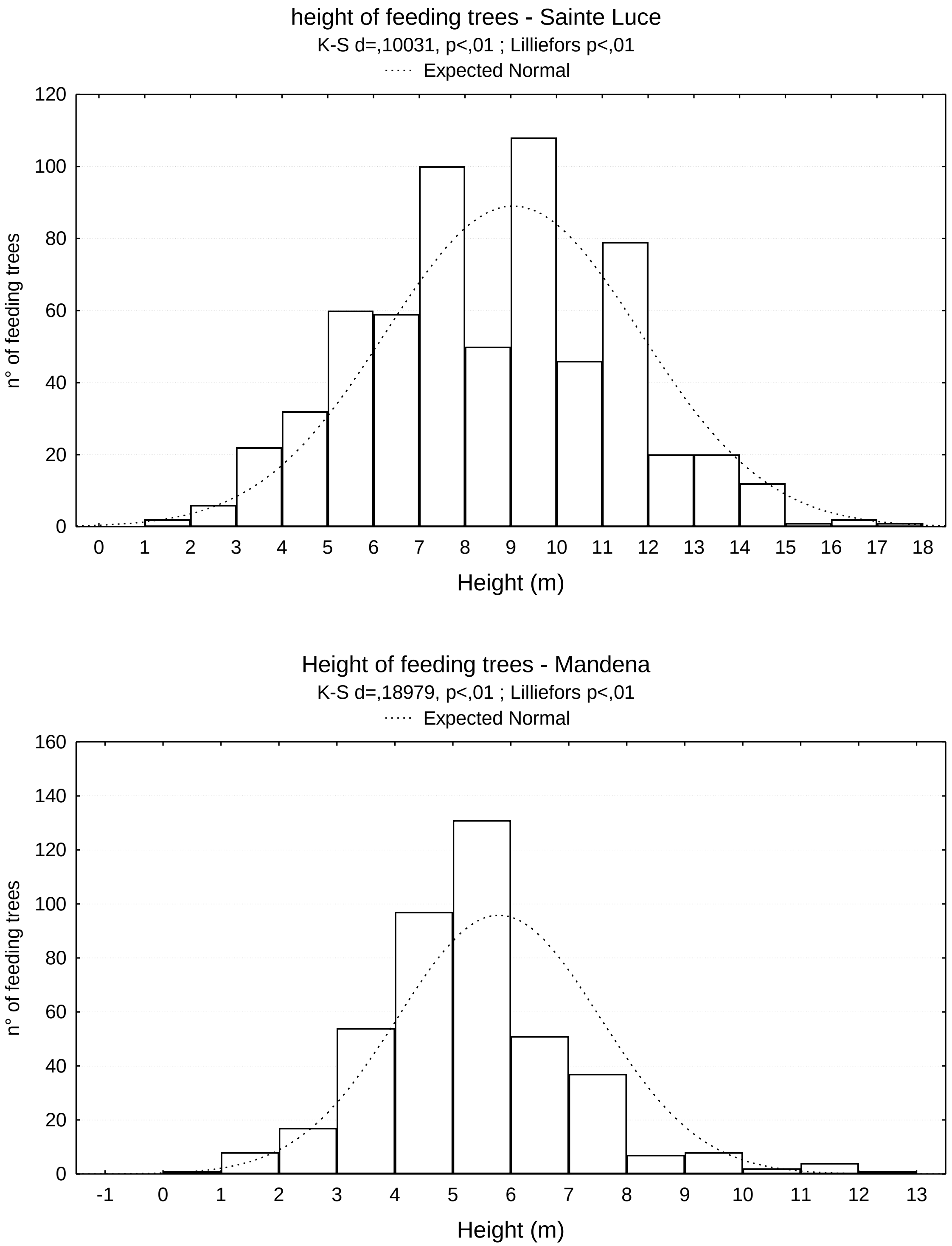


Fig. 4.5: Frequency classes of height of feeding trees in Mandena and Sainte Luce. Normal distribution tested via Kolmogorov-Smirnov (K-S) and Lilliefors test for normality. Graphs performed with Statistica 8.0.

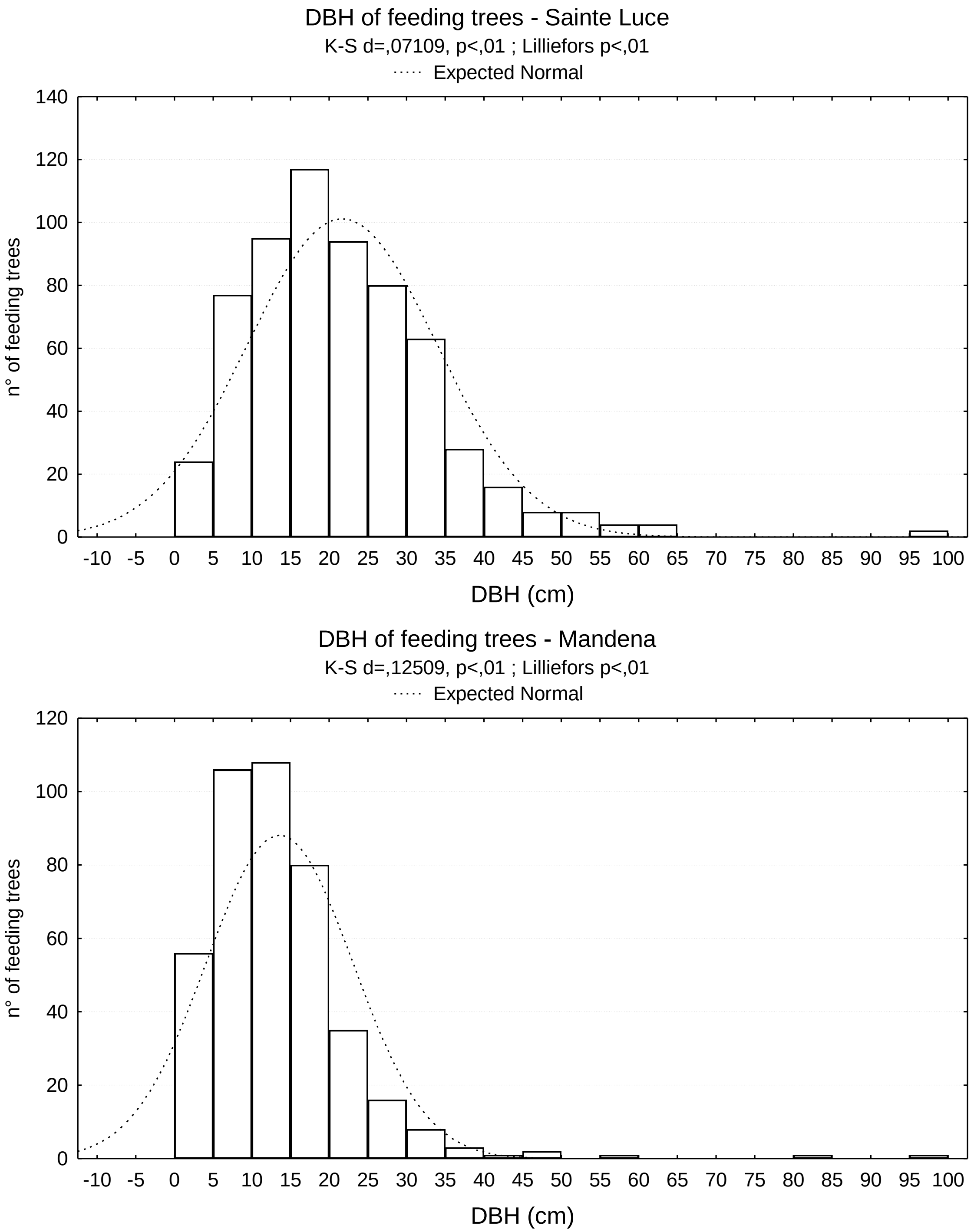


Fig. 4.6: Frequency classes of DBH of feeding trees in Mandena and Sainte Luce. Normal distribution tested via Kolmogorov-Smirnov (K-S) and Lilliefors test for normality. Graphs performed with Statistica 8.0.

4.4 Discussion

As expected on the basis of previous studies (Donati *et al.*, 2011), home ranges were larger in the degraded forest fragments of Mandena as compared to the intact forest fragments of Sainte Luce. In particular, group C had exceptionally high home range values as compared to other brown lemurs. In fact, we found an overall home range of 112.80 ha with the minimum convex polygon method, while according to literature, brown lemurs living in eastern rainforests tend to have ranges from 12 to 100 ha (Overdorff, 1991; Vasey, 1997). In particular, *Eulemur fulvus rufus* is known to have the widest home ranges (between 85 and 100 ha) found so far in the brown lemurs group (Overdorff, 1996; Vasey, 1997). Considering that Mandena Conservation Zone is almost 240 ha (see chapter 3), and that group C and group AB had a limited home range overlap, we can argue that the two groups used almost 160 ha of Mandena forests and swamps, almost 65 % of the Conservation Zone. Group C used also M20 occasionally, which is a fragment out of the Conservation Zone. We saw another group (about 5 individuals) of *Eulemur collaris* living in Mandena (approximately between *analamafotra* and M20), showing a home range overlap with group C, and we know that Tina (group C) left the group and joined a solitary male, remaining in M15. Those four groups are the only known in Mandena, and we noted that they tend to exploit at maximum forest fragments and swamps. In fact, Mandena hosted approximately 17 individuals of *E. collaris* at the moment of our study, having a low interspecific competition. Probably, group size reduction in Mandena was a crucial step for *E. collaris* to minimize intra-group resource competition, that in a degraded habitat is more intense and challenging. Decrease in group size has been reported also for other primate species that inhabit fragmented and/or degraded forests, such as the black-and-white colobus (Onderdonk and Chapman, 2000; Marshall *et al.*, 2005), the red colobus (Marshall *et al.*, 2005), the black spider monkey (Symington, 1988), the crowned lemur (Wilson *et al.*, 1989), and the barbary macaque (Machairas *et al.*, 2003).

Home ranges in Sainte Luce were smaller as compared to those at Mandena, but in line with other brown lemurs. We found home ranges near 20 ha. Home range of group B (17.5 ha) was in line with Donati, 2002 (20.5 ha), while the home range of group A (20.1 ha) was very different (96.8 ha). This was mainly due to the fact that we analyzed the data between July 2011 and January 2012, while in Donati, 2002 data were collected for 14 months. In fact, from February 2011 to June 2011, the other students, Valentina Serra and Marta Barresi, noted a different habitat use in group A, and overall home ranges were higher. Additionally, Donati (2002) found the highest monthly home range (56.4 ha) on March. Thus, we will join our data in order to have one year of data.

The highest monthly home range during our study period was reached by group C on September (69.3 ha, via MCP). While group A reached at maximum 15.7 ha on November, group B 15.9 ha in October and group AB 37.4 ha on January. Group B had monthly home ranges (from 5.6 to 15.9 ha) slightly lower as compared to those found by Donati, 2002 (from 11.6 to 17.1 ha), while group A had monthly home ranges (from 6.9 to 15.7 ha) much lower as compared to those found by Donati, 2002 (from 22.5 to 56.4 ha). In addition to the fact that our study had a shorter duration, we can also notice that resource availability was higher in our study period (see also chapter 6). In fact, the graphs obtained via the Kernel method (fig. 4.2) show that groups at Sainte Luce remained in the same area, well exploited by the two groups. Group A seemed to have a more uniform exploitation of his vital area, while group B had three more important *core areas*.

In Mandena, Kesch (unpub. data) collected data between August and December 2007. Group AB in that period was still divided in group A and group B. She found overall home ranges for group A and C near 70 ha, but the group composition was different. In particular group C was composed by three adults, while group A by five adults and one juvenile. Home range size and the percentage of feeding and moving are positively correlated with group size (Isbell and Young, 1993; Barton *et al.*, 1992; Janson, 1988; de Ruiter, 1986; van Schaik *et al.*, 1983). This might explain why we found an higher home range for group C (now composed by 5 individuals and one infant) and a lower home range for group AB (now composed by 3 individuals and one infant). However, in Sainte Luce we had smaller home ranges as compared to Mandena. This seems to be mainly due to the lower density distribution of productive feeding trees, that is the consequence of the higher level of degradation in Mandena (Ganzhorn *et al.*, 2007). Thus, the animals need large home ranges to find enough feeding trees, possibly also to visit some especially productive feeding trees. In fact, the conservation status of the habitat plays a fundamental role in shaping home range size, in relation to resource distribution and availability (Merker *et al.*, 2005; Schwitzer *et al.*, 2007b).

By contrast, daily home ranges and daily distance traveled were higher at Sainte Luce as compared to Mandena. Curiously, group B, which had the lowest overall home range, had the highest daily range and distance traveled. We must consider that Kernel density estimators (Worton, 1987) are not reliable to calculate daily range, because they tend to be inconsistent and to overestimate the size of the area when sample size is low (Boyle *et al.*, 2009). Thus, in this case it is better to consider daily ranges calculated via the minimum convex polygon (Odum and Kuenzler, 1955). We must also take into account the different contact hours with the lemurs, that varied daily and between groups. Thus, the most reliable comparisons were done considering the areas used per hour, calculated via the minimum convex polygons. In this case we did not found a significant difference between Mandena and Sainte Luce, but a strong tendency. Distance traveled per hour remained significantly different between Sainte Luce and Mandena.

The lower values of overall home ranges and the higher values of daily ranges and distance traveled by lemurs at Sainte Luce as compared to lemurs at Mandena suggested a higher food availability and a more uniform distribution of food resources at Sainte Luce. In figure 4.2 we can see that at Mandena, especially for group C, lemurs had different and distant *core areas*. The higher values of daily ranges and distance traveled, in particular, suggested that lemurs at Mandena had to save energy more than lemurs at Sainte Luce, as food availability and quality in Mandena was lower (see chapter 6 and 7).

In the degraded forest of Mandena, lemurs used smaller feeding trees (considering tree height and DBH) than those living in the intact forest of Sainte Luce. The DBH (diameter at breast height) is positively correlated to biomass of fruits in a tree (Chapman *et al.*, 1992). Moreover, our results showed that Mandena groups used a lower number of feeding plants per day than those of Sainte Luce, contrary to previous findings (Donati *et al.*, 2011). However, the data cannot be considered reliable considering the different amount of time spent feeding by lemurs. As we will see in chapter 5, time spent feeding was higher in lemurs at Sainte Luce. In Donati *et al.*, 2011 lemurs at Mandena spent more time feeding than those at Sainte Luce, and this can explain our different findings. In fact, we found a higher number of feeding plants per hour of feeding at Mandena as compared to Sainte Luce. This seems to support the hypothesis that lemurs at Mandena had lower and more scattered food resources (i.e. trees at Mandena offered a lower amount of fruits since their DBH was significantly lower compared to those at Sainte Luce, therefore lemurs at Mandena have to feed on more trees in proportion of feeding time).

In conclusion, red collared brown lemurs showed two different strategies on habitat use: in a more degraded forest, such as Mandena, lemurs cope with the lower amount and more scattered distribution of food resources by reducing group size in order to reduce food competition and increase their ranging areas, while in a more intact forest, such as Sainte Luce, lemurs have in general lower ranging areas and groups can support more individuals. However, daily ranges and distance travelled was higher at Sainte Luce, suggesting an influence of energy-saving behaviors at Mandena (see chapter 7). Moreover, habitat use can vary monthly, depending on food availability.

CHAPTER 5

ACTIVITY PATTERN

5.1 Introduction

Until about 30 years ago, primates were classified as either diurnal or nocturnal (Curtis and Rasmussen, 2006). Since the late 1970s, however, it was found that some lemur species of the genus *Eulemur* regularly exhibited both nocturnal and diurnal activity; i.e. they were active throughout the 24 h cycle (Curtis and Rasmussen, 2006; Tattersall, 1987). This pattern was first described in the wild by Tattersall (1979) for *Eulemur fulvus* on the island of Mayotte, between northern Madagascar and northern Mozambique. Later on, this pattern was also described for the congeneric species *E. albifrons, E. albocollaris, E. collaris, E. coronatus, E. macaco macaco, E. mongoz, E. rubriventer, E. rufus and E. sanfordi* (Wright, 1999; Vasey, 2000; Donati and Borgognini-Tarli, 2006; Colquhoun 2006). Tattersall (1987) formally introduced the term 'cathemeral': "the activity pattern of an organism can be regarded as cathemeral when it is about evenly distributed over the 24 h daily cycle, or when significant amounts of activity, particularly feeding and/or travelling, occur within both light and dark portions of the cycle" (p. 201). A cathemeral activity cycle has also been reported in a number of other lemur genera, such as *Hapalemur alaotrensis* (Mutschler *et al.*, 1998; Mutschler, 2002) and *Prolemur simus* (Tan, 2000; Grassi, 2001), and in neotropical owl monkeys of the genus *Aotus* (Wright, 1994; Kinzey, 1997; Fernandez-Duque, 2003). Furthermore, cathemerality may occur in 2 howler monkey species, *Alouatta pigra* and *A. palliata* (Dahl and Hemingway, 1988; Curtis and Rasmussen, 2002; Mutschler, 2002; Fernandez-Duque, 2003; Kirk, 2006).

E. collaris, as other *Eulemur* species, shows cathemeral behavior (Curtis and Rasmussen, 2002; Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006; Schwitzer *et al.*, 2007a), considered by Engqvist and Richard (1991) as an adaptation to cope with a diet having a high fiber and a low carbohydrate content, especially during lean periods, in order to minimize the time in which no food is being processed. In support to this hypothesis *Eulemur* does not show anatomical or physiological adaptations that allow it to retain food in the gut for extended periods of time, thus increasing food energy absorption (Overdorff and Rasmussen, 1995). Other studies supported the “dietary theory” (Wright, 1999; Tarnaud, 2006; Donati *et al.*, 2007a) and demonstrated that cathemerality is also influenced by lunar phases and by light intensity (Donati *et al.*, 2001; Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). Further hypotheses on the origin of cathemerality involve antipredator strategy (van Schaik and Kappeler, 1996) and interspecific competition (Tattersall and Sussman, 1998). In the first case cathemerality has been interpreted as a response to predation pressure by diurnal raptors, while for the second theory, it might be an ecological adaptation to minimize competition for food resources with other sympatric primate species.

In this chapter we will examine diurnal and nocturnal activity of *E. collaris*, making comparisons between study sites. Moreover, we will evaluate the influence of different ecological parameters in nocturnal activity and in diurnal *vs*. nocturnal activity ratio.

5.2 Materials and methods

We collected behavioral data using the instantaneous sampling method, with records every five minutes (Altmann, 1974). To determine diurnal time budget we calculated the daily percentages of each activity of the focal animal, grouping them into four principal categories: resting (including R, H, SB, G, MG, LK and SC; see Appendix I), moving, feeding and other (all the behaviors not included in the previous categories). During the night it was not possible to use the instantaneous sampling method. Therefore, auditory group sampling method (Andrews and Birkinshaw, 1998) was applied during nocturnal observation, where the general activity of the entire group was recorded every five minutes based on visual and auditory clues. The auditory method might overestimate general activity levels, as “active” is also used in cases when part of the group may be resting. However, this approximation is acceptable considering the usual synchrony of *Eulemur collaris* groups. We additionally estimated nocturnal ranges and home ranges per hour of nocturnal observations via the 100% Minimum Convex Polygons (see chapter 4), nocturnal distance traveled, and distance traveled per hour of nocturnal observations.

Astronomical data such as sunset and sunrise, moon phases and nocturnal luminosity were obtained from the Moon® program (version 1.0), using Sainte Luce and Mandena's geographical coordinates as entries (see chapter 3). Nocturnal luminosity index (I) derived from the lunar phase (P), using sunrise, sunset, moonrise and moonset times as shown in the following formula:

$$I = \int_{a}^{b} P \, \mathrm{d}t$$

where a < b (dt = 0.24 h). When sunset precedes moonset, 'a' corresponds to sunset time; when sunset precedes moonrise, 'a' corresponds to moonrise time; when moonset precedes sunrise, 'b' corresponds to moonset time; when sunrise precedes moonset, 'b' corresponds to sunrise time. During nocturnal observations, the above index ranged from 0 to 0.6. At the study sites, night length (time from sunset to sunrise) varied between 10.3 and 13.3 h.

We considered activity to be nocturnal if it occurred between the end of astronomical evening twilight (after sunset, when the sun is at 18° below the horizon) and the beginning of astronomical morning twilight (before sunrise, when the sun is at 18° below the horizon). At the study site, the astronomical twilights lasted about 73 min. Considering the astronomical twilight, the amount of nocturnal observation hours used in our analysis was 111.11 h (STL: 55.08 h; MAN: 56.03 h).

The daily percentages were compared between groups and sites using the non-parametric Mann-Whitney U test. We used the Spearman correlation index to test the relation between nocturnal activity, lunar phase and luminosity. All tests were performed with STATISTICA for Windows, version 8.0, and we considered $p<0.05$ as the significant level.

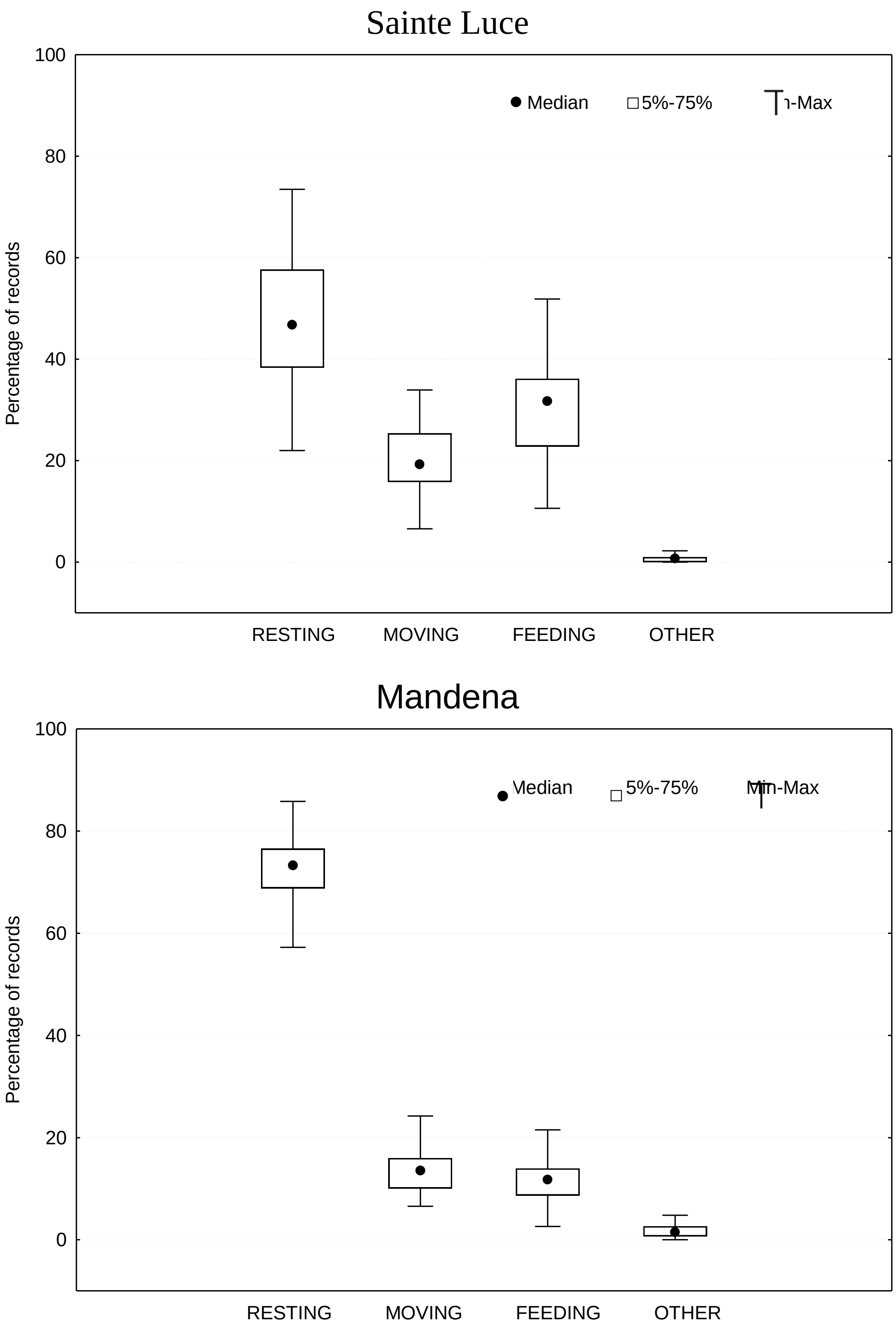
5.3 Results

Concerning diurnal time budget, percentages of records in which lemurs spent time in different activities are shown in Table 5.1 and are represented in Figure 5.1. Statistically significant differences between Sainte Luce and Mandena were found in every categories of diurnal time budget ($U_{50,52}$=125, p<0.001 for resting; $U_{50,52}$=506.50, p<0.001 for moving; $U_{50,52}$=101, p<0.001 for feeding; $U_{50,52}$=861, p=0.003 for other behaviors). Differences between groups living in the same site were found only between group A and group B ($U_{25,25}$=178.50, p=0.009 for moving).

Table 5.1: Diurnal time budget of the four groups. Percentage of records in which *E. collaris* spent time in the various categories of time budget at the two study sites. Values are in medians (in bold) and quartiles. N is the sample size, i.e. days of diurnal observation.

	N	Resting	Moving	Feeding	Other
Group A	**25**	**51.08**	**18.25**	**32.12**	**0.72**
		43.61-60.53	13.19-21.28	24.82-34.59	0.00-1.60
Group B	**25**	**42.34**	**23.36**	**30.39**	**0.71**
		37.25-50.00	16.55-28.47	21.01-37.24	0.00-0.75
STL	**50**	**46.78**	**19.27**	**31.75**	**0.71**
		38.35-57.66	15.79-25.38	22.81-36.15	0.00-0.98
Group AB	**28**	**74.35**	**13.29**	**11.71**	**0.83**
		70.76-76.73	9.62-16.06	8.69-13.79	0.69-1.92
Group C	**24**	**71.79**	**13.82**	**11.78**	**2.16**
		65.97-76.55	10.23-15.50	8.18-15.78	0.36-2.94
MDN	**52**	**73.32**	**13.57**	**11.78**	**1.48**
		68.81-76.57	10.06-16.00	8.69-13.99	0.69-2.66

Fig. 5.1: Diurnal time budget of *Eulemur collaris* at the two study sites.



Monthly variation of diurnal time budget is shown in Figure 5.2.

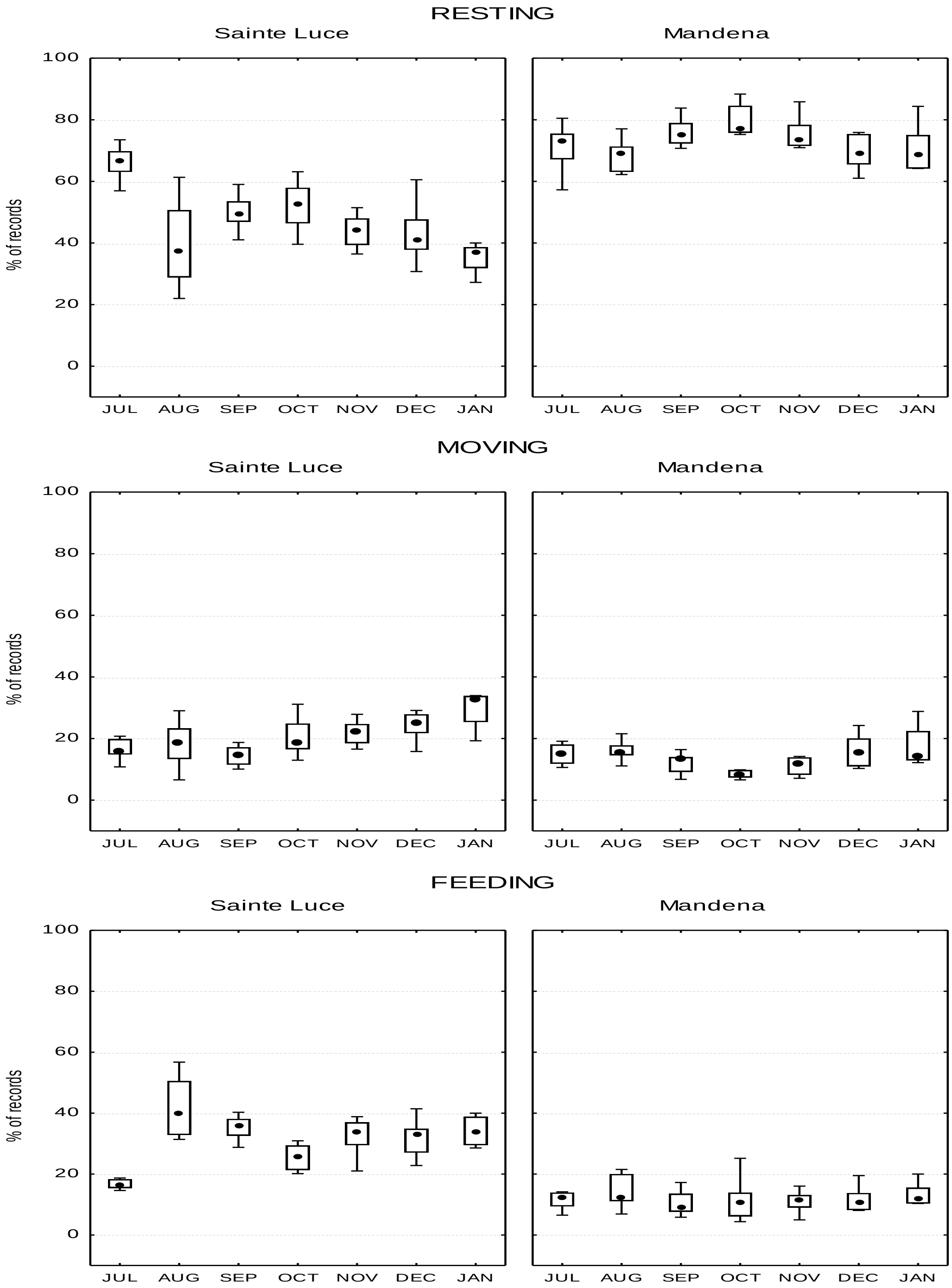
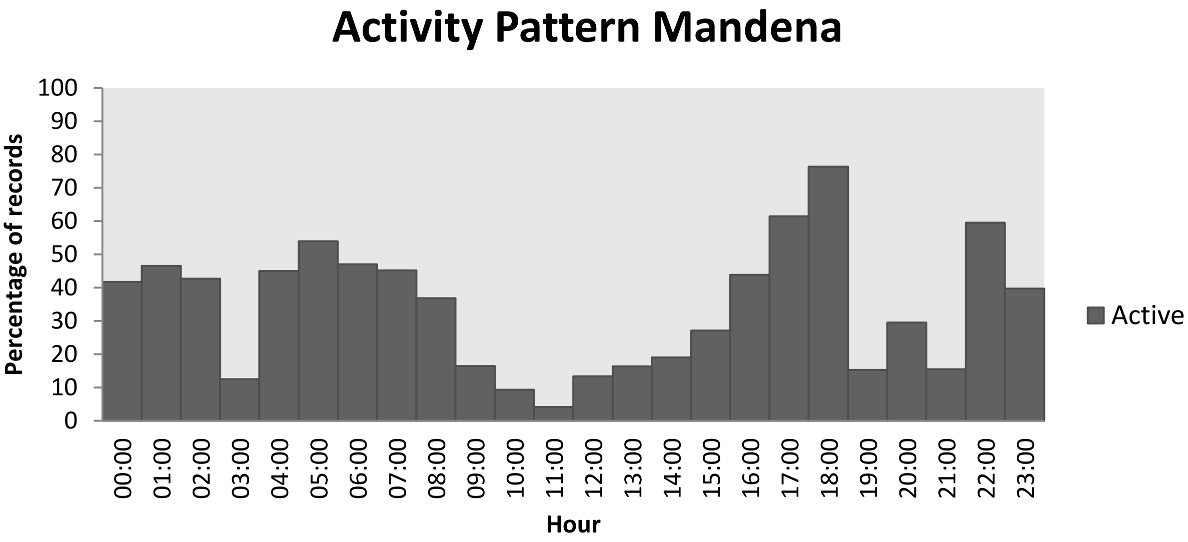


Fig 5.2: Monthly variation of resting, moving and feeding at the two study sites.

● Median □ 25%-75% ┬ Min-Max

Eulemur collaris showed cathemeral behavior over the study period in both forests, with peaks of activity occurring at dawn and dusk, especially at Mandena (Fig. 5.3).



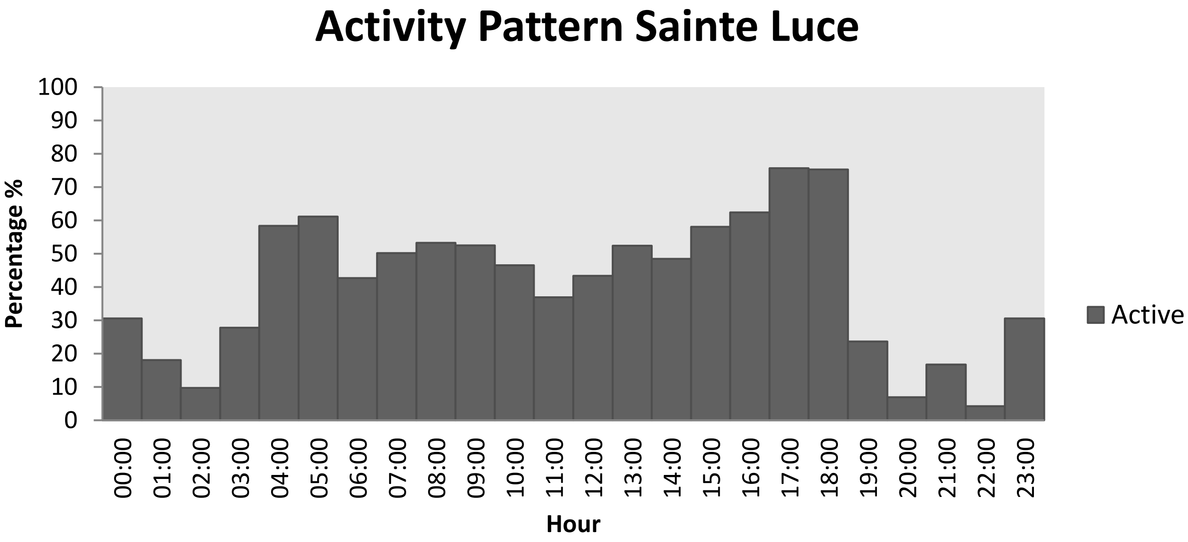


Fig. 5.3: Average 24 h activity pattern in the two forests over the study period. Sunrise ranges between 4:54 and 6:35, sunset ranges between 17:19 and 18:40.

Nocturnal activity in comparison with diurnal activity is shown in Table 5.2 and is represented in figure 5.4. No significant differences in nocturnal activity between the two forests were found ($U_{6,6}$=8, p=0.110). On the other hand, significant differences were found in diurnal *vs*. nocturnal activity ratio ($U_{6,6}$=5, p=0.037).

Table 5.2: Nocturnal and diurnal activity (in percentage of records) at Mandena and Sainte Luce. Values are in medians (in bold) and quartiles.

	N	Nocturnal activity	Diurnal activity	D/N activity ratio
STL	**6**	**16.75**	**53.55**	**2.79**
		13.27-22.86	47.87-57.42	2.09-4.33
MDN	**6**	**37.64**	**26.70**	**0.73**
		16.41-42.59	24.06-30.71	0.53-1.75

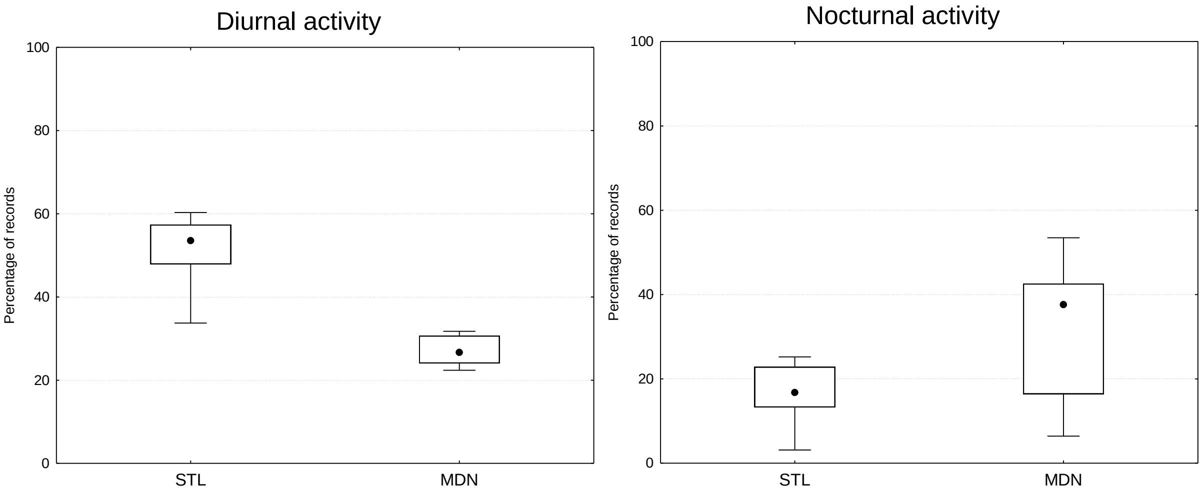


Fig. 5.4: Diurnal and nocturnal activity of *Eulemur collaris* at the two study sites.

● Median □ 25%-75% ┬ Min-Max

Considering the home ranges and the distance traveled during nocturnal observations (Table 5.3), lemurs at Mandena seemed to have higher nocturnal ranges and distance traveled during the night. Monthly variations in nocturnal ranges are shown in figure 5.5.

	N	Nocturnal home range (ha)	Home range per hour (ha)	Distance traveled (m)	Distance traveled per hour (m)
STL	**6**	**0.26**	**0.03**	**238.4**	**27.5**
		0.14-0.44	0.01-0.05	210.6-270.2	24.6-31.1
MDN	**5**	**1.17**	**0.14**	**513.3**	**55.4**
		0.75-1.72	0.08-0.18	497.2-516.3	25.9-65.1
U		4*	4*	4*	5
p-level		0.045	0.045	0.045	0.068

Table 5.3: Nocturnal home ranges and distance traveled at Mandena and Sainte Luce. Home ranges were evaluated via 100% Minimum Convex Polygons as overall nocturnal home ranges and home ranges per hour of nocturnal observations; distance traveled valued as overall distance traveled during the night and distance traveled per hour of nocturnal observation. Values are in medians (in bold) and quartiles, considering the astronomical twilight. Bottom: results of Mann-Whitney test between nocturnal ranges and distance traveled at Sainte Luce and Mandena. *p<0.05

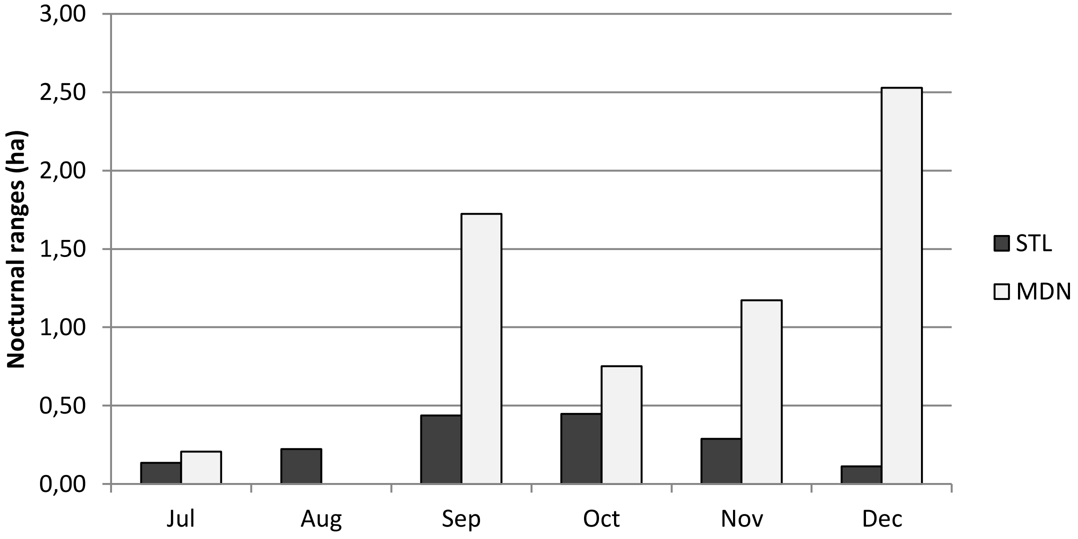


Fig. 5.5: Monthly variation in nocturnal ranges between Sainte Luce (STL) and Mandena (MDN). Nocturnal ranges evaluated via 100% Minimum Convex Polygon. In MDN on August we had no data.

Nocturnal activity appeared not to be significantly influenced by lunar phase (ρs=0.550, p=0.064), and by the relative lunar luminosity index (ρs=0.294, p=0.354). Instead, nocturnal activity was negatively influenced by humidity (ρs=-0.880, p<0.001) (Table 5.4).

Diurnal *vs* nocturnal activity ratio was significantly influenced by lunar phase (ρs=-0.687, p=0.014), and by humidity (ρs=0.880, p<0.001). Nocturnal activity and diurnal *vs*. nocturnal activity ratio seemed not to be significantly influenced by night length and ambient temperature (Table 5.4).

Table 5.4: Nocturnal activity and possible correlates. Moon phase ranges between 0.00 (new moon) and 1.00 (full moon).

Day	N. activity (%)	Night length (h)	Moon phase	Nocturnal luminosity	Humidity (%)	Temp. (°C)	D/N activity
				Sainte Luce			
15-jul	16.15	13.27	1.00	0.54	100.00	19.38	2.09
26-aug	17.36	12.53	0.13	0.02	97.14	19.80	3.48
20-sep	25.22	11.95	0.56	0.14	94.37	21.65	1.99
25-oct	22.86	11.12	0.05	0.01	99.16	22.12	2.09
24-nov	13.27	10.54	0.02	0.00	98.34	24.34	4.33
22-dec	3.16	10.32	0.10	0.01	100.00	23.11	18.05
				Mandena			
26-jul	16.41	13.13	0.24	0.05	96.26	18.61	1.75
12-aug	6.45	12.83	0.97	0.47	100.00	15.25	4.92
12-sep	34.23	12.14	1.00	0.49	87.45	20.10	0.70
12-oct	42.59	11.42	1.00	0.46	91.71	20.81	0.53
9-nov	53.47	10.75	0.97	0.40	90.08	20.78	0.46
9-dec	41.05	10.36	0.98	0.38	93.64	23.34	0.75

5.4 Discussion

Diurnal time budget and diurnal *vs.* nocturnal time budget ratio appeared to be influenced by the study site during the study period. At Mandena resting time was significantly higher than at Sainte Luce in diurnal observations, with a decrease in feeding and moving time. This is in contrast with previous studies (Donati *et al.*, 2011) on *Eulemur collaris* at the same sites, where resting time was not different between Mandena and Sainte Luce, and feeding time was significantly higher at Mandena. However, this strategy has already been observed, with decreased feeding and increased resting, in *Colobus guereza* (Oates, 1977), in *Procolobus rufomitratus* (Marsh, 1981), and in *Macaca sylvanus* (Machairas *et al.*, 2003) living in fragmented and degraded forests.

As we can see from our results, diurnal *vs.* nocturnal activity ratio was influenced by lunar phase, and nocturnal activity in general was influenced by lunar phase and luminosity (Donati and Borgognini-Tarli, 2006; Donati *et al.*, 2009), even if in our study period this is not evident, probably due to the low amount of nocturnal observation. Our analysis could be partially influenced by the observation periods. In fact we made almost all the observations at Sainte Luce during the lower luminosity lunar phases, and at Mandena during the period of high lunar luminosity. This fact could determine a bias, as lemur diurnal activity might decrease with the increase of nocturnal activity, influenced by a higher lunar luminosity, as in the case of Mandena. The higher nocturnal activity and the lower diurnal activity shown by lemurs at Mandena can by explained also by the antipredator strategy (van Schaik and Kappeler, 1996), since we noted an higher risk of diurnal raptors at Mandena (see also chapter 7). Further information will be provided by the study of stress levels which will be performed by Michela Balestri. Additionally, we found higher nocturnal ranges and distance traveled during the night at Mandena. Ranges per hour during the night were lower compared to diurnal ranges, however the difference is higher at Sainte Luce. In fact, at Sainte Luce we found a median of 0.37 ha/h (0.24-0.48 ha/h the quartile range) during diurnal observations and a median of 0.03 ha/h (0.01-0.05 ha/h the quartile range) during the night, and at Mandena we found a median of 0.26 ha/h (0.16-0.44 ha/h the quartile range) during diurnal observations and a median of 0.14 ha/h (0.08-0.18 ha/h the quartile range) during the night. We had the same pattern considering the distance traveled per hour during the day (median, min-max: 93.0 m/h, 36.9-172.2 m/h at Sainte Luce; 70.9 m/h, 19.8-158.8 m/h at Mandena) and during the night (median, min-max: 27.5 m/h, 16.2-43.3 m/h at Sainte Luce, 55.4 m/h, 20.9-68.4 m/h at Mandena). Thus, lemurs at Mandena seemed to move more and to have higher ranges as compared to lemurs at Sainte Luce during the night, while lemurs at Sainte Luce moved more during the day and had higher daily ranges. This seems to support our hypothesis that a low amount of nocturnal observations may overestimate the differences between the two sites, especially for the diurnal time budget. In fact, in Donati *et al.*, 2011 time budget of *Eulemur collaris* considered the same amount of diurnal and nocturnal observations (3 days and 3 nights per months on each group), having a 24h activity pattern. They found more moving and feeding at Mandena than at Sainte Luce. We chose not to balance diurnal and nocturnal observation hours, because cathemerality was not the focus of this research, whose main aim is the evaluation of energy-saving behaviors and feeding strategies in intact and degraded habitats.

However, the high differences in time budget found between the two forests could be explained not only by the influence of lunar phases, but mostly by ecological factors. The lower percentage of activity observed at Mandena throughout the study period could be due to lower availability of resources, so animals might be obliged to use energy saving strategies (see chapter 7 and 8 for further information). In fact primates vary their time budget with changing ecological conditions. There are two possible adjustments: 1) to increase feeding time, and 2) to minimize energy expenditure and reduce metabolic activity by decreasing time devoted to high cost behavior or by resting more (Huang *et al.*, 2003).

Furthermore, we have to consider that group size at Sainte Luce was two times higher than that at Mandena, and this might influence activity patterns. In fact, to obtain enough food for all group members, large groups need to travel more and rest less than small groups, as also seen in the case of red colobus monkeys (*Procolobus badius*), (Gillespie and Chapman, 2001).

In conclusion, lemurs in more degraded forests can supply to the low quality and scattered food resources in two ways: they can increase moving and feeding time (as in Donati *et al.*, 2011) or they can increase resting in order to save energy (as we found). Additionally, we must consider that diurnal time budget in cathemeral lemurs is influenced by lunar phase and by luminosity. Thus, it is better to balance diurnal and nocturnal observations in order to have a 24-h time budget.

CHAPTER 6

FEEDING ECOLOGY

6.1 Introduction

Primates exhibit a broad range of foraging strategies and dietary preferences, including mainly folivorous (e.g. *Lepilemur*, *Colobus*, *Brachyteles*), gummivorous (e.g. *Euoticus, Phaner, Callithrix*), frugivorous (e.g. *Hylobates, Pongo*), insectivorous (faunivorous) (e.g. *Tarsius, Loris*), as well as omnivorous feeding patterns (e.g. *Microcebus, Papio, Pan*) (Clutton-Brock and Harvey, 1977; Nash, 1986; Garber, 1987; Gursky, 2000; Nekaris and Rasmussen, 2003). The relationships between dietary preferences for certain food sources of highly different distribution patterns and quality have been generally recognized as an important factor explaining inter- and intra-specific variation in ecology and behavior of primates (Clutton-Brock, 1974; Clutton-Brock and Harvey, 1977; Wrangham, 1980). Folivores, for example, are usually larger, live in larger groups and have smaller group home ranges than comparable frugivores (Clutton-Brock and Harvey, 1977). Also, the competitive regime and resulting social organization of folivores differ from those of frugivores because they usually experience weaker within-group feeding competition (Wrangham, 1980; van Schaik, 1989). Insectivores (faunivores), in contrast, are usually small, forage solitarily and have large home ranges in relation to their population group size (Clutton-Brock and Harvey, 1977; Gursky, 2007), a feeding pattern that has been linked to intense within-group scramble competition for small resources of high quality that cannot be shared (van Schaik, 1989). However, the classification into frugivores, folivores and insectivores is not possible for numerous primate species of all large radiations, because they use food from several trophic levels.

Eulemur collaris is a mainly frugivorous species, even if it can feed on leaves or less nutritious food when fruits are not available (Donati *et al*., 2011). Malagasy rainforests represent a challenging environment for arboreal frugivorous primates as compared to other tropical forests (Ganzhorn *et al*., 1999; Wright, 1999; Ganzhorn, 2002; Bollen and Donati, 2005; Wright *et al*., 2005). The unpredictable phenology and seasonal lean periods make these forests a hard challenge also for our study species, *Eulemur collaris*, despite its social and ecological flexibility (Donati *et al*., 2011). This feature allows red collared brown lemurs not only to overcome the hostile season, but also to cope with degraded habitats, as, for example, the Mandena forest fragments. In this site, lemurs, introduced in 2000, initially responded well to translocation (Donati *et al*., 2007b), but in recent years the population declined from 25 individuals in 2004 to 12 in 2011. The causes of this reduction are still unknown, but we can advance some hypotheses, such as predation by diurnal raptors (*Polyboroides radiatus* and *Accipiter henstii*), or undocumented movements towards other forest fragments. More likely, however, the secondary forest would not be able to provide adequate food support for groups with an average size greater than the current one

(4-5 individuals per group). Previous studies have already considered group size reduction as an adaptive response of primates to habitat degradation (Symington, 1988; Wilson *et al.*, 1989; Onderdonk and Chapman, 2000; Marshall *et al.*, 2005; Donati *et al.*, 2011), but given the extreme variability in annual food availability for Malagasy littoral rainforests, long-term studies are required to have a more reliable picture of the whole situation.

This chapter deals with the alimentary strategies used by *Eulemur collaris* to survive in such environment. We will consider the plant species eaten, the percentage of food items and their nutrient content, to obtain the actual energy content of the diet of the various groups. Using the Sainte Luce groups as a control, we will compare the data of the two study sites to assess the possible presence of dietary deficiencies for Mandena groups. We expect to find a significant change in diet composition from frugivory to folivory and/or nectarivory in the degraded habitat of Mandena, mainly during lean periods, as reported in previous studies on *E. collaris* (Donati *et al.*, 2011) as well as on other primates living in forest fragments (Tattersall, 1979; Overdorff, 1993; Chiarello, 1994; Tutin, 1999; Martins, 2009). The results on habitat use and on time budget shown in the previous Chapters will be integrated here with the data on diet and nutrition in order to ascertain whether or not the reduction in population density occurred at Mandena can be related to insufficient food quality.

6.2 Materials and methods

Diurnal and nocturnal ethological data collected during the study period by the instantaneous focal method are used in this analyses (see chapter 3). To determine food quality we calculated the daily percentages of each food type eaten by the focal animal. Food types were noted as ripe fruits, unripe fruits, mature leaves, young leaves, flowers, invertebrates, and other (stems, roots, mushrooms, petioles, resin). Differentiation between unripe/ripe fruits and mature/young leaves was based on differences in color, size, and texture. We estimated lemur diet by using the proportion of feeding records, as the poor visibility conditions in dense littoral forests precluded a reliable quantification of the absolute amount of food items consumed. Although temporal measures of diet may produce significant distortions of actual food intake (Kurland and Gaulin, 1987; Zinner, 1999), since we focus on the relative proportion of food items between the two forests and not on the absolute quantification of food consumed, this method can be considered adequate for our purposes. We analyzed arboreal species eaten by calculating the total number and the relative percentage of trees visited per group. We also calculated the percentages of the item eaten per species, which allows us to calculate the Shannon index per group, in order to estimate dietary diversity. The Shannon index formula used is the following:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

where *s* is the number of species consumed, *p* the abundance of each species in the diet (records spent feeding on species *i* over the total feeding records). The greater the dietary diversity, the greater is H'. This measure is particularly suitable when comparing similar dietary regimes, as it considers both the number of food species and their evenness in the diet.

To better evaluate diet composition and its energetic content we performed biochemical analyses on the food items eaten by *Eulemur collaris*. Some nutritional analysis were already available in literature from other field studies (Donati, 2002; Donati unpub. data, 2004; see Appendix III), but for many plants data were not available yet (also depending from annual phenology). So we tried to fill the lack of data by collecting the missing samples. Nevertheless, some food item is still missing, and we put an equivalent food item in our analyses to act as a stopgap (e.g. we replaced a missing ripe fruit energetic composition with another ripe fruit energetic composition, provided that the substitute fruit was of the same plant family of the substituted fruit). Fourteen food items from a total of 129 food items used by lemurs in our study period were substituted. Most of them were marginal fruits (used for less than 1% of feeding time) or occasional food items, the lahinampoly ripe fruits (substituted with ampoly ripe fruits) and the falinandro kely nectar excepted (substituted with another nectar). Considering the potential nutritional variation in time and space, an effort was made to collect food items where and when lemurs were actually feeding, preferably from the same feeding plant. When this was not possible (if animals were feeding high in the canopy or at night, or the food items were entirely consumed), food items were collected on the same trees in a subsequent day, or on other trees of the same species. A total of 41 food samples eaten by *E. collaris* were collected and dried on plates under sun warmth (at least for 2 days). Fresh weight was taken before drying with an electronic balance (LAICA BX9310) in order to calculate water content. Biochemical analyses were conducted at the Department of Animal Ecology and Conservation of Hamburg University in 2011-2012. Samples were weighed again (dry weight), ground to pass a 2-mm sieve and dried again at 50–60°C before the analyses. The lipid content was determined by extraction using petroleum ether, followed by evaporation of the solvent. The amount of crude protein (total nitrogen × 6.25 = crude protein) was determined using the Kjeldahl procedure. As not all nitrogen is bound in proteins and not all proteins are available for digestion, soluble proteins were assessed by BioRad after extraction of the plant material with 0.1 N NaOH for 15 h at room temperature. Soluble carbohydrates and procyanidin (condensed tannins) were extracted with 50% methanol. Amount of soluble sugars was determined as the equivalent of galactose after acid hydrolization of the 50% methanol extract. Concentrations of procyanidin tannins was measured as equivalents of quebracho tannin (Oates *et al.*, 1977). Samples were analyzed for neutral (NDF) and acid (ADF) detergent fibers. NDF represents all the insoluble fiber (cellulose, hemicellulose and lignin) partly digestible in species with hindgut fermentation. ADF represents the fiber fraction containing cellulose and lignin, which are mostly indigestible for *Eulemur spp*.

Polyphenol concentration was estimated as equivalents to pyrogallic acid units. A detailed review of the procedures and their biological relevance is provided by Ortmann *et al.* (2006). To evaluate diet quality, we calculated the metabolizable energy (ME) in the monthly diet. We calculated the weighted proportion of dry matter per month for each nutritional compound, with the proportion of feeding records for each food item as the weighted coefficient (Kurland and Gaulin, 1987). Energy content from food was obtained by standard conversion factors such as 4 kcal/g for carbohydrates, 4 kcal/g for crude proteins and 9 kcal/g for lipids. We used a fiber conversion factor of 3 kcal/g rather than 4 kcal/g usually used for carbohydrates, since the anaerobic microbes take ~1 kcal/g of fibers for their own growth during fermentation processes (Conklin-Brittain *et al.*, 2006). The metabolizable energy was then obtained via the following equation:

$$ME = (9 \times L) + (4 \times SP) + (4 \times SC) + [3 \times (NDF \times 0.415)]$$

where ME is the metabolizable energy per 100 grams (kcal/100 g) of diet; L is the proportion of lipids; SP the proportion of soluble proteins; SC the proportion of soluble carbohydrates and [NDF x 0.415] the fraction of NDF which are digested by brown lemurs (Campbell *et al.*, 2004). Statistical comparisons between sites or groups were made by the non parametric Mann-Whitney U test for independent data. We performed all tests with STATISTICA for Windows, version 8.0 and we considered $p<0.05$ as the significant level.

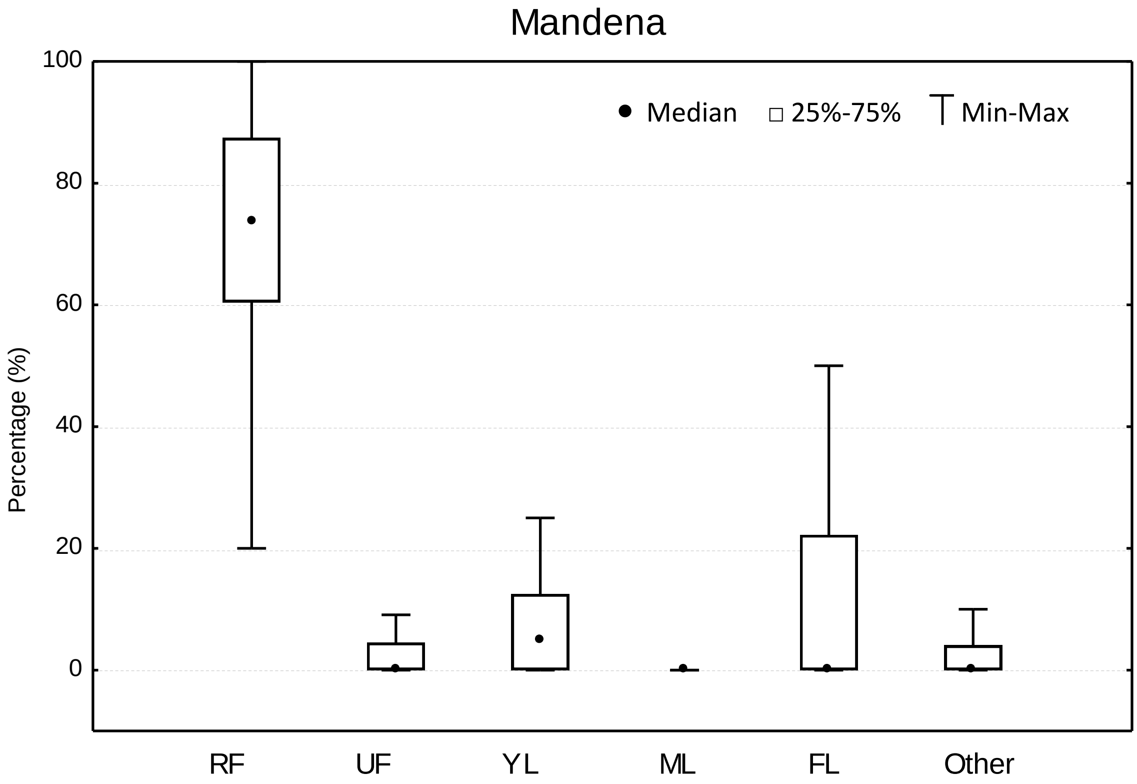
6.3 Results

Eulemur collaris was mainly frugivorous (median, quartile range; ripe fruits: 76.0%, 58.3-88.2%; unripe fruits: 0.0%, 0.0-2.1% of total feeding time) at the two sites during our study period, integrating its diet with flowers (4.3%, 0.0-21.7%), leaves (young leaves: 4.3%, 0.0-12.5%; mature leaves: 0.0%, 0.0-2.9%) and other food items (0.0%, 0.0-3.6%), (see Appendix I). Differences in groups living in the same site were found in Mandena between group AB and group C for mature leaves ($U_{28,24}$=214, p=0.025) and for flowers ($U_{28,24}$=227, p=0.045). No significant differences in diurnal diet were found between Mandena and Sainte Luce (see Table 6.1 and Figure 6.1). Monthly variation is shown in Table 6.2.

Table 6.1: Diurnal diet of the four groups. Percentage of feeding records in which *E. collaris* ate the various categories of food items at the two study sites. Values are in medians (in bold) and quartiles. N is the sample size, i.e. days of diurnal observation. Bottom: results of Mann-Whitney test between diet proportion in diurnal time budget at Sainte Luce and Mandena. *p<0.05

	N	RF	UF	YL	ML	FL	Other
Group A	**25**	**82.5**	**0.0**	**5.4**	**0.0**	**5.7**	**1.9**
		65.7-87.0	0.0-2.1	2.1-11.6	0.0-2.1	0.0-13.6	0.0-4.3
Group B	**25**	**75.9**	**0.0**	**2.1**	**0.0**	**6.3**	**0.0**
		38.3-90.3	0.0-0.0	0.0-14.3	0.0-3.4	0.0-22.2	0.0-1.7
STL	**50**	**78.8**	**0.0**	**3.4**	**0.0**	**5.8**	**0.0**
		48.6-88.2	0.0-0.0	0.0-14.3	0.0-3.2	0.0-21.4	0.0-2.6
Group AB	**28**	**76.0**	**0.0**	**5.6**	**0.0**	**0.0**	**0.0**
		66.7-88.6	0.0-5.9	0.0-12.9	0.0-0.0	0.0-8.9	0.0-2.8
Group C	**24**	**67.7**	**0.0**	**2.0**	**0.0**	**5.4**	**0.0**
		41.4-87.0	0.0-0.0	0.0-10.8	0.0-7.5	0.0-52.9	0.0-4.1
MDN	**52**	**73.6**	**0.0**	**4.9**	**0.0**	**0.0**	**0.0**
		60.4-87.5	0.0-4.5	0.0-12.5	0.0-0.0	0.0-22.2	0.0-4.1
U		1299	1218	1200	1175	1081	1251
p-level		0.995	0.583	0.669	0.401	0.142	0.743

RF: ripe fruits, **UF**: unripe fruits, **YL**: young leaves, **ML**: mature leaves, **FL**: flowers



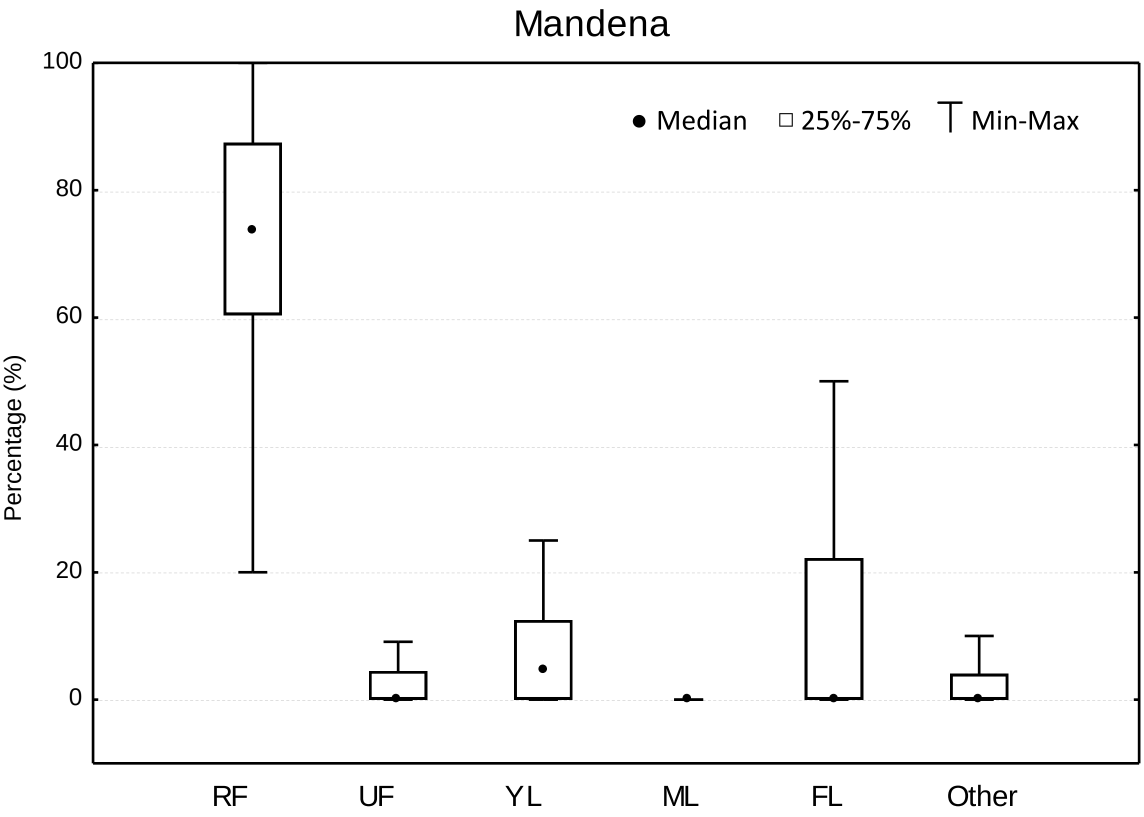


Fig. 6.1: Percentage of food types present in diurnal diet of *Eulemur collaris* at the two study sites. RF: ripe fruits, **UF**: unripe fruits, **YL**: young leaves, **ML**: mature leaves, **FL**: flowers.

		RF	UF	YL	ML	FL	Other
Jul	A	70.31	7.81	7.61	2.17	12.10	0.00
	B	69.19	4.66	15.05	3.04	4.81	3.26
	AB	71.25	8.37	7.64	1.56	8.06	3.13
	C	48.62	0.00	0.00	8.61	40.40	2.36
Aug	A	51.74	0.58	17.62	1.98	27.53	0.54
	B	26.22	0.00	0.57	0.00	71.28	1.93
	AB	79.51	14.58	4.51	0.00	0.00	1.39
	C	16.75	1.33	1.33	11.13	68.27	1.19
Sep	A	86.69	1.42	9.38	0.00	1.89	0.63
	B	87.95	3.27	4.17	1.93	2.68	0.00
	AB	74.62	2.27	3.19	0.00	14.14	5.77
	C	66.84	9.20	20.31	3.65	0.00	0.00
Oct	A	48.68	0.00	36.62	0.81	7.71	6.19
	B	33.28	0.60	40.11	2.05	20.99	2.98
	AB	90.71	1.67	5.24	0.00	2.38	0.00
	C	60.12	0.00	0.00	0.00	39.14	0.74
Nov	A	79.76	1.99	0.54	1.26	14.50	1.95
	B	70.84	0.00	1.55	2.33	25.28	0.00
	AB	78.75	0.00	10.83	0.00	8.33	2.08
	C	74.60	0.00	9.49	3.57	8.25	4.09
Dec	A	93.55	0.00	2.05	0.00	2.17	2.22
	B	93.50	0.00	1.25	2.15	1.58	1.52
	AB	72.50	2.64	18.19	1.39	0.00	5.28
	C	91.11	0.00	6.72	0.00	2.17	0.00
Jan	A	83.28	0.00	6.93	3.91	1.06	4.81
	B	84.22	0.00	14.21	0.00	1.56	0.00
	AB	80.17	0.00	10.06	0.00	4.78	5.00
	C	69.19	0.00	9.97	2.78	8.33	9.72

Table 6.2: Variation in diurnal diet between months of the four groups. Percentage of feeding records in which *E. collaris* ate the various categories of food items at the two study sites. Values are in means. **RF:** ripe fruits, **UF**: unripe fruits, **YL**: young leaves, **ML**: mature leaves, **FL**: flowers.

Group A and group B at Sainte Luce fed on a total of 54 and 48 plant species respectively, while at Mandena group AB used 56 and group C 45 species (see Appendix II). Preferred food items (used for more than 1% of feeding time) accounted for 89.4% and 81.6% of feeding time for Sainte Luce and Mandena groups, respectively (Table 6.4 and Table 6.5). The preferred plant species in common between Sainte Luce and Mandena were: *Uapaca littoralis*, *Cynometra cloiselii*, *Vepris elliotii* and *Cryptocarya sp*.

Monthly dietary diversity evaluated by the Shannon index (H'±SD: 1.83±0.29 in STL and 2.14±0.46 in MAN) differ significantly between sites ($U_{14,14}$=53, p=0.039), due to group AB that had the highest dietary diversity (Table 6.3). In fact, group AB differs significantly from the other groups ($U_{7,7}$=7, p=0.025 with group C, $U_{7,7}$=2, p=0.004 with group A and $U_{7,7}$=1, p=0.003 with group B).

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Mean±SD
STL								
Group A	1.81	1.64	1.52	1.75	2.15	2.12	2.03	**1.86±0.25**
Group B	1.89	1.22	1.43	1.91	2.21	2.04	1.96	**1.81±0.35**
MDN								
Group AB	2.65	2.42	2.11	2.29	2.34	2.35	2.74	**2.42±0.21**
Group C	1.34	1.41	2.14	1.85	2.14	1.50	2.61	**1.86±0.47**

Table 6.3: Shannon index (H') calculated on species eaten per month by *Eulemur collaris* at the two study sites.

Vernacular name	Scientific name	Family	Part eaten	% in diet TOT	A	B
Voapaky vavy	*Uapaca littoralis*	Euphorbiaceae	RF	**24.4**	28.1	20.9
Mampay	*Cynometra cloiselii*	Fabaceae	FL,YL	**11.5**	5.0	17.6
Ampoly	*Vepris elliotii*	Rutaceae	UF,RF	**6.9**	6.4	7.4
Vahabatra	*Cinnamosma madagascariensis*	Canellaceae	UF,RF	**5.7**	6.2	5.2
Zoramena	*Scolopia orientalis*	Flacourtiaceae	UF,RF	**5.7**	3.0	8.2
Berонono	*Trilepisium sp*	Moraceae	FL,UF,RF	**5.0**	5.7	4.3
Harandrato	*Intsia bijuga*	Fabaceae	YL	**4.9**	8.5	1.4
Merana	*Sarcolaena multiflora*	Sarcolaenaceae	FL,RF	**4.5**	4.1	5.0
Hazomamy marécage	*Apodytes dimidiate*	Icacinaceae	RF	**4.1**	2.6	5.6
Falinandro kely	*Dracaena reflexa*	Conavallariaceae	FL,RF	**2.8**	3.9	1.7
Tavolohazo marécage	*Cryptocarya sp.*	Lauraceae	RF	**2.6**	4.3	1.0
Kambatrikambatry	*Drypetes madagascariensis*	Euphorbiaceae	RF	**2.1**	2.6	1.6
Tsilavimbinanto	*Rhopalocarpus coriaceus*	Sphaerosepalaceae	UF,RF	**1.9**	3.0	0.9
Belavenoka	*Noronhia sp*	Oleaceae	UF,RF	**1.8**	0.3	3.3
Lahinampoly	*Olea sp.*	Oleaceae	UF,RF	**1.3**	2.5	0.1
Invertebrates	?	?	ALL	**1.1**	1.7	0.5
Roandria	*Campnosperma micranteium*	Anacardiaceae	RF	**1.1**	0.4	1.7
Velomihanto	*Bakerella clavata*	Loranthaceae	RF	**1.0**	0.4	1.7
Vahiazo	*Dichaepetalum sp.*	Dichapetalaceae	YL	**1.0**	0.6	1.4

Table 6.4: Preferred food items in *Eulemur collaris'* diet at Sainte Luce. Vernacular name, scientific name, family, part eaten (RF: ripe fruits, UF: unripe fruits, FL: flowers, YL: young leaves, ML: mature leaves), percentage in the diet (%), i.e. percentage of time spent by collared lemurs feeding on the plants visited during >1% of total feeding time at Sainte Luce. . TOT: percentage in Sainte Luce; A: percentage in group A; B: percentage in group B.

Vernacular name	Scientific name	Family	Part eaten	% in diet TOT	AB	C
Ampoly	*Vepris elliotii*	Rutaceae	UF,RF	**15.5**	17.7	12.5
Voakarepoka	*Brexia madagascariensis*	Celastraceae	FL,RF	**13.1**	1.5	29.7
Sivory be	*Mammea sessiliflora*	Clusiaceae	UF,RF	**10.5**	12.0	8.3
Mampay	*Cynometra cloiselii*	Fabaceae	FL,YL	**4.7**	4.6	4.9
Nonoka	*Ficus reflexa*	Moraceae	ML,RF	**4.6**	5.6	3.1
Menahihy marécage	*Erythroxilum platicladum*	Erythroxylaceae	RF	**4.5**	4.9	3.9
Voapaky vavy	*Uapaca littoralis*	Euphorbiaceae	RF	**4.2**	3.1	5.7
Tomizo	*Memecylon delphinense*	Melastomataceae	RF	**3.3**	5.5	0.3
Fantsikaitry	*Psychotria sp.*	Rubiaceae	UF,RF	**3.2**	2.4	4.4
Tavoloazo marécage	*Crypctocarya sp.*	Lauraceae	RF	**2.7**	4.0	0.8
Rotrimena	*Syzygium sp.*	Myrtaceae	RF	**2.5**	4.0	0.3
Invertebrates	*?*	?	ALL	**2.0**	2.4	1.6
Ramy	*Canarium boivinii*	Burseraceae	UF,RF	**1.9**	3.3	0.0
Ambora	*Tambourissa purpurea*	Monimiaceae	UF,RF	**1.7**	2.4	0.8
Harongana	*Harungana madagascariensis*	Clusiaceae	RF	**1.7**	0.0	4.2
Nofotrako marécage	*Vitex tristis*	Verbenaceae	FL,RF	**1.6**	1.8	1.3
Fandranabo	*Pandanus sp*	Pandanaceae	FL	**1.5**	2.6	0.0
Meramavo	*Sarcolaena eriophora*	Sarcolaenaceae	FL	**1.2**	0.9	1.6
Sarigavo	*Malleastrum mandenense*	Meliaceae	RF	**1.1**	1.3	0.8

Table 6.5: Preferred food items in *Eulemur collaris'* diet at Mandena. Vernacular name, scientific name, family, part eaten (RF: ripe fruits, UF: unripe fruits, FL: flowers, YL: young leaves, ML: mature leaves), percentage in the diet (%), i.e. percentage of time spent by collared lemurs feeding on the plants visited during >1% of total feeding time at Mandena. TOT: percentage in Mandena; AB: percentage in group AB; C: percentage in group C.

In Table 6.6 and 6.7 we can see the monthly contribution of preferred food species in lemur’s diet. At Sainte Luce (Table 6.6), *Uapaca littoralis* was the most important food item during the lean period (approximately from July to September), with important contribution of flowers of *Cynometra cloiselii* and *Dracaena reflexa* on August, and of ripe fruits of *Apodytes dimidiata* in September. On October, *Uapaca littoralis* remained the most consumed plant species in the diet, with an important contribution of young leaves of *Cynometra cloiselii* and *Intsia bijuga*.

Vernacular name	Jul	Aug	Sep	Oct	Nov	Dec	Jan	N_M
Voapaky vavy	53.01	26.02	52.28	33.23	9.50	-	-	4
Mampay	-	38.71	-	25.71	-	0.27	-	2
Ampoly	0.55	-	-	3.13	29.45	6.32	-	1
Vahabatra	-	-	-	0.31	1.90	21.70	25.30	2
Zoramena	-	0.65	0.80	-	2.14	27.47	9.04	1
Beronono	0.55	-	-	-	1.19	17.31	27.11	2
Harandrato	3.28	9.25	5.09	13.48	-	0.27	-	1
Merana	-	1.08	-	9.09	15.91	-	1.81	1
Hazomamy marécage	-	-	25.20	0.31	-	-	-	1
Falinandro kely	-	12.90	0.80	0.31	-	-	-	1
Tavolohazo marécage	5.46	-	0.80	0.31	6.65	4.95	-	0
Kambatrikambatry	-	-	-	-	11.16	0.27	-	1
Tsilavimbinanto	-	-	-	-	0.48	7.14	9.64	0
Belavenoka	0.55	4.52	5.36	-	-	-	-	0
Lahinampoly	1.64	3.01	2.41	0.94	-	-	-	0
Invertebrates	0.55	-	-	4.08	0.71	1.37	1.81	0
Roandria	-	-	-	-	5.94	-	-	0
Velomihanto	-	-	-	-	5.70	-	-	0
Vahiazo	0.55	0.22	0.54	1.88	0.71	1.10	3.61	0

Table 6.6: Contribution (%) of preferred food species to monthly feeding records at Sainte Luce. **-**: species not consumed; N_M: number of months in which the species was eaten more than 10% of feeding records.

On November, ripe fruits of *Vepris elliotii* and *Drypetes madagascariensis* as the flowers of *Sarcolaena multiflora* had the most important contribution in lemur's diet. On December and January, lemurs at Sainte Luce preferred ripe fruits of *Cinnamosma madagascariensis*, *Scolopia orientalis* and *Trilepisium sp*.

Vernacular name	Jul	Aug	Sep	Oct	Nov	Dec	Jan	N_M
Ampoly	-	2.48	24.14	21.47	25.49	26.05	2.27	4
Voakarepoka	28.47	38.02	-	14.72	0.65	0.84	10.23	4
Sivory be	2.08	0.83	-	9.20	23.53	33.61	3.41	2
Mampay	-	3.31	15.17	1.23	7.19	2.52	2.27	1
Nonoka	14.58	6.61	8.28	-	-	-	2.27	1
Menahihy marécage	4.86	14.88	10.34	-	1.31	-	-	2
Voapaky vavy	-	0.83	7.59	16.56	-	-	-	1
Tomizo	6.94	10.74	4.83	-	0.65	-	-	1
Fantsikaitry	-	-	2.76	8.59	4.58	-	-	0
Tavoloazo marécage	4.86	5.79	3.45	-	0.65	3.36	1.14	0
Rotrimena	-	-	1.38	8.59	4.58	-	-	0
Invertebrates	1.39	0.83	0.69	0.61	2.61	5.04	4.55	0
Ramy	-	-	0.69	7.36	-	0.84	4.55	0
Ambora	0.69	2.48	2.07	3.07	1.96	0.84	-	0
Harongana	10.42	0.83	-	-	-	-	-	1
Nofotrako marécage	5.56	-	-	3.68	0.65	-	-	0
Fandranabo	2.78	1.65	5.52	-	-	-	-	0
Meramavo	-	-	-	6.13	0.65	-	-	0
Sarigavo	-	-	-	-	-	0.84	10.23	1

Table 6.7: Contribution (%) of preferred food species to monthly feeding records at Mandena. **-**: species not consumed; N_M: number of months in which the species was eaten more than 10% of feeding records.

At Mandena (Table 6.7), during the lean period the major resources were the ripe fruits of *Ficus reflexa* (mature leaves were also eaten in this species), *Erythroxilum platicladum*, *Harungana madagascariensis*, *Memecylon delphinense* and *Vepris elliotii*, the flowers of *Brexia madagascariensis* (mostly used by group C) and the young leaves of *Cynometra cloiselii*. *Vepris elliotii* was the most consumed species also on October and November, with the important contribution of *Brexia madagascariensis* (flowers and fruits) and *Uapaca littoralis* (ripe fruits) on October, and of *Mammea sessiliflora* (ripe fruits) on November. Ripe fruits of *Mammea sessiliflora* and *Vepris elliotii* remained the most important food items at Mandena also on December, while on January food items changed, whit the important contribution of *Malleastrum mandenense* (ripe fruits) and *Brexia madagascariensis* (flowers and fruits).

Table 6.8: Monthly nutritional contents at Mandena (MDN, mean between group AB and group C) and Sainte Luce (STL, mean between group A and group B). Percentage of 100 g of dry matter in the monthly diet of *Eulemur collaris*.

		Lipids(%)	CP(%)	SP(%)	SC(%)	NDF(%)	ADF(%)	CT(%)	PP(%)
Jul	**MDN**	4.88	8.48	5.63	9.70	33.99	24.42	0.10	1.73
	STL	2.84	7.57	4.47	9.10	39.32	27.25	0.37	2.93
Aug	**MDN**	4.95	9.45	6.06	11.51	31.98	21.42	0.58	2.47
	STL	2.16	13.17	5.64	14.56	35.17	23.73	0.71	2.96
Sep	**MDN**	7.40	8.73	4.72	15.45	34.85	24.32	1.03	2.74
	STL	2.68	7.09	4.02	22.58	33.87	22.89	0.28	2.67
Oct	**MDN**	7.21	7.63	4.58	16.52	34.43	24.92	0.53	2.12
	STL	2.46	14.98	7.03	12.04	32.43	22.47	1.30	3.65
Nov	**MDN**	8.67	9.04	3.90	21.58	32.96	23.63	0.50	2.56
	STL	7.52	7.31	3.16	19.05	33.63	22.97	0.12	2.91
Dec	**MDN**	11.19	9.33	3.36	20.64	33.04	23.45	0.21	1.67
	STL	4.12	7.18	2.69	21.19	29.47	21.17	0.23	2.11
Jan	**MDN**	4.85	10.82	4.15	15.30	36.63	25.38	0.89	2.21
	STL	2.63	7.93	2.14	16.26	32.05	23.66	0.14	1.70

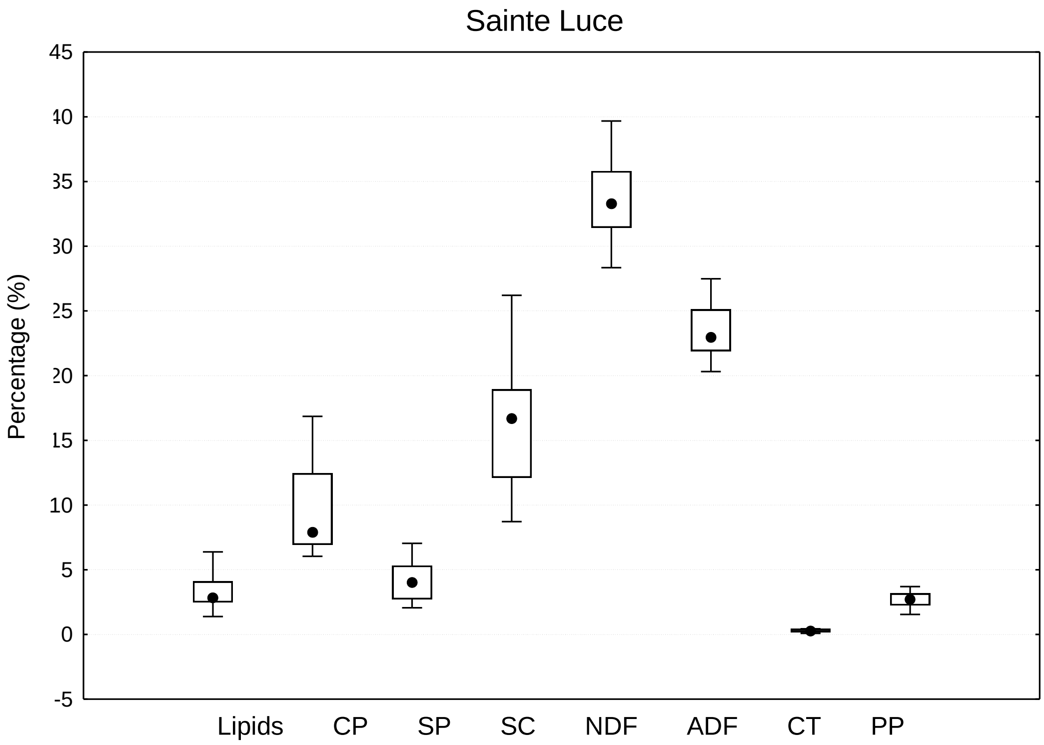
Crude Proteins (**CP**), Soluble Proteins (**SP**), Soluble Carbohydrates (**SC**), Neutral and Acid Detergent Fibers (**NDF** and **ADF**), Condensed Tannins (**CT**) and Polyphenols (**PP**).

The evaluation of monthly nutritional contents (Table 6.8) indicated that the largest percentage of food (dry weight) ingested by red collared brown lemurs was represented by fibers (median, quartile range; NDF: 33.4%, 31.7-36.6%; ADF: 23.5%, 22.1-25.1%), followed by carbohydrates (15.9%, 12.3-18.9%), crude proteins (8.5%, 7.4-10.5%), lipids (4.5%, 2.8-7.9%), soluble proteins (4.0%, 3.2-5.4%), polyphenols (2.5%, 1.9-2.8%) and by tannins (0.4%, 0.2-0.6%). Overall nutritional content (Figure 6.2) shows that diet at Mandena was significantly richer in lipids and lower in polyphenols (Table 6.9). No significant differences were present between groups at the same site, group AB excepted, that had a diet significantly richer in NDF as compared to group C (U7,7=8, p=0.041).

Table 6.9: Overall nutritional contents of the four groups (group A and B at Sainte Luce, group AB and C at Mandena). Percentage of 100 g of dry matter in the diet of *Eulemur collaris* during the study period. Values are in medians (in bold) and quartiles. Bottom: results of Mann-Whitney test between nutritional content of the diet at Sainte Luce and Mandena.

	Lipids(%)	CP(%)	SP(%)	SC(%)	NDF(%)	ADF(%)	CT(%)	PP(%)
Group A	**2.9**	**8.3**	**4.3**	**16.7**	**33.5**	**23.1**	**0.3**	**2.9**
	2.8-4.1	7.5-13.9	2.7-5.9	12.0-18.2	31.4-35.8	21.9-25.1	0.1-0.4	2.0-3.2
Group B	**2.5**	**6.9**	**3.8**	**16.7**	**33.1**	**22.8**	**0.3**	**2.6**
	2.5-4.1	6.7-12.5	2.7-5.3	12.1-24.2	30.6-37.4	20.9-25.6	0.2-1.0	2.2-3.0
STL	**2.8**	**7.9**	**4.0**	**16.7**	**33.3**	**23.0**	**0.3**	**2.7**
	2.5-4.1	6.9-12.5	2.7-5.3	12.1-18.9	31.4-35.8	21.9-25.1	0.2-0.4	2.2-3.2
Group AB	**8.4**	**9.4**	**4.0**	**15.9**	**36.6**	**24.9**	**0.5**	**2.1**
	6.8-9.3	7.5-10.4	3.7-4.3	13.9-18.9	33.2-38.1	23.6-25.6	0.2-0.7	1.7-2.4
Group C	**5.5**	**8.8**	**5.4**	**15.3**	**32.9**	**23.3**	**0.6**	**2.5**
	3.1-8.3	7.5-10.5	3.7-7.0	9.4-20.1	29.3-33.8	21.2-24.1	0.2-0.7	1.7-2.8
MDN	**7.1**	**9.1**	**4.0**	**15.4**	**33.6**	**23.9**	**0.5**	**2.2**
	4.9-9.0	7.5-10.4	3.7-5.4	13.9-18.9	32.1-36.6	23.1-25.1	0.2-0.7	1.7-2.6
U	29*	88	82	89	91	79	69	49*
p-level	0.002	0.646	0.462	0.679	0.748	0.383	0.183	0.024

Crude Proteins (**CP**), Soluble Proteins (**SP**), Soluble Carbohydrates (**SC**), Neutral and Acid Detergent Fibers (**NDF** and **ADF**), Condensed Tannins (**CT**) and Polyphenols (**PP**). *p-level<0.05



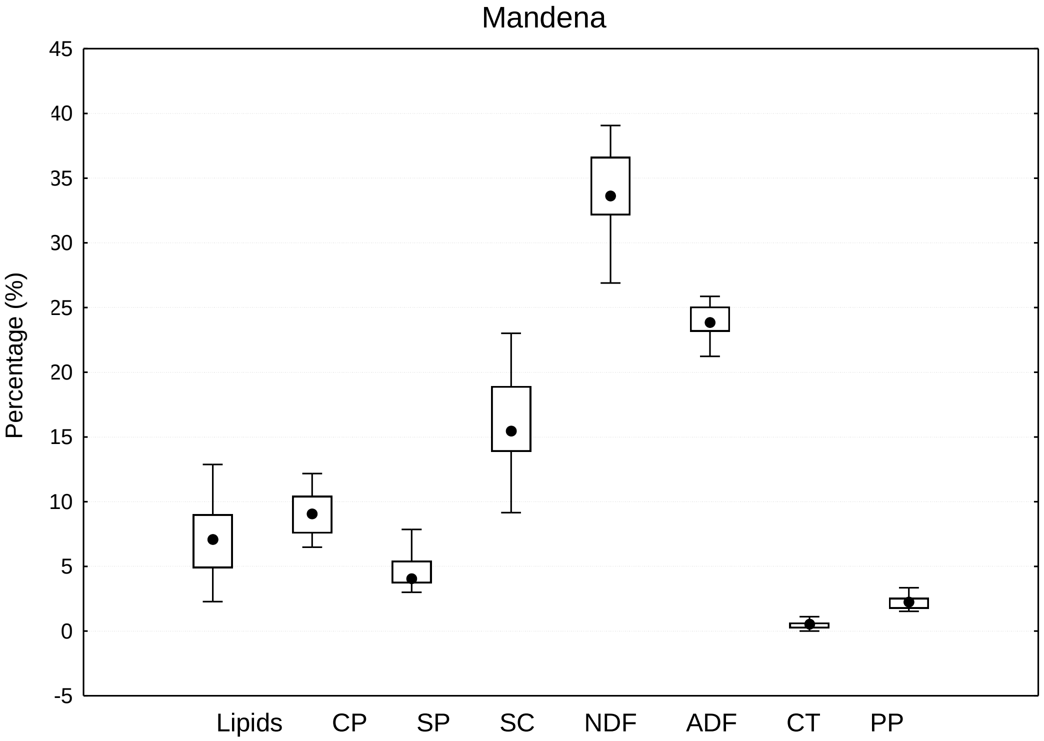


Fig. 6.2: Overall nutritional content at the two study sites. Percentage of 100 g of dry matter in the diet of *Eulemur collaris* during the study period.

Crude Proteins (CP), Soluble Proteins (SP), Soluble Carbohydrates (SC), Neutral and Acid Detergent Fibers (NDF and ADF), Condensed Tannins (CT) and Polyphenols (PP).

Nutritional analyses indicate that marginal fruits at STL contained a lower proportion of lipids as compared to MAN fruits (Table 6.10). No other differences were present between sites, a trend in NDF and ADF in primary fruits excepted. No significant differences were found between groups at the same site.

Table 6.10: Nutritional contents of primary (used for more than 1% of feeding time) and marginal fruits (used for less than 1% of feeding time), leaves and flowers present in *Eulemur collaris* diet at the two study sites as percentage of 100 g of dry matter. Values are in medians (in bold) and quartiles. At the bottom of each category, results of Mann-Whitney test between Sainte Luce and Mandena.

	Lipids(%)	CP(%)	SP(%)	SC(%)	NDF(%)	ADF(%)	CT(%)	PP(%)
				PRIMARY FRUITS				
Group A	**3.8**	**6.5**	**2.2**	**15.2**	**34.3**	**22.4**	**0.0**	**1.5**
	2.1-12.8	3.8-7.6	1.5-3.7	7.5-33.4	23.4-38.2	18.6-27.9	0.0-0.2	0.5-3.9
Group B	**2.4**	**6.1**	**2.1**	**17.6**	**31.4**	**19.8**	**0.1**	**1.7**
	1.5-3.3	4.1-8.4	1.4-4.2	8.2-26.5	23.3-36.3	13.7-25.7	0.0-0.2	0.7-1.6
STL	**2.8**	**6.5**	**2.2**	**16.9**	**32.2**	**20.8**	**0.0**	**1.5**
	1.7-5.3	3.8-7.6	1.5-3.7	7.5-33.4	23.3-38.1	14.6-26.1	0.0-0.2	0.5-3.9
Group AB	**3.1**	**5.5**	**3.6**	**13.1**	**38.5**	**26.3**	**0.4**	**2.2**
	1.6-12.6	3.8-7.8	2.1-4.8	7.0-29.3	28.7-48.8	19.0-32.5	0.0-1.1	1.3-3.5
Group C	**5.9**	**5.6**	**3.4**	**25.0**	**36.8**	**26.3**	**0.1**	**1.3**
	2.1-12.4	4.5-6.7	2.2-4.7	10.7-34.0	22.4-46.2	17.5-32.8	0.0-0.7	0.5-1.7
MDN	**3.5**	**5.5**	**3.4**	**17.1**	**38.1**	**26.3**	**0.4**	**1.5**
	2.0-12.4	4.4-7.3	2.2-4.7	7.5-33.0	24.1-46.7	18.9-32.8	0.0-1.0	0.7-3.1
U	272	287	217	281	209	207	143	298
p-level	0.589	0.810	0.100	0.718	0.070	0.064	0.051	0.976
				MARGINAL FRUITS				
Group A	**2.5**	**5.6**	**2.3**	**12.3**	**42.3**	**27.7**	**0.2**	**1.7**
	1.3-3.9	4.5-7.6	1.6-4.0	6.5-19.3	32.0-50.1	19.3-34.5	0.0-1.0	0.6-3.1
Group B	**2.9**	**6.5**	**2.2**	**10.3**	**42.3**	**27.9**	**0.0**	**1.2**
	1.4-5.1	4.9-7.7	1.5-4.0	5.2-17.9	32.2-55.7	21.9-38.2	0.0-0.6	0.5-2.5
STL	**2.8**	**5.8**	**2.3**	**10.9**	**42.3**	**27.8**	**0.2**	**1.6**
	1.4-4.9	4.6-7.7	1.6-4.0	5.2-18.3	32.1-51.1	20.1-36.2	0.0-0.7	0.6-2.9
Group AB	**4.5**	**5.1**	**2.7**	**11.3**	**45.3**	**32.2**	**0.0**	**0.9**
	2.5-7.0	3.4-6.8	1.8-5.1	5.6-21.3	27.7-56.7	18.6-43.1	0.0-0.4	0.6-1.7
Group C	**3.1**	**4.9**	**2.7**	**13.6**	**42.0**	**24.4**	**0.2**	**1.2**
	2.0-5.2	2.9-7.6	1.8-3.8	9.3-25.9	24.1-50.1	18.6-35.7	0.0-1.1	0.6-2.5

Table 6.10 (continued)

MDN	**3.8**	**4.9**	**2.7**	**11.8**	**43.7**	**28.0**	**0.1**	**0.9**
	2.4-6.0	2.9-7.6	1.8-5.0	8.0-25.9	24.1-55.7	18.6-42.3	0.0-0.5	0.6-2.1
U	1120*	1224	1347	1366	1527	1526	816	1348
p-level	0.015	0.070	0.278	0.332	0.986	0.979	0.603	0.280
LEAVES								
Group A	**2.2**	**8.9**	**2.6**	**5.6**	**46.7**	**29.3**	**0.0**	**0.5**
	1.3-3.2	8.0-15.0	1.7-5.0	2.4-6.8	31.1-53.0	20.9-38.7	0.0-0.2	0.5-2.1
Group B	**2.0**	**13.4**	**3.3**	**3.0**	**32.6**	**22.9**	**0.0**	**0.5**
	1.5-2.7	8.9-16.1	1.9-5.4	2.3-10.1	29.6-48.9	20.2-29.7	0.0-0.2	0.5-2.1
STL	**2.0**	**8.9**	**2.6**	**5.2**	**44.6**	**25.2**	**0.0**	**0.5**
	1.5-3.2	8.1-16.1	1.9-5.4	2.3-7.3	29.6-50.4	20.2-38.3	0.0-0.2	0.5-2.1
Group AB	**3.0**	**10.4**	**2.7**	**5.2**	**41.3**	**28.3**	**0.0**	**0.9**
	1.7-3.8	8.5-15.6	1.5-4.6	4.9-7.1	36.9-48.9	25.2-36.0	0.0-0.5	0.5-2.6
Group C	**2.5**	**8.5**	**2.8**	**5.6**	**42.0**	**27.0**	**0.0**	**1.0**
	1.3-3.0	7.2-12.5	2.0-5.0	3.5-6.2	34.9-50.0	21.3-37.3	0.0-1.4	0.5-3.0
MDN	**2.7**	**8.9**	**2.7**	**5.2**	**41.3**	**28.3**	**0.0**	**0.9**
	1.7-3.2	8.1-15.6	1.5-4.6	4.8-6.2	36.9-49.5	22.2-36.3	0.0-0.7	0.5-2.6
U	192	203	210	211	214	208	179	192
p-level	0.466	0.660	0.792	0.801	0.860	0.744	0.977	0.473
FLOWERS								
Group A	**1.3**	**9.3**	**4.7**	**15.3**	**31.4**	**23.1**	**0.5**	**3.0**
	1.2-2.3	6.2-13.2	3.9-6.1	7.1-23.4	21.5-41.2	15.2-29.0	0.1-1.4	2.2-5.1
Group B	**1.5**	**8.8**	**4.9**	**15.3**	**32.5**	**23.3**	**0.5**	**2.7**
	1.3-2.3	6.2-11.0	4.0-6.1	9.2-23.4	21.5-39.5	15.2-28.6	0.3-1.4	2.2-4.9
STL	**1.3**	**9.3**	**4.7**	**15.3**	**31.4**	**23.1**	**0.5**	**3.0**
	1.3-2.3	6.2-11.0	4.0-6.1	9.2-23.4	21.5-39.5	15.2-28.6	0.2-1.4	2.2-4.9
Group AB	**1.5**	**7.9**	**6.0**	**8.9**	**30.0**	**23.1**	**0.5**	**4.0**
	1.3-2.2	4.8-13.2	3.7-6.4	7.1-17.5	18.4-49.3	11.5-28.6	0.2-1.4	1.9-6.3
Group C	**2.1**	**8.9**	**7.8**	**7.9**	**23.2**	**17.2**	**0.4**	**5.6**
	1.8-4.9	7.5-11.6	6.2-9.4	6.6-15.7	20.7-26.7	14.1-20.4	0.1-2.9	3.6-9.7
MDN	**1.5**	**7.9**	**6.1**	**8.7**	**23.3**	**17.7**	**0.5**	**4.9**
	1.4-2.2	7.1-13.2	5.2-9.2	7.1-17.5	18.4-39.5	11.5-25.8	0.2-1.4	2.3-6.3
U	95	113	74	83	89	88	114	82
p-level	0.416	0.905	0.096	0.197	0.293	0.275	0.953	0.177

Crude Proteins (**CP**), Soluble Proteins (**SP**), Soluble Carbohydrates (**SC**), Neutral and Acid Detergent Fibers (**NDF** and **ADF**), Condensed Tannins (**CT**) and Polyphenols (**PP**). *****p-level<0.05

Concerning metabolizable energy, diet quality at Mandena was significantly higher as compared to Sainte Luce (Table 6.11). The greatest amount of metabolizable energy was due to primary fruits (median, quartile range; 116.6 Kcal/100g of diet, 78.9-159.5 Kcal/100g of diet), followed by marginal fruits (10.4 Kcal/100g, 5.4-20.0 Kcal/100g), leaves (9.9 Kcal/100g, 3.3-20.3 Kcal/100g), flowers (9.6 Kcal/100g, 4.2-36.7 Kcal/100g) and by other food items (2.6 Kcal/100g, 0.4-4.6 Kcal/100g). No significant differences were found between groups at the same site.

Table 6.11: Diet quality. Metabolizable energy (in Kcal/100 g of diet) for each food category used by *Eulemur collaris* during the study period. Values are in medians (in bold) and quartiles. Bottom: results of Mann-Whitney test between Sainte Luce and Mandena.

	PF	MF	L	FL	Other	ME
Group A	**113.0**	**10.1**	**11.2**	**9.6**	**3.0**	**141.6**
	67.1-141.8	2.8-13.5	3.1-22.9	3.6-34.9	0.9-5.9	137.3-163.4
Group B	**92.3**	**5.1**	**3.8**	**5.5**	**2.9**	**147.1**
	44.1-151.2	2.1-20.0	2.8-23.8	2.5-40.6	0.0-4.2	132.7-182.0
STL	**102.6**	**8.6**	**9.8**	**7.5**	**2.9**	**144.3**
	67.1-144.9	2.7-18.4	3.0-22.9	3.6-38.6	0.0-4.2	137.3-179.7
Group AB	**170.7**	**17.3**	**6.3**	**7.8**	**3.3**	**206.9**
	105.8-180.4	8.9-44.1	3.4-21.3	5.6-10.1	1.3-4.9	172.5-217.6
Group C	**112.1**	**11.3**	**15.2**	**12.2**	**1.3**	**174.4**
	49.2-171.3	6.7-32.6	6.9-19.3	3.5-60.8	0.0-5.8	131.0-213.8
MDN	**131.6**	**14.3**	**11.9**	**9.6**	**2.1**	**178.1**
	99.1-171.3	8.9-32.6	4.3-19.3	5.6-27.7	1.1-4.9	171.2-213.8
U	64	64	88	95	92	49*
p-level	0.118	0.118	0.646	0.890	0.783	0.024

Food categories: primary fruits (**PF**), marginal fruits (**MF**), leaves (**L**), flowers (**FL**), other. **ME**: monthly metabolizable energy during the study period. *p-level<0.05

6.4 Discussion

Contrary to our expectation, the percentages of food items eaten between the two sites did not differ significantly. In addition, considering the total amount of food eaten, lemurs at Mandena seemed to have a more caloric diet, richer in lipids. As we observed in chapter 5, lemurs showed different activity patterns: lemurs at Mandena spent more time resting and less time feeding compared to lemurs at Sainte Luce, in contrast with Donati *et al.*, 2011. Low habitat quality is associated with increased feeding and decreased resting also in baboons (*Theropithecus gelada* (Iwamoto and Dunbar, 1983), *Papio cynocephalus* (Altmann and Muruthi, 1988)), while an increased feeding on leaves or some fall-back food is also observed in guenons (*Cercopithecus cephus* (Tutin, 1999)), macaques (*Macaca tonkeana* (Riley, 2007)), howling monkeys (*Alouatta palliata* (Dunn *et al.*, 2009) and lemurs (*Propithecus diadema* (Irwin, 2008)) living in fragments. The situation may be different from 2004 and 2007 (data collection at Mandena by Donati *et al.*, 2011), having more food resources. Unfortunately, we do not have phenological data to compare food availability, but we can argue that the situation in Mandena forest fragments (M15 and M16) is improving. However, the opposite feeding strategy with decreased feeding and increased resting, has been observed in *Colobus guereza* (Oates, 1997), in *Procolobus rufomitratus* (Marsh, 1981), and in *Macaca silenus* (Menon and Poirier, 1996) living in fragmented forests.

Eulemur collaris showed a high dietary flexibility during the study period, adapting the diet to food availability. Red collared brown lemurs' diet was mainly frugivorous, but other food items (such as flowers and young leaves) were frequently used, especially when ripe fruits were scarce. Effectively, young leaves of *Intsia bijuga* and *Cynometra cloiselii*, and flowers of *Brexia madagascariensis* and *Sarcolaena eriophora*, preferred food items at Sainte Luce and Mandena, have a very high content of soluble proteins (table 6.12). Invertebrates only (preferred food items in *Eulemur collaris* diet both at Mandena and Sainte Luce) have a soluble proteins content higher than the above mentioned food items. Ripe fruits are a preferred food item, as they have a high lipid and soluble carbohydrates content as compared to the other food items (table 6.12). However, ripe fruits usually last for one or two months, and lemurs change their diet frequently. At Sainte Luce, *Uapaca littoralis* was the most important plant species as its fruits were eaten from July to November, including the lean period. Other important tree species producing ripe fruits eaten by *E. collaris* were: *Apodytes dimidiata* (on September), *Vepris elliotii* and *Drypetes madagascariensis* (on November), *Cinnamosma madagascariensis*, *Scolopia orientalis* and *Trilepisium sp*. (on December and January). At Mandena, *Vepris elliotii* was the most important plant species as its fruits were eaten from September to December. *Erythroxilum platicladum* (on August and September) and *Mammea sessiliflora* (on November and December) can be considered as the other two very important tree species for ripe fruits eaten by *E. collaris*. *Uapaca littoralis* ripe fruits were important also at Mandena, especially on October, but voapaky vavy density appeared to be lower (pers. obs.).

Table 6.12: list of first and last 10 food items as percentages of lipids, soluble proteins (SP), soluble carbohydrates (SC). *preferred food items at Mandena (M) or Sainte Luce (SL).

Vernacular Name	Scientific Name	Site	Item	Lipids (%)
Ampoly	*Vepris elliotii*	M*,SL*	RF	17.74
Menahihy marécage	*Erythroxilum platicladum*	M*	RF	13.42
Ramy	*Canarium boivinii*	M*	RF	12.98
Tavolohazo marécage	*Cryptocarya sp.*	M*,SL*	RF	12.83
Sikondrokondro	*Rhodocolea sp.*	M	RF	12.63
Sivory be	*Mammea sessiliflora*	M*	RF	12.36
Haziny	*Garcinia aphanophlebia*	M	RF	11.12
Faritsaty	*Bursaia madagascariensis*	M,SL	RF	8.77
Sanira	*Tinopsis conjugata*	SL	RF	8.27
Sizena	*Croton louvelii*	M	RF	8.00
Fantsikaitry	*Pyrostria sp*	M*,SL	RF	0.83
Zoramena	*Scolopia orientalis*	SL*	RF	0.75
Sisikandrongo	*Poupartia chapelieri*	SL	RF	0.65
Hazomainty	*Diospyros sp.*	SL*	RF	0.55
Fandranabo	*Pandanus sp.*	SL	RF	0.43
Voakarepoka	*Brexia madagascariensis*	M	RF	0.41
Mampay	*Cynometra cloiselii*	M*,SL*	YL	0.29
Hazomainty	*Diospyros sp.*	SL	FL	0.29
Belavenoka	*Noronhia sp.*	SL*	RF	0.26
Vahimety	*Monathotaxus sp.*	M	YL	0.17

Vernacular Name	Scientific Name	Site	Item	SP(%)
Insects	*?*	M*,SL*	All	11.45
Mampay	*Cynometra cloiselii*	M*,SL*	YL	11.22
Voakarepoka	*Brexia madagascariensis*	M*	FL	9.57
Meramavo	*Sarcolaena eriophora*	M*	FL	9.15
Harandrato	*Intsia bijuga*	SL*	YL	8.63
Sanira	*Tinopsis conjugata*	SL	RF	8.11
Hazomainty	*Diospyros sp*	M,SL	RF	7.84
Taolana	*Rothmannia mandenensis*	SL	FL	7.71
Nanto	*Faucherea exandra*	M,SL	RF	7.05
Mokarana	*Macaranga perrieri*	M,SL	RF	6.40

Table 6.12 (continued)

Fandranabo	*Pandanus sp.*	SL	RF	1.09
Vahifotsy	*Jasminium kitchingii*	M,SL	YL	1.09
Fantsikaitry	*Pyrostria sp*	M*,SL	RF	0.94
Belavenoka	*Noronhia sp*	SL*	RF	0.72
Nofotrako marécage	*Vitex tristis*	M*	RF	0.71
Falinandro kely	*Dracaena reflexa*	M,SL	RF	0.71
Vahilengo	*Morinda sp.*	M	YL	0.65
Voakarepoka	*Brexia madagascariensis*	M	RF	0.62
Vahabatra	*Cinnamosma madagascariensis*	SL*	RF	0.61
Vahimbokatepoka	*Senecio sp.*	M	YL	0.49

Vernacular Name	**Scientific Name**	**Site**	**Item**	**SC(%)**
Hazomamy marécage	*Apodytes dimidiata*	SL*	RF	64.06
Tsilanitria	*Vaccinum ermirnense*	M	RF	50.39
Tavolo	*Tacca leontopetaloides*	SL	RF	48.31
Merana	*Sarcolaena multiflora*	SL*	FL	46.62
Rotrimena	*Syzigium sp.*	M*,SL	RF	43.36
Haziny	*Garcinia aphanophlebia*	M	RF	43.26
Lona	*Oncostenum subcuspidatum*	M	RF	40.76
Vahabatra	*Cinnamosma madagascariensis*	SL*	RF	38.53
Menahihy marécage	*Erythroxilum platicladum*	M*	RF	36.00
Fanstikaitry	*Pyrostria sp*	M*,SL	RF	33.96
Beronono	*Trilepisium sp*	SL*	RF	2.63
Vahy 2	*Senecio sp.*	SL	YL	2.59
Roandria	*Campnosperma micranteium*	SL*	RF	2.50
Vahiazo 1	*Dichaepetalum sp.*	M,SL	YL	2.29
Voapaky lahy	*Uapaca ferruginea*	M,SL	RF	2.26
Ramy	*Canarium boivinii*	M*	RF	2.17
Tavolohazo	*Cryptocarya retusa*	SL	YL	2.07
Mushroom harandrato	*?*	SL	All	1.82
Vahiboatsimatra	*Salacia madagascariensis*	M,SL	YL	1.48
Insects	*?*	M*,SL*	All	0.86

In some primate species, the need for efficient extraction of nutrients and energy and the digestion of fibrous components is achieved by specific anatomic adaptations such as the sacculated stomach of colobines (Chivers, 1995) or the enlarged caecum-colon of leaf-eating lemurs (Chivers and Hladik, 1980; Martin, 1990). However, *Eulemur spp.* do not possess specializations of their digestive tract (Hill, 1953). On the contrary, they show an extremely rapid food transit time (between 1.5 and 3.2 h according to Overdorff and Rasmussen, 1995; Campbell *et al.*, 2004). Holding anatomy and diet constant, shorter transit times result in lower levels of fermentation and reduced energy extraction from fibrous food (Milton, 1998; Lambert, 2002). Scaled on body mass (mean transit time in hours/mean body mass in kilograms), the food transit time of brown lemurs is not only shorter than that recorded for specialized, folivorous primates (*E. fulvus*: ≈0.9; *Hapalemur griseus*: ≈35.0; Overdorff and Rasmussen, 1995; Campbell *et al.*, 2004), but it is short even when compared to frugivore/folivore primates lacking gut specializations (e.g. *Cercopithecus spp.*, between 3.0 and 8.0; Lambert, 2002). In fact, *Eulemur* food transit time approaches the values recorded for specialized fruit-eaters (*Pan troglodytes*, 0.5; Lambert, 2002; *Ateles geoffroyi*, 0.6; Milton, 1984). In line with the above observations, *Eulemur* fibre digestion ability is low as compared to other frugivore/ folivore primates (Lambert, 2002; Campbell *et al.*, 2004). In summary, lacking anatomical adaptations to cope with a fibrous diet *Eulemur spp.* seem to adopt a “power feeding strategy” that consists in processing a large volume of food per unit time to meet nutritional requirements (Milton, 1998; Simmen *et al.*, 2003). One of the most important criterion for *Eulemur collaris* dietary choices is the low amount of acid detergent fibers, not digested by those lemurs. In fact, low ADF content food items were preferred in both sites, especially at Sainte Luce (Table 6.13).

Table 6.13: list of last and first 10 food items as percentages of acid detergent fibers (ADF). *preferred food items at Mandena (M) or Sainte Luce (SL).

Vernacular Name	Scientific Name	Site	Item	ADF(%)
Belavenoka	*Noronhia sp*	SL*	RF	5.45
Harandrato	*Intsia bijuga*	SL*	YL	5.83
Hazomamy marécage	*Apodytes dimidiata*	SL*	RF	9.78
Fandramana	*Aphloia theaeformis*	M	RF	9.90
Vahabatra	*Cinnamosma madagascariensis*	SL*	RF	10.38
Lona	*Oncostenum subcuspidatum*	M	RF	10.99
Menahihy marécage	*Erythroxilum platicladum*	M*	RF	10.99
Sivory be	*Mammea sessiliflora*	M*	RF	11.69
Zoramena	*Scolopia orientalis*	SL*	RF	12.78
Tavolo	*Tacca leontopetaloides*	SL	RF	13.72
Vahilengo	*Morinda sp.*	M	UF	42.40
Fantsikaitry marécage	*Gaertnera sp.*	M	RF	43.10
Tavolohazo marécage	*Cryptocarya sp.*	SL	ML	43.90
Tavolohazo	*Cryptocarya retusa*	SL	YL	45.59
Lendemibe	*Anthocleista madagascariensis*	M,SL	RF	45.90
Nofotrakoho marécage	*Clerodendrum arenarium*	SL	FL	47.49
Fandranala (vakoa)	*Pandanus sp.*	M	RF	48.18
Voapaky lahy	*Uapaca ferruginea*	M,SL	RF	51.01
Fandranabo	*Pandanus sp.*	SL	RF	55.23
Mushroom harandrato	*?*	SL	All	60.48

Concerning ADF and NDF (acid and neutral detergent fibers), we found no differences in dietary content between Mandena and Sainte Luce (Table 6.9). However, this data may be incorrect, as we considered the percentage in diet as the percentage of the food items eaten in feeding records during our diurnal and nocturnal observations. In fact, we don’t have a reliable amount of food ingested by lemurs (food intake, Zinner, 1999), as the processing time of different food items is different. For example, drupes of

Uapaca littoralis or *Vepris elliotii* require high processing times, as they need to be opened to swallow the pulp discarding the husk. Other fruits, as for example *Erythroxilum platicladum, Apodytes dimidiata* and *Trilepisium sp*. have small berries that can be easily and quickly swallowed without processing. Thus, it is more reliable the comparison between primary fruits (eaten for more than 1% of feeding time), as we don't have the effective food intake (see Donati *et al*., 2011). In this perspective, primary fruits at Mandena had a higher content in NDF, ADF and condensed tannins as compared to Sainte Luce primary fruits (Table 6.10). We can argue that, in general, *Eulemur collaris* tend to avoid 'bad fruit' consumption, searching for 'good fruits'. When possible, 'bad fruits' are eaten occasionally, tested and then discarded, and can be considered as 'marginal fruits' eaten during less than 1% of feeding records. However, it is not possible in each period to avoid 'bad fruit' consumption, especially at Mandena. So, the higher content of NDF, ADF and condensed tannins in comparison with Sainte Luce must be due to the higher consumption of 'bad fruits', which were included in the 'primary fruits', i.e. eaten more than 1% of feeding records. In fact, ripe fruits of *Malleastrum mandenense, Harungana madagascariensis*, *Tambourissa purpurea*, *Ficus reflexa* were 'primary fruits' in Mandena even if their NDF, ADF and CT content is high (see Table 6.13, Table 6.14 and Appendix III).

Tannins, in particular, are known to bind proteins and reduce their digestibility (De Gabriel *et al*., 2009), therefore limiting tannin ingestion might be necessary for lemurs. In fact, a low fruit protein content seems to be a general rule in Madagascar as compared to other continents (Ganzhorn *et al.*, 2009).

Table 6.14: list of first 10 food items as percentages of condensed tannins (CT) and polyphenols (PP). *preferred food items in Mandena (M) or Sainte Luce (SL).

Vernacular Name	**Scientific Name**	**Site**	**Item**	**CT(%)**
Sarigavo	*Malleastrum mandenense*	M*	RF	6.70
Nofotrako marécage	*Vitex tristis*	M*	FL	5.44
Sanira	*Tinopsis conjugata*	SL	RF	4.74
Mampay	*Cynometra cloiselii*	M*,SL*	YL	4.11
Nanto	*Faucherea exandra*	M,SL	RF	3.51
Taolana	*Rothmannia mandenensis*	SL	FL	3.16
Menahihy marécage	*Erythroxilum platicladum*	M*	RF	2.58
Ambora	*Tambourissa purpurea*	M*,SL	RF	2.53
Vahabatra 1	*Cinnamosma madagascariensis var. namororensis*	SL	RF	1.74
Vahiazo A	*Secamone sp.*	M	YL	1.41

Vernacular Name	**Scientific Name**	**Site**	**Item**	**PP(%)**
Meramavo	*Sarcolaena eriophora*	M*	FL	13.01
Kambatrikambatry	*Drypetes madagascariensis*	M,SL*	RF	11.41
Sisikandrongo	*Poupartia chapelieri*	SL	RF	10.56
Sanira	*Tinopsis conjugata*	SL	RF	7.58
Nanto	*Faucherea exandra*	M,SL	RF	6.41
Nofotrako marécage	*Vitex tristis*	M*	FL	6.29
Sarigavo	*Malleastrum mandenense*	M*	RF	6.01
Mampay	*Cynometra cloiselii*	M*,SL*	YL	5.73
Randramboay	*Euphorbia lophogona*	SL	FL	5.19
Taolana	*Rothmannia mandenensis*	SL	FL	5.05

In conclusion, *Eulemur collaris* is able to cope with degraded forests changing his feeding behavior. In a more degraded forest, such as Mandena, lemurs spend less time feeding and more time resting compared to a more intact forest, such as Sainte Luce. *E. collaris* is mainly frugivorous, integrating its diet especially with young leaves, flowers and invertebrates. Due to their dietary flexibility, collared brown lemurs are able to select better food items, avoiding ‘bad’ food items. However, this is not possible in each season, especially in a more degraded forest, and *E. collaris* must integrate his diet with marginal fruits, mature leaves and fall-back foods.

CHAPTER 7

BEHAVIORAL THERMOREGULATION

7.1 Introduction

Primates are able to cope with the thermic fluctuation of the environment by both physiological processes and behavioral mechanisms of thermoregulation (Stelzner and Hausfater, 1986; Bicca-Marques and Calegaro-Marques, 1998; Schino and Troisi, 1990; Hill, 2006; Kobbe *et al.*, 2010). In fact, primates have been shown to reduce the physiological cost of thermoregulation in behavioral ways, such as adjustment in postures and activity, huddling and microhabitat selection (Iwamoto and Dumbar, 1983; Schino and Troisi, 1990; Bicca-Marques and Calegaro-Marques, 1998; Hanya *et al.*, 2007; Campos and Fedigan, 2009). Adjustment in postures and huddling allows the animal to reduce heat dissipation during the coolest periods, due to changing in body surface/volume ratio (Hanya *et al.*, 2007). Primates also move to different microhabitats whose thermal condition is closest to their thermoneutral zones (Hanya *et al.*, 2007). The thermal environment can vary within microhabitats such as sunshine, shade, on the ground, or on trees. Additionally, other climatic factors, such as humidity, wind velocity and solar radiation may affect the perception of external temperature (Hill *et al.*, 2004). A high relative humidity, for instance, increases perceived temperature, because of a decrease in evaporation rate, while perceived temperature decreases in the presence of wind because of the higher efficiency of heat loss by convection (Mount, 1979). It was also demonstrated that climatic variables are not the only variables affecting thermoregulatory strategies, but dietary energy content, feeding time and food availability are strongly related to the use of various thermoregulatory strategies (Cruz-Neto and Bozinovic, 2004; Canale *et al.*, 2010).

Malagasy island environment is characterized by a pronounced seasonality and a climatic unpredictability, with temperatures dropping as low as 5°C during the coolest period (Wright, 1999). Fluctuations in food availability, with the relative decrease during the cooler period represent a serious challenge to primate survival. Many smaller lemur species cope with adverse periods by reducing their metabolism and entering a state of temporary torpor (*Microcebus murinus, Microcebus griseorufus*) or of a prolonged hibernation (*Cheirogaleus medius*) (Dausmann *et al.*, 2005; Dausmann *et al.*, 2008; Canale *et al.*, 2010). Such physiological adaptations are unknown in red collared brown lemurs, but previous studies have demonstrated that they face the cooler season using thermoregulatory strategies such as modifications of the activity pattern, by postural and social thermoregulation, and by microhabitat selection (Donati *et al.*, 2010). The aim of this part of the research is to investigate the role of climatic and dietary-related factors on behavioral thermoregulation in groups of red collared brown lemurs living in a secondary forest fragment (Mandena), comparing them with groups living in an almost intact forest fragment (Sainte Luce), in order to identify possible thermoregulatory stress due to habitat degradation. In fact we expected to find a more marked thermoregulatory behavior in *Eulemur collaris* groups living at Mandena, due to the lower protection of the canopy from climatic factors and to a lower food availability. We correlated with seasonal fluctuations in temperature the activity adjustments (percentage of time spent resting), the social thermoregulation (frequency of huddling behavior), the postural thermoregulation (resting in curled and prone positions), and the microhabitat selection. If seasonality is influential, we predicted that lemurs would rest more and use huddling and curled postures more frequently during cooler periods and would huddle less and spend more time in prone postures during warmer periods. We further examined the role of some climatic and dietary-related factors in determining frequencies of the various types of behavioral thermoregulation. Especially, we investigated the influence of dietary energy content. Given the overall resource seasonality of Madagascar, we predicted that lemur thermoregulatory behaviors would be shaped not only by climatic, but also by dietary-related factors: when food is scarce or has lower energy content lemurs should use energy saving behaviors more often.

7.2 Materials and methods

Diurnal ethological data collected during the study period by the instantaneous focal method are used in this analyses (see chapter 3). We considered separately active behaviors (feeding, foraging, moving, and social behaviors) from nonactive behaviors (resting alone or huddling with one or more others), and we also collected the food type consumed (see chapter 6), the level above ground (measured at 1-m intervals) and the position in the tree crown (distance from the trunk). We also recorded climatic conditions (meteorology and wind presence) by the *ad libitum* method. The daily proportion of huddling with another animal weighted by the total number of instantaneous records was used to quantify social thermoregulation. We considered as thermoregulatory postures those that allowed animals to retain ('curled' positions) or dissipate ('prone' positions) body heat when environmental conditions required it (see Appendix I for a detailed description of thermoregulatory postures). Postural thermoregulation was quantified using two variables: the daily proportion of instantaneous observations in postures 1 and 2, 'curled' postures, and the daily proportion in postures 4 and 5, 'prone' postures. We excluded posture 3 from the analysis because its significance for thermoregulatory function was affected by the fact that this posture is used during activities such as feeding, grooming, inspecting, etc. When taken alone posture 3 was often transitorily maintained for very short periods, so it cannot be considered a purely "resting posture" (Donati *et al.,* 2010). Microhabitat selection was quantified as the daily proportion of records in the canopy, (i.e., above 6 m at Sainte Luce and 4 m at Mandena). This is the lower limit of the forest canopy and the animals were on average more exposed to meteorological factors when resting/moving above this height. In fact, appreciable differences in terms of daily temperature and relative humidity was recorded between the understory of the littoral forest and the canopy, i.e., larger fluctuations characterize the upper levels (up to 18°C for temperatures and up to 10% for relative humidity; Donati and Borgognini, 2006). Differences between the upper canopy limit between Mandena and Sainte Luce are due to the fact that the forest height at Mandena is lower than at Sainte Luce (see chapter 3 and 4). We considered the upper canopy as the 60 % of the mean tree height. Moreover, we distinguished among three positions in the crown during nonactive behaviors: 1) lemurs resting near the trunk (the most protected from climatic variables); 2) lemurs resting in the middle of the crown; 3) lemurs resting in the external part of the crown (the most exposed to climatic variables).

Temperature and relative percentage humidity were registered at 30 minutes intervals by five data loggers (Hobo H8 Pro) operated by custom software (BoxCar 3.51 for Windows, Onset Computer Corporation). Two data loggers were placed at Mandena: one in M16 forest, in the middle of group AB home range, and one in the forest near the plant nursery, used by group C. It was not possible to place the data logger in *analamafotra* (see chapter 3) because of the impossibility to enter into the swamp during the rainy season. Therefore, we considered the data logger near the plant nursery as the one to get data for group C. Three data loggers were placed at Sainte Luce: one near the little swamp in the middle of group B home range, one in the middle of group A home range, and one near the biological station (group A used this part of the forest, but not in our study period). Data were downloaded on computer via

HOBOware® software, version 3.3.0 (Onset Computer Corporation).

Thermoregulatory behaviors were related to climatic factors and to metabolizable energy (ME), as a measure of diet quality (see chapter 6). Statistical comparisons between sites or groups were made by the non parametric Mann-Whitney U test for independent data. We used the Spearman correlation index to test relations between climatic variables (temperature and humidity) and dietary related data with thermoregulatory variables (resting time, thermoregulatory postures, huddling and microhabitat selection). Additionally, we tested relations between daily home ranges/h (calculated via 100% MCP) and distance traveled/h (see chapter 4) with climatic and dietary variables. We performed all tests with STATISTICA for Windows, version 8.0 and we considered $p<0.05$ as the significant level.

7.3 Results

Climatic data from data loggers are shown in Figure 7.1.

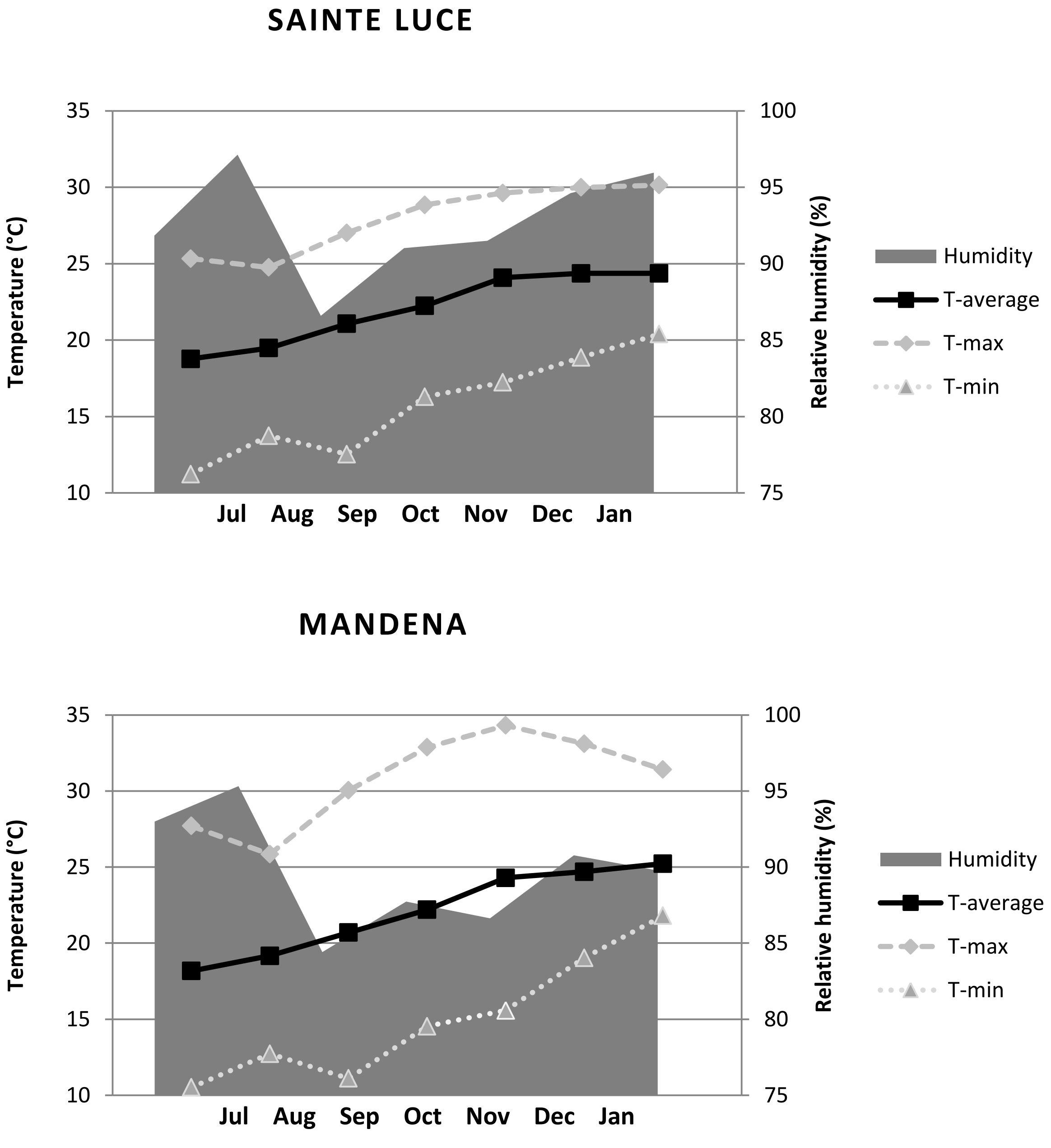


Fig. 7.1: Climatic profile at the two study sites. Monthly maximum temperature (T-max), minimum temperature (T-min), average temperature (T-average) and mean relative humidity trends for Sainte Luce (group A data logger) and Mandena (group AB data logger).

Fluctuations in temperature seemed to be more relevant for Mandena (T-max – T-min = 23.79 °C) as compared to Sainte Luce (T-max – T-min = 18.92 °C) (Table 7.1). At Mandena the minimum ambient temperature was registered on July (10.52°C) as at Sainte Luce (11.22°C), while the maximum ambient temperature at Mandena was registered on November (34.31°C) and at Sainte Luce on January (30.14°C).

	T-average (°C)	**T-max (°C)**	**T-min (°C)**	**Humidity (%)**
STL	22.04	30.14	11.22	92.66
MDN	22.06	34.31	10.52	89.66

Table 7.1: Climatic mean values at Mandena and Sainte Luce. Maximum temperature (T-max), minimum temperature (T-min), average temperature (T-average) and mean relative humidity trends for Sainte Luce (group A data logger) and Mandena (group AB data logger) during the study period.

In chapter 5 we saw that groups at Mandena showed a significantly higher percentage of resting as compared to those living in Sainte Luce (Mandena: median, quartile range; 73.32 %, 68.81-76.57 %; Sainte Luce: median, quartile range; 46.78 %, 38.35-57.66 %), with $U_{50,52}$=125, p<0.001 as result of Mann-Whitney U test. Now we will consider differences in postural and social thermoregulation. Postural thermoregulation was different between Mandena and Sainte Luce considering curled postures, that were significantly more used at Mandena (Table 7.2). No significant differences were found between groups living at Sainte Luce, while at Mandena group C used more curled postures ($U_{28,24}$=220, p=0.032) and more huddling ($U_{28,24}$=201, p=0.013) as compared to group AB.

Table 7.2: Postural thermoregulation at Mandena and Sainte Luce. Percentages of "curled" and "prone" postures, and huddling in resting time of groups living at Mandena and Sainte Luce during the study period. Values are in medians (in bold) and quartiles. Bottom: results of Mann-Whitney test between resting percentages in diurnal time budget at Sainte Luce and Mandena. *p<0.05, **p<0.01

	Curled postures	Prone postures	Huddling
Group A	**73.24**	**0.00**	**40.91**
	56.45-82.89	0.00-1.72	27.27-61.22
Group B	**60.78**	**0.00**	**35.09**
	56.34-76.12	0.00-1.96	15.69-51.47
STL	**67.01**	**0.00**	**38.06**
	56.34-78.26	0.00-1.96	19.64-59.78
Group AB	**72.81**	**0.00**	**33.97**
	64.98-79.69	0.00-4.17	14.75-63.33
Group C	**82.10**	**0.45**	**65.28**
	72.73-87.77	0.00-3.58	32.24-77.55
MDN	**78.50**	**0.00**	**38.85**
	66.17-84.73	0.00-3.66	24.25-74.23
U	861**	1203	1136
p-level	0.003	0.516	0.271

During the study period, thermoregulatory postures seemed to be correlated to ambient temperature (Fig. 7.2) . In fact, a strong negative correlation was found between curled postures and corresponding temperatures (ρs=-0.487; p<0.001), and a strong positive correlation between prone postures and relative temperatures (ρs=0.567, p<0.001). Huddling was also negatively correlated to ambient temperature (ρs=-0.582; p<0.001). Curled postures were also negatively correlated to humidity (ρs=-0.251; p=0.011). In the comparison between Mandena and Sainte Luce, we had not correlation with humidity (Table 7.3).

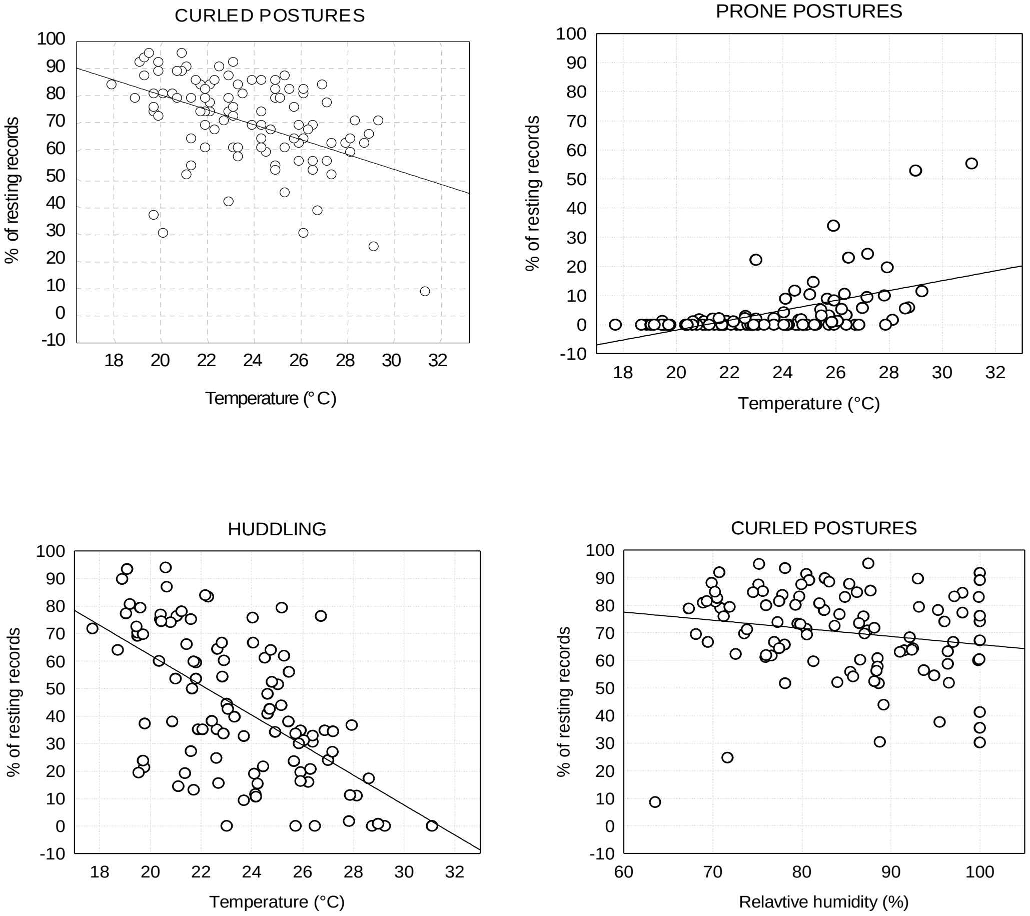


Fig. 7.2: Significant correlations between thermoregulatory ('curled' and 'prone') postures, huddling and climatic variables (temperature and humidity).

		N		Temperature	Humidity
Sainte Luce	**Curled**	50	ρs	-0.347*	-0.158
			p-level	0.014	0.272
	Prone	50	ρs	0.456**	-0.075
			p-level	0.001	0.607
	Huddling	50	ρs	-0.455**	0.020
			p-level	0.001	0.891
Mandena	**Curled**	52	ρs	-0.692**	-0.035
			p-level	0.000	0.807
	Prone	52	ρs	0.693**	-0.185
			p-level	0.000	0.188
	Huddling	52	ρs	-0.671**	0.128
			p-level	0.000	0.368

Table 7.3: Spearman correlation values between thermoregulatory ('curled' and 'prone') postures, huddling and climatic variables (temperature and humidity) at Sainte Luce and Mandena. ρs=Spearman's coefficient *p<0.017, **p<0.003 after Bonferroni adjustment.

Concerning microhabitat selection, the factors examined here are shown in table 7.4. Statistically significant differences were found also between groups living at Sainte Luce (group B rested significantly more frequently in position 1 of the crown: $U_{25,25}$=196, p=0.023; group A rested significantly more frequently in the upper canopy: $U_{25,25}$=195, p=0.022) and at Mandena (group AB rested significantly more frequently in the upper canopy as compared to group C: $U_{28,24}$=197, p=0.010).

Table 7.4: Microhabitat selection. Percentages of resting time spent in crown 1, crown 3 and upper canopy (i.e. above 6 m at Sainte Luce and above 4 m at Mandena) of groups living at Mandena and Sainte Luce during the study period. Values are in medians (in bold) and quartiles. Bottom: results of Mann-Whitney test between resting percentages in diurnal time budget at Sainte Luce and Mandena. *p<0.05, **p<0.01

	Crown 1 (%)	Crown 3 (%)	Upper canopy (%)
Group A	**12.50**	**4.55**	**77.38**
	4.08-19.48	1.72-11.11	54.55-88.16
Group B	**17.74**	**6.45**	**50.98**
	13.95-38.04	2.33-18.31	41.07-70.97
STL	**16.23**	**5.81**	**65.75**
	5.71-25.64	2.17-14.61	47.89-80.90
Group AB	**36.86**	**0.00**	**51.59**
	21.20-54.64	0.00-0.45	31.31-79.50
Group C	**23.92**	**0.00**	**18.30**
	6.31-56.36	0.00-1.06	6.38-53.60
MDN	**32.60**	**0.00**	**41.36**
	15.78-54.64	0.00-0.95	12.50-67.71
U	792**	354**	779**
p-level	0.001	0.000	0.000

We found a significant positive correlation between temperature and percentage of time spent by lemurs resting in position 1 of the crown at Sainte Luce, and a tendency at Mandena (table 7.5). Moreover, we found a significant negative correlation between temperature and frequency of resting in the upper canopy at Sainte Luce, while at Mandena we had no significant correlation.

		N		Temperature	Humidity
Sainte Luce	**Crown 1**	50	Ps	0.353*	-0.185
			p-level	0.012	0.199
	Crown 3	50	Ps	-0.062	-0.216
			p-level	0.671	0.133
	Upper canopy	50	Ps	-0.415**	0.102
			p-level	0.003	0.482
Mandena	**Crown 1**	52	Ps	0.265	0.008
			p-level	0.058	0.955
	Crown 3	52	Ps	0.005	-0.169
			p-level	0.974	0.232
	Upper canopy	52	Ps	-0.101	-0.154
			p-level	0.476	0.275

Table 7.5: Spearman correlation values between microhabitat selection and climatic variables (temperature and humidity). Microhabitat selection were valued as percentages of resting time spent in crown 1, crown 3 and upper canopy (i.e. above 6 m at Sainte Luce and above 4 m at Mandena) of groups living in Mandena and Sainte Luce during the study period. ρs=Spearman's coefficient *p<0.017, **p<0.003 after Bonferroni adjustment.

Statistical analysis between dietary related factors (see chapter 6) and thermoregulatory variables showed that at Sainte Luce, the use of curled positions and huddling was negatively correlated with time spent feeding and with diet quality (measured as the metabolic energy contained in 100g of diet) (table 7.6). Percentages of ripe fruits eaten was not correlated whit thermoregulatory variables at Sainte Luce, while at Mandena we found a positive correlation between the percentage of ripe fruits in diurnal diet and the percentage of time spent by lemurs resting in position 1 of the crown. At Mandena we found no significant correlation between feeding time and thermoregulatory variables, while we found a significant negative correlation between metabolic energy and the use of curled positions and huddling frequency (tendency), and a positive correlation between metabolic energy and time spent by lemurs resting in position 1 of the crown (tendency).

		N		Feeding	Ripe fruits	ME
	Curled	50	ρs	-0.485**	0.152	-0.398*
			p-level	0.000	0.292	0.004
Sainte Luce	**Prone**	50	ρs	0.050	0.127	0.129
			p-level	0.728	0.378	0.373
	Huddling	50	ρs	-0.434**	-0.049	-0.430*
			p-level	0.002	0.733	0.002
	Crown 1	50	ρs	0.112	-0.016	0.182
			p-level	0.439	0.914	0.206
	Crown 3	50	ρs	-0.036	-0.139	0.025
			p-level	0.805	0.334	0.865
	Upper canopy	50	ρs	-0.121	-0.075	-0.238
			p-level	0.402	0.604	0.096
	Curled	52	ρs	-0.039	-0.218	-0.362*
			p-level	0.786	0.121	0.008
Mandena	**Prone**	52	ρs	-0.088	0.051	0.148
			p-level	0.533	0.718	0.295
	Huddling	52	ρs	0.100	-0.179	-0.325
			p-level	0.480	0.231	0.019
	Crown 1	52	ρs	-0.176	0.369*	0.304
			p-level	0.213	0.007	0.028
	Crown 3	52	ρs	-0.273	0.073	0.038
			p-level	0.050	0.606	0.790
	Upper canopy	52	ρs	0.093	0.004	0.192
			p-level	0.513	0.975	0.174

Table 7.6: Correlation between dietary related factors and thermoregulatory variables. We considered feeding time in diurnal time budget, percentage of ripe fruits in diurnal diet and metabolic energy as dietary related factors. As thermoregulatory variables we used prone and curled postures (postural thermoregulation), huddling (social thermoregulation) and position in crown 1, crown 3 and upper canopy (microhabitat selection). ρs=Spearman's coefficient *p<0.008, **p<0.002 after Bonferroni adjustment.

Finally, we correlated the percentage of resting time in diurnal time budget (shown in chapter 5), and the daily ranges/h (calculated via 100% MCP) and the daily distances traveled/h (shown in chapter 4) with climatic and dietary variables (Table 7.7 and 7.8). Concerning resting time, we found a strong negative correlation with the percentage of feeding time and the metabolizable energy at Sainte Luce, and with humidity and the percentage of feeding time at Mandena. Concerning daily ranges/h and distance traveled/h, we found a possible influence of temperature and metabolizable energy at Sainte Luce.

	N		Temperature	Humidity	Feeding	Ripe fruits	ME
Sainte Luce	50	Ps	-0.196	-0.304	-0.783**	0.061	-0.459**
		p-level	0.174	0.032	<0.001	0.675	<0.001
Mandena	52	Ps	0.230	-0.455**	-0.723**	0.132	0.184
		p-level	0.101	<0.001	<0.001	0.350	0.191

Table 7.7: Correlation between resting time in diurnal time budget and climatic/dietary variables. We considered feeding time in diurnal time budget, percentage of ripe fruits in diurnal diet and metabolizable energy as dietary related variables. As climatic variables we considered mean temperature and mean humidity during diurnal observation. ρs=Spearman's coefficient *p<0.01, **p<0.002 after Bonferroni adjustment.

	N		Temperature	Humidity	Feeding	Ripe fruits	ME
Sainte Luce							
Daily ranges/h	47	Ps	0.315	0.154	0.063	0.134	0.328
		p-level	0.031	0.302	0.673	0.371	0.024
Distance traveled/h	47	ρs	0.453**	0.171	0.228	0.067	0.381*
		p-level	0.001	0.251	0.123	0.654	0.008
Mandena							
Daily ranges/h	49	Ps	0.108	0.186	0.253	0.118	0.165
		p-level	0.458	0.201	0.079	0.420	0.258
Distance traveled/h	49	Ps	0.038	0.186	0.250	0.142	0.028
		p-level	0.796	0.200	0.083	0.330	0.847

Table 7.8: Correlation between daily ranges/h, distance traveled/h and climatic/dietary variables. We considered feeding time in diurnal time budget, percentage of ripe fruits in diurnal diet and metabolizable energy as dietary related variables. As climatic variables we considered mean temperature and mean humidity during diurnal observation. ρs=Spearman's coefficient *p<0.01, **p<0.002 after Bonferroni adjustment.

7.4 Discussion

Our results confirm the role of temperature fluctuations in shaping behavioral thermoregulation in *Eulemur collaris*, as already shown in literature (Donati *et al.*, 2010). As predicted, proportion of time spent in postures which reduce the surface/volume ratio, i.e., huddling and curling, increased when ambient temperature decreased, indicating that these strategies were used to minimize the dissipation of body heat. By contrast, the proportion of time spent in prone, extended postures increased when ambient temperature increased, following the same principle of body surface/volume ratio; elongation maximizes dissipation of heat when the thermal environment is particularly warm. Lemurs used this strategies both at Mandena and at Sainte Luce, confirming the important role of postural and social thermoregulation in coping with the pronounced seasonality of climate in Madagascar (Jolly, 1966; Tattersall, 1982; Pereira *et al.*, 1999; Ostner, 2002, Donati *et al.*, 2010). In contrast with Donati *et al.*, 2010, we did not found a significant correlation between ambient temperature and resting time. Previous studies indicated the importance of time budget changes in relation to climatic factors: *Colobus badius rufomitratus* (Marsh, 1981), *Alouatta caraya* (Bicca-Marques and Calegaro-Marques, 1998), *Eulemur rufus* (Ostner, 2002), and *Macaca fuscata* (Hanya, 2004; Hanya *et al.*, 2007). In our study we found a negative correlation trend as expected between resting time and temperature at Sainte Luce, while we found a positive correlation trend at Mandena. Of course, it has to be noted that trends give weaker indications than statistically significant differences.

As predicted, lemurs at Mandena spent more time resting, indicating that the animals needed to save energy more than at Sainte Luce. Additionally, the proportion of time spent in ‘curled’ postures was higher at Mandena.

Sunning or basking in early morning is a common behavior in ringtailed lemurs, sifakas, and ruffed lemurs (Jolly, 1966; Tattersall, 1982; Morland, 1993; Pereira *et al.*, 1999). In contrast with Donati *et al.*, 2010, we observed occasional sunbathing at Sainte Luce during the coolest period (July-August), while we did not found this behavior at Mandena. In a primary forest the only opportunity for sunbathing is on the emergent part of the canopy, where predation risk by diurnal raptors is expected to be high. Between 1999-2001 (data collection by Donati *et al.*, 2010) and 2011 predation risk at Sainte Luce can be lowered, and this can explain the presence of sunbathing behavior. At Mandena, we noted more diurnal raptors (the new born in group C, Olivia, was attacked by a diurnal raptor, *Accipiter hernstii*, on November, risking its life). This difference in predation risk can explain the differences in microhabitat selection between Sainte Luce and Mandena. Lemurs at Sainte Luce rested more time in the upper canopy and in the most external part of the crown, while lemurs at Mandena rested more time in the internal part of the crown. Additionally, we found a positive correlation between temperature and resting in the internal part of the crown and a negative correlation between temperature and resting in the upper canopy at Sainte Luce, meaning that lemurs had the possibility to rest more frequently in the shade (internal part of the crown and lower canopy) during the hottest periods, and to rest in the sun (upper canopy) during the coolest periods. At Mandena, we did not find any correlation between temperature and microhabitat selection, only a tendency to rest in the internal part of the crown when the temperature was higher. This findings can be related to the fact that lemurs at Mandena had less possibilities to use microhabitat selection in order to face with different climatic conditions, considering that predation risk was higher.

Two dietary-related variables, i.e., feeding time and the amount of metabolizable energy in the diet had a strong correlation with thermoregulatory behaviors, in agreement with the findings by Donati *et al.*, 2010. In particular, at Sainte Luce, the proportion of resting and the frequency of huddling and curled postures increased as feeding time and metabolizable energy decreased, while at Mandena feeding time was negatively correlated only with resting time and metabolizable energy was negatively correlated with the frequency of huddling (tendency) and curled postures. Percentage of ripe fruits in the diet as a measure of fruit availability seemed to have a lower correlation with thermoregulatory behaviors compared to the other two dietary-related variables, as already shown by Donati *et al*. 2010.

Daily ranges and distance traveled as measures of energy expenditure seemed to be positively correlated to ambient temperature and metabolizable energy at Sainte Luce. During warmer periods, when fruit availability and metabolizable energy were higher, lemurs at Sainte Luce had higher daily ranges, and traveled higher distances. At Mandena, we did not found this correlation, and we found lower daily ranges and daily distance traveled (chapter 4). We can argue that at Mandena we do not have a real season with abundant resource availability, and lemurs must adopt energy saving behaviors more often also during the warmer period.

In conclusion, the effect of a secondary-type forest on *Eulemur collaris* thermoregulatory strategies appears to be decisive in activity adjustment, by increasing the time spent resting for energy conservation (as seen in Chapters 5 and 6). Additionally we found that proportion of 'curled' postures was higher at Mandena, confirming that energy saving behaviors were more frequent. On the whole, however, postural and social thermoregulation seem to be influenced mostly by seasonal temperature fluctuations, which are similar in the two forests. Microhabitat selection seems to be an important thermoregulatory strategy, but its use can be limited by predation risk. Finally, diet appears to be important in determining the proportion of thermoregulatory behaviors, especially considering energy-saving behaviors.

CHAPTER 8

HOMEOTHERMY IN *Eulemur collaris*

8.1 Introduction

Homeothermic mammals have the capacity to maintain a constant body temperature (T_b) within a wide range of ambient temperatures (T_a) (Speakman, 1997). They are known to adjust their metabolism and thermal biology to unpredictable environments and seasonality through adjustments of their basal metabolic rates and thermal conductances (McNab, 1979; Satinoff, 1978). However, the cost of homeothermic thermoregulation is very high in cold and dry environments, especially in small species: because the surface area/volume ratio of animals increases with decreasing size, many small endotherms must produce substantial amounts of endogenous heat to compensate for high heat loss during cold exposure (Speakman, 1997). As prolonged periods of high metabolic heat production require high food intake and food availability in the wild often fluctuates, the cost of thermoregulation may become prohibitively expensive. Thus, small mammals in certain periods of the day or of the year may show poikilothermy as extreme adaptation to cope with seasonal energy shortages and low temperatures. These animals, defined heterotherms (from the Greek: heteros = "other", thermē = "heat"), are able to shift from homeothermy to poikilothermy, reducing their metabolic rate by controlled hypothermia (Geiser and Ruf, 1995).

There are two categories of heterothermy: daily torpor and hibernation. The distinction is typically based on two variables only: the minimum T_b reached during torpor and the duration of torpor bouts (periods in which T_b is low and bodily functions are reduced to a minimum), even if the maximum torpor bouts duration is the only variable that shows no overlap between daily heterotherms and hibernators (Geiser and Ruf, 1995). Daily torpor is characterized by a controlled reduction of Tb, metabolic rate (MR), and other physiological functions (Geiser, 2004). The T_b during daily torpor falls from high normothermic values of ~32°-42°C to values between 5°C and 30°C, and the minimum torpid metabolic rate (TMR) is on average reduced to 5–30% of the basal metabolic rate (BMR) (Geiser, 2004). BMR is defined as the minimum rate of metabolism measured under the following specific conditions: animals must be adult (to eliminate the cost of growth), nonreproductive, postabsorptive (to eliminate the specific dynamic action of food), and inactive. Furthermore, animals must be measured within the thermoneutral zone and during a major resting period of their daily cycle (Genoud, 2002). Thus, BMR is free of direct behavioral and environmental effects on the rate of metabolism and is therefore a fundamental parameter in the comparative study of physiological adaptation relative to energy turnover. In hibernation (or prolonged torpor), torpor bouts last for several days or weeks, but are interrupted by periodic rewarming and brief (usually less than one day) normothermic resting periods with high T_b and high energy turnover (Humphries *et al.*, 2003). Hibernating species usually reduce T_b to below 10°C, with a minimum of -3°C in arctic ground squirrels, *Spermophilus parryii* (Barnes, 1989), and most, with the exception of large carnivores and perhaps tropical hibernators, have T_b minima around 5°C (Barnes *et al.*, 2000; Dausmann *et al.*, 2000; Geiser, 2004). The TMR in hibernators is on average reduced to about 5% of the BMR but can be less than 1% of the resting metabolic rate (RMR) in normothermic individuals at low T_a. Even when the high cost of periodic arousals is considered, energy expenditure during the mammalian hibernation season is still reduced to below 15% of that the animal would have expended if it remained normothermic throughout winter (Wang, 1978). Heterothermy is used by a wide range of mammals and also by birds, from the smallest insectivore *Suncus etruscus* (2 g) to the largest carnivore *Ursus americanus* (80 kg) (Watts *et al.*, 1981; Geiser, 2004).

Torpid animals of the tropics experience climatic conditions that are very different from those of their temperate and arctic counterparts. Ambient temperatures (T_a) in the tropics are generally above those in temperate areas, and minimal T_a rarely drops to temperatures below 5°C (Lovegrove, 2000). Contrary to temperate and artic hibernators, tropical animals, some of which are known to use tree holes with poor thermal insulation capacities as sleeping sites, face recurrent high T_a and strong daily fluctuations of T_a during the tropical winter. Minimizing the difference between T_b and T_a, hibernators reduce their metabolism and energy expenditure while avoiding the energetic costs of arousals (Dausmann *et al*, 2004). The Malagasy fat-tailed dwarf lemur (*Cheirogaleus medius*) is unique among primates, because it is the only primate known to hibernate for extended periods of time (Petter, 1978; Dausmann *et al.*, 2004). In preparation for this period of inactivity, the animals store considerable amounts of fat, increasing their body weight from about 130 g to over 250 g (Hladik *et al.*, 1980; Fietz and Ganzhorn, 1999; Dausmann *et al.*, 2005). *Cheirogaleus major* may hibernate obligatory as well (Wright and Martin, 1995), but no evidence is present in literature. In primates daily torpor has been observed in *Microcebus murinus*, *M. berthae*, *M. ravelobensis*, *M. griseorufus*, *M. rufus*, *Mirza coquereli* (Canale *et al.*, 2010; Kobbe *et al.*, 2010). The frequency of heterothemic species in the family Cheirogaleidae is very high. In fact, one of the most reliable hypothesis is that the ability to enter torpor has been a crucial feature for Madagascar forests colonization by ancestral lemurs. This plesiomorpic trait, in theory, should also be found in mainland relatives (i.e. Lorisiformes), but right now some evidence was found in *Galago moholi* only, where torpor bouts are rare (Nowack *et al.*, 2010).

In the case of *Eulemur collaris* there are no data in literature showing that it is capable of heterothermy. No primate of the same size (~2300 g) is known to enter a state of torpor. In fact, the size of daily heterotherms is, usually, very small (2-200 g), but there are some exceptions in non-primate mammals: *Taxidea taxus* (9000 g), *Tachyglossus aculeatus* (~2000 g), *Marmota marmota* (~4000 g) (Harlow, 1981; Nicol *et al.*, 1992, Ortmann and Heldmaier, 2000). However, the low metabolic rate of *E. collaris* (supposed to be similar to that of its sister species *E. fulvus*: minimal metabolic rate of 0.139 cm^2 O_2 g^{-1} h^{-1} which is 28% of the basal value expected from the Kleiber relationship for a mammal of 2.33 kg.; Daniels, 1984) and the need to cope with restrictive seasonal changes under the energy profile, make it a possible candidate to show torpor bouts. Given the lower temperature reached in South-eastern Malagasy forests (<15°C), have red collared brown lemurs relied only on their thermoregulatory behavior during the cool and lean period?

The aim of this piece of research is to shed some light on this aspect not yet investigated, testing the hypothesis that *E. collaris* might enter daily torpor to cope with the adverse season, thereby minimizing the dissipation of body heat and energy expenditure.

8.2 Materials and methods

We collected ethological data with the instantaneous sampling method, with records every five minutes, the all occurrences method and the *ad libitum* method (Altmann, 1974, see chapter 3). We considered as thermoregulatory postures those that allowed animals to retain (curled positions) or dissipate (prone positions) body heat when environmental conditions required it (see chapter 7). Description of thermoregulatory postures are available in Appendix I.

Records of thermoregulatory postures, proximity to other individuals (huddling), sun exposition, height and position in the tree crown, were integrated by measurement of body temperature by radio-collars. Temperature-sensitive collars (TW-3, medium mammal tag, Biotrack) were present in each group (one female in group A, one male in groups B, AB, C). The temperature-sensitive transmitters were calibrated in a water bath (14–45 °C, steps of ~2°C) with a mercury thermometer. To extrapolate skin-temperatures (Ts) from seconds we used a regression line, built with the calibration data of the collars. We used the data in logarithmic form to obtain more reliable predictions. Temperature data were collected during the study period (from July to January), during diurnal and nocturnal observations. To evaluate skin temperature (T_s) we used the receiver's signal (SIKA receiver, Biotrack), whose frequency changes depending upon temperature. So we noted the seconds spent to count 20 pulses with a stopwatch. T_s from radio collar transmitters precisely reflect core body temperature (T_{core}) of resting individuals over a wide range of ambient temperature (Dausmann *et al.*, 2005). This is valid for *Cheirogaleus medius* and *Microcebus sp.*, due to the low body mass. In fact, in small animals, the high thermal conductivity and small distance between the surface and the core precludes the establishment of a steep and variable temperature gradient between T_s and T_{core} (McNab, 1969; Brown and Bernard, 1991; Audet and Thomas, 1996). In large animals, these distances can be substantial, and the resulting temperature gradient can therefore be considerable, limiting the use of external transmitters. Thus, in our analyses we considered only prolonged resting sessions in curled postures to provide reliable measurement of T_{core}. Temperature was measured after five minutes the animal was motionless, and then every 15 minutes of the same resting session. To differentiate between artificial fluctuations and true decreases of T_s due to the initiation of torpor bouts, animals were defined to have entered torpor when T_s showed a distinct and stable decrease (<30°C) for longer time periods (>1 hours). Termination of a torpor bout was defined as the moment T_s increased above 30°C (see Nowack *et al.*, 2010). However, this limits could not be valid for *Eulemur collaris*, as in literature we have no data on body temperatures. We integrated T_s data with abiotic data from data loggers (chapter 7).

8.3 Results

During our study period we collected a total of 62 T_s set of data in prolonged resting sessions (more than 1 hour in the same resting position): 22 for Octavio (group AB), 18 for Apollo (group C), 11 for Fotsy (group B), 11 for Fana (group A). In Figure 7.1 and 7.2 we can see some examples of T_s of *Eulemur collaris* in resting sessions. In particular in Figure 7.1a we can see that we have to wait 30 minutes from the first resting instantaneous in order to have reliable T_s, and we must consider the resting session finished when the animal changed posture or became active. The same resting session continued when the animal passed from curled posture 1 to curled posture 2 and *vice versa* because the variation is only on the position of the tail. T_s didn't change between 14°C and 31°C of T_a.

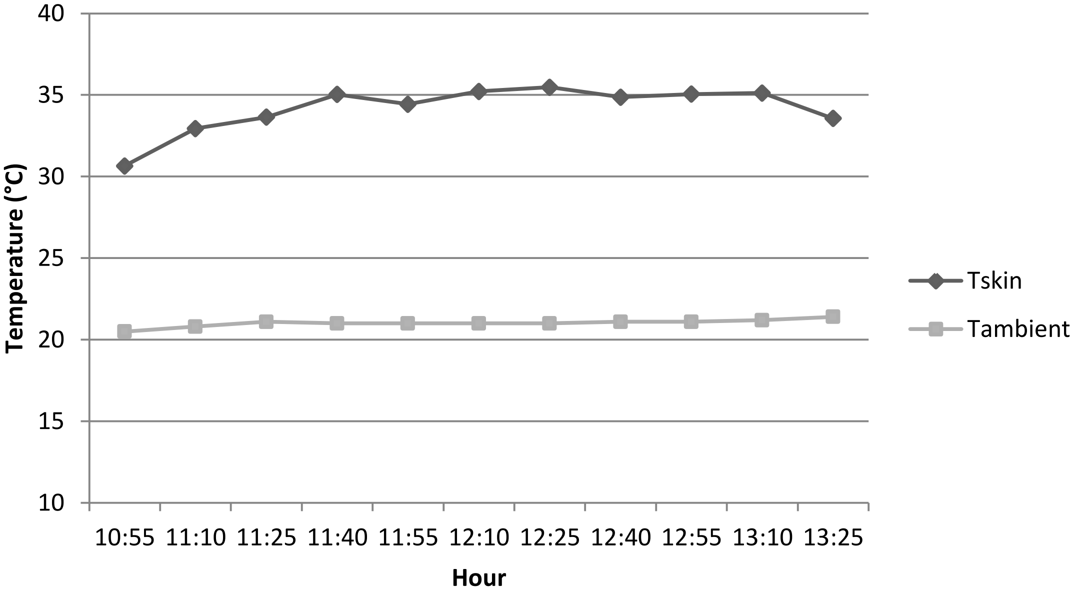
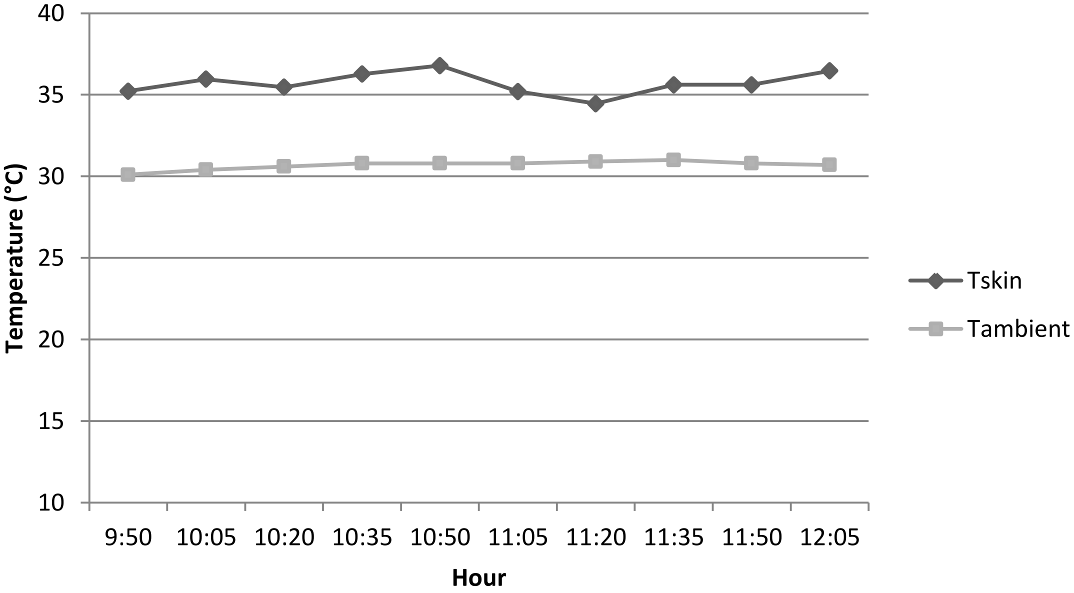


Fig. 7.1: Typical T_s in resting session of *Eulemur collaris*: a) above, data from Apollo (lemur in group C with temperature-sensitive collar) on October 6th 2011. Skin temperature started below 32 °C, and after 30 min in curled posture 1 reached ~35°C that was the usual T_s registered. So we needed 30 minutes to have a reliable T_s. After 1h and 30 minutes in which Apollo stayed in curled posture 1, the animal passed in resting 3 (non-thermoregulatory posture) and T_s dropped a little. In this case we can consider as reliable T_s from 11:40 to 13:10, and we can see no variation in T_s.

b) below, data from Octavio (lemur in group AB with temperature-sensitive collar) on December 8th 2012. In this case we considered only reliable temperatures in curled posture 2. T_s remained near 35-36°C even if T_a was higher than above (reached 31°C).



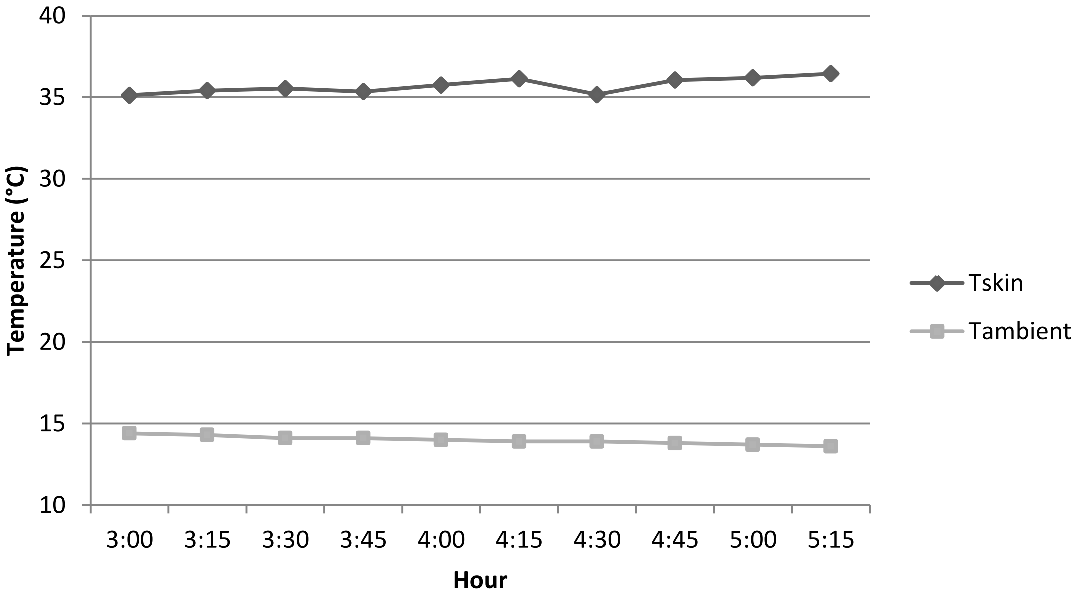


Fig. 7.2: Nocturnal resting session of *Eulemur collaris*: data from Octavio (lemur in group AB with temperature-sensitive collar) on October 13th 2011. Even if T_a was under 15°C, T_s remained near 35-36°C.

We found no torpor bouts in which T_s remained more than 1 hour under 30°C. However we have no literature on *Eulemur collaris* or other Lemuridae. Thus, we analyzed mathematically our data, trying to extrapolate some results.

A total of 546 T_s were present in the data set, and the mean ($\bar{x}$+SD) was 35.40±1.22 °C. We considered as the T_s* (T_s at possible torpor bouts) the T_s which was below the case ($T_s<\bar{x}$-2SD), so T_s<32.96°C. In figure 7.3 and 7.4 we can see the only three T_s* set from the set of 62 T_s of prolonged resting sessions. All the three sets were registered on July, during the lean and cool period.

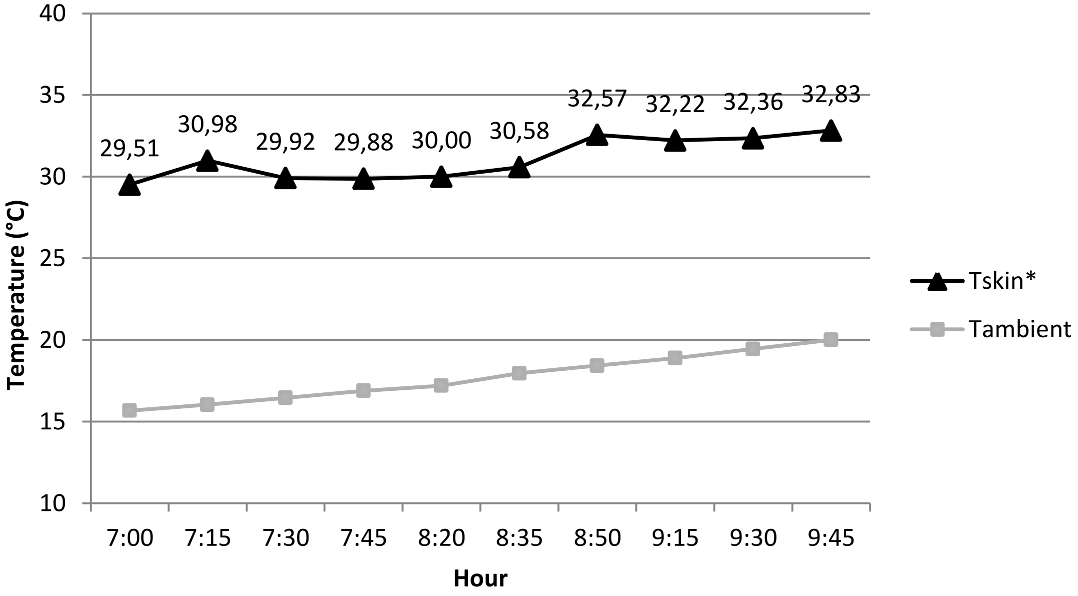
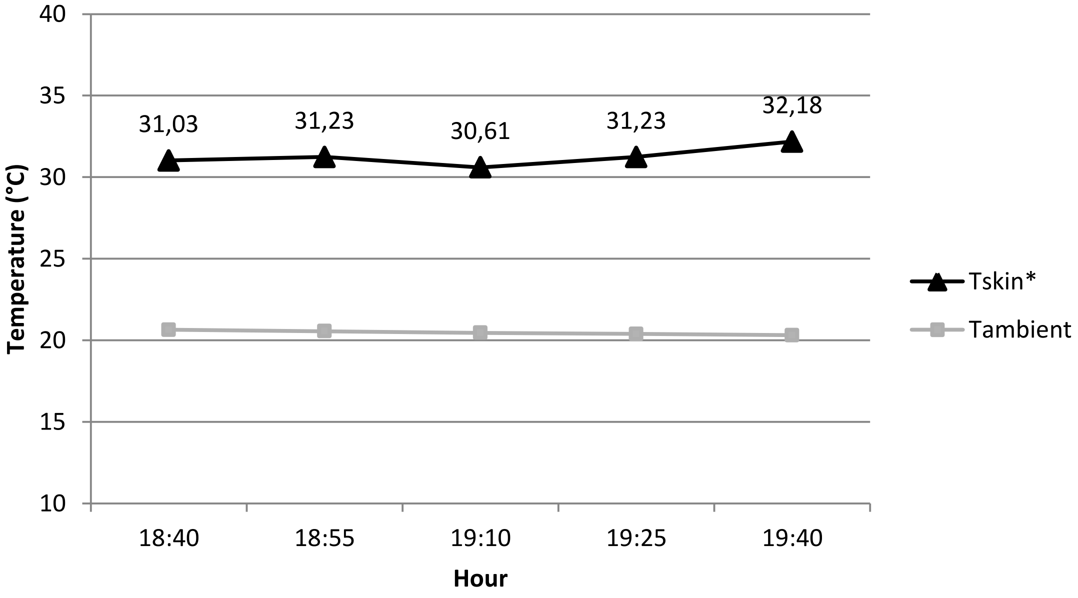


Fig. 7.3: Possible torpor bouts in Sainte Luce: data from Fana (lemur in group A with temperature-sensitive collars) on July 11th 2011 (above) and on July 15th 2011 (below). **a)** Above, Fana was in huddling with other lemurs and in curled posture 1. T_s remained constantly under 33°C for 2 hours and 45 minutes, of which more than 1 hour T_s was near 30°C. T_a passed from 15.7°C to 20°C, the day was sunny/variable. **b)** Below, Fana was in resting (probably huddling in curled posture 1, but there was no visibility). T_s remained under 32°C for 1 hour, and T_a was near 20°C, the night was limpid.



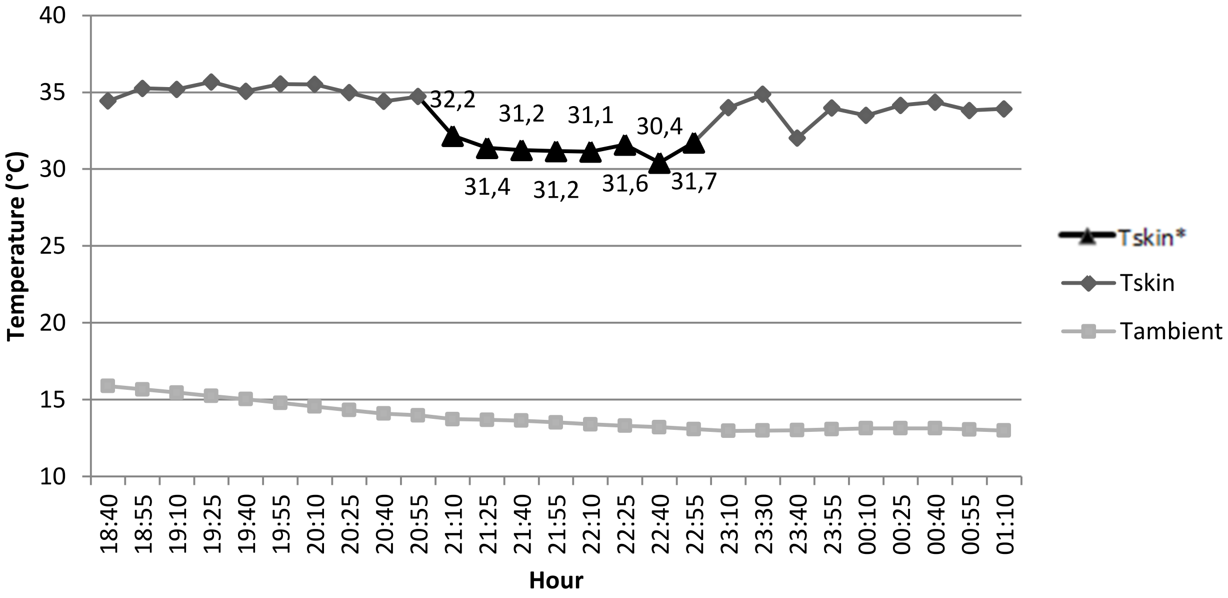


Fig. 7.4: Possible torpor bouts at Mandena: data from Octavio (lemur in group AB with temperature-sensitive collars) on the night between the 5th and the 6th of July 2011. Octavio was in huddling, posture 1 with Abelardo and Barabarà. After a period in which the T_s remained near 35°C, from 21:10 to 22:55 T_s dropped and remained under 32 °C. After that period, T_s returned near 34-35 °C, while T_a was decreasing. The night was limpid.

Overall, T skin fluctuation under the case (T_s<32.96°C) were noted only on July (Figure 7.5). We distinguished between T_s collected in posture 1 and T_s collected in other postures or unknown postures (e.g. during nocturnal observations), in order to see if the possible T_s* can be due to a non-registered change in posture. We did not found any data under 32.96°C, excepted for July also when the animal rested in unknown postures (i.e. during nocturnal observations), meaning that possible torpor bouts were not due to non-registered postural changes. On September we collected one T_s under 32.96°C, but it was a single event, probably caused by counting error.

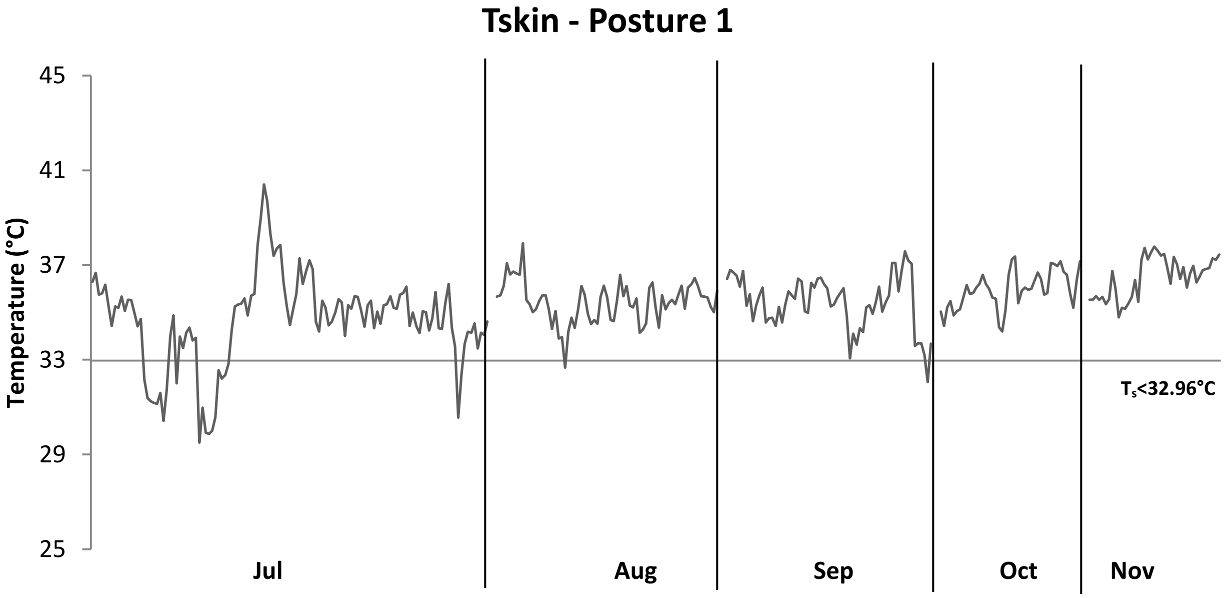
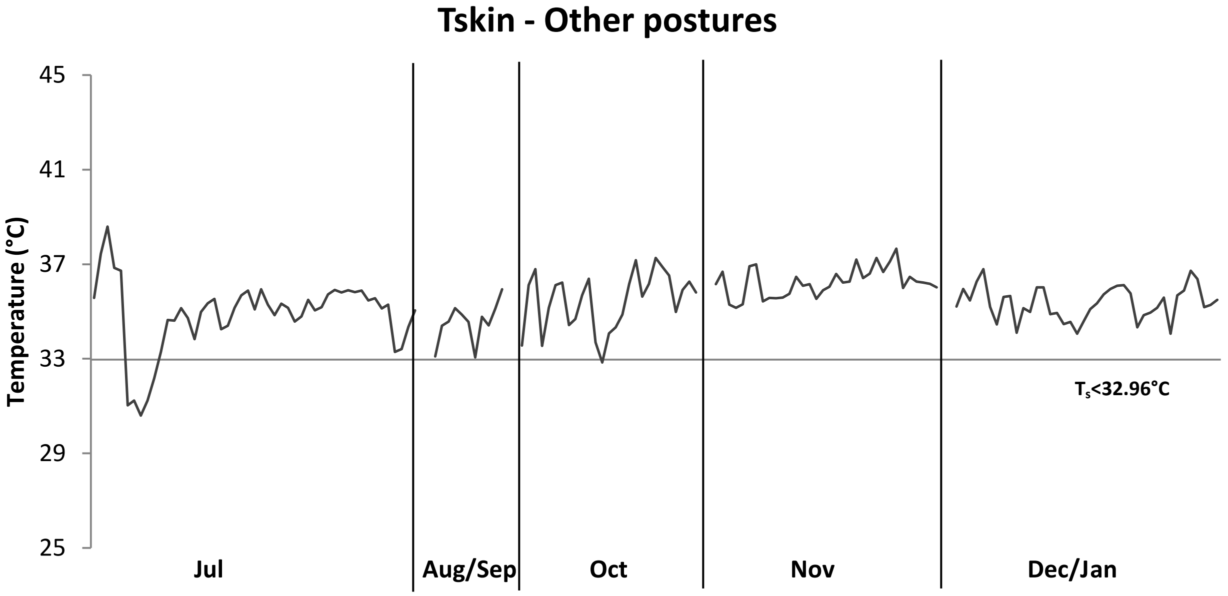


Fig. 7.5: Overall skin temperatures during the entire study period. Above, data collected when the animal rested alone or in huddling with other lemurs in posture 1. Prolonged resting bouts under 32.96°C were present on July. On December and January lemurs did not use posture 1 for more than one hour. Below, data collected when the animal rested alone or in huddling with other lemurs in posture 2,3,4,5. Prolonged resting bouts under 32.96°C were present on July.



8.4 Discussion

The mean T_s of *Eulemur collaris* recorded by radio-collars during resting, 35.4±1.2°C, is slightly below 38.2°C, the T_b of *E. fulvus* maintained constant at T_a from -2°C to 40°C, detected by Daniels (1984) with a rectal probe. Assuming that the internal temperature of *E. collaris* is the same as *E. fulvus*, given their phylogenetic closeness, the T_s measured by radio collars was on average 2.8±1.2°C lower than expected. Neither the standard error of the instruments, nor the statistical error is large enough to fill this gap. Therefore, although the measurement of skin temperature has proved to be reliable for predicting T_b in *Cheirogaleus medius* (Dausmann, 2005), in our case the T_s is not indicative of absolute T_b in *E. collaris*. The causes are probably to be found in scarce adhesion of the collars (lemurs are subject to significant seasonal variations in weight and a collar too tight would seriously compromise the health of an individual when it had increased its body mass), in the more thicker hair cover and in the different surface/volume ratio as compared to *C. medius*. In fact, it was demonstrated that animal size influences the distribution of the heat surface and therefore its detection. So, taking into account that our measurements are ~ 3°C lower than the actual T_b of *E. collaris*, we can say that no resting T_s or T_s* reflected inner temperatures lower than 30°C, the threshold below which the temperature of an animal should drop to be defined in torpor. However, our research aimed at observing the variations of T_s, so the measurement by radio-collars turned out to be a suitable method for this kind of study. In fact, when the animal assumes a curled position the radio-collar sensor is in close contact with the body surface and is almost completely shielded from T_a. For this reason, the T_s measured under these conditions is much closer to the actual surface temperature. When an animal moves its T_s drops sharply due to increased exposure of the sensor to T_a. Sharp peaks are easily distinguishable, remaining below 30°C. Instead, when an animal begins a resting phase, the temperature reported by the sensor increases gradually, stabilizing at around 35-36°C. Sometimes there are fluctuations due to movements of the animal, which moves or changes position, exposing the collar to T_a. The most interesting changes were observed in three resting bouts, where the T_s is lowered by about 4°C and remained constant (~31°C) for ~ 1-2 h. We could rule out, such causes of this drop in temperature, prolonged exposure of the collars to T_a during resting phases (i.e. when the animal changed resting position during the same resting phase), because in that case T_s remained near 35-36°C (see Figure 7.5), and occasional movements of animals, because the peaks were short, isolated and inconsistent. According to our interpretation, these T_s* reflect an actual change in surface temperature of *E. collaris*, in response to a T_a (14-20°C) below its zone of thermoneutrality (supposed to be 22-30°C). This drop in temperature, probably not due to torpor, could be due to other physiological processes that would reduce the loss of body heat, as the decrease of thermal conductance. This phenomenon has already been observed in *E. fulvus*, which exposed to low T_a (<19°C) would have reduced its thermal conductance below that observed at T_a = 30°C. Decreased peripheral circulation probably also contributed to the decreased conductance at T_a below

19°C (Daniels, 1984). Nevertheless, we cannot totally exclude that the T_s* plateau might be due to a slight form of torpor. In fact, we cannot exclude a certain flexibility in torpor behavior, as it is yet not well known. For example, *Galago moholi* has the potential to enter torpid states, but probably only does so under especially adverse conditions, so torpor bouts are relatively rare (Nowack *et al.*, 2010). Other studies on free living *G. moholi* did not find any incidence of torpor (Mzilikazi *et al.*, 2006), demonstrating the potential flexibility of torpor behavior. Further data collection, especially during lean and cool periods, will be useful to clarify the T_s* origin and determine if heterothermy is actually absent in *E. collaris*.

CHAPTER 9

SOCIAL STRUCTURE

9.1 Introduction

Group composition and social structure are highly variable among lemur species. Solitary, pair bonded, and group living lemurs have been described in literature (Jolly, 1966; Kappeler, 1993a; van Schaik and Kappeler, 1993; Kappeler and van Schaik, 2002; Pochron and Wright, 2003). A peculiar trait of Malagasy primates is the high frequency of female dominance in lemur societies, i.e. the capacity of adult females to evoke submissive behavior in adult males in dyadic agonistic interactions (Marolf *et al*., 2007). This particular trend was observed in *Lemur catta*, *Indri indri*, *Varecia variegata*, *Propithecus verreauxi*, *P. diadema*, *Microcebus murinus*, *Phaner furcifer*, *Eulemur coronatus*, *E. flavifrons*, *E. rubriventer*, and, *Hapalemur griseus alaotrensis* (Pollock, 1979; Jolly, 1984; Pereira *et al*., 1990; Kubzdela *et al*., 1992; Pereira and Kappeler, 1997; Radespiel and Zimmermann, 2001; Pochron and Wright, 2003; Waeber and Hemelrijk, 2003; Overdorff *et al*., 2005; Marolf *et al*., 2007). However, some species are more clearly female dominant than others and there is a continuum in between. The causes of such hierarchy, unusual among primates, are still uncertain and under debate, but the most reliable hypothesis involve the peculiar conditions of Malagasy environment, especially resource distribution and availability. Moreover "the lack of sexual dimorphism seems to be a crucial prerequisite for female dominance” (Kappeler, 1993b).

Data on social structure and sexual dominance in *Eulemur collaris* are not yet available in literature, but some studies have been done on the phylogenetically closest species, the redfronted lemurs (*Eulemur rufus*). Redfronted lemurs live in groups of 5-12 individuals with an even or male-biased sex ratio (Sussman, 1974; Overdorff, 1998; Wimmer and Kappeler, 2002; Ostner and Kappeler, 2004). Females have concealed ovulation during the estrus period, that is brief and partially synchronized (Pereira and McGlynn, 1997). Genetic analyses have indicated that closely related coresident females form the core of stable groups whereas males typically migrate (Wimmer and Kappeler, 2002). Sexual dominance was not always clear. In particular, data from three wild and two semi-freeranging social groups of redfronted lemurs showed that females do not dominate males in this species (Pereira *et al.*, 1990). Other analyses extended early reports that dominance relations are actually ambiguous or nonexistent between most adult redfronted lemurs (Harrington, 1975). Moreover, Pereira and McGlynn (1997) found special relationships instead of female dominance, Overdorff (1998) showed the presence of highly variable male-female dyads within the larger social group, while Ostner and Kappeler (1999) found a “central male” involved in most social interactions with all the resident females.

In this Chapter we will provide a description of the social structure of *E. collaris*, analyzing sexual dominance and making comparisons between Mandena and Sainte Luce groups, in order to identify the possible influence of a degraded habitat on social behavior.

Our expectations are 1) to find social composition and organization similar to that of *E. rufus* and 2) to observe a more rigid hierarchy in Mandena groups, due to the more challenging habitat conditions, that could impose more rigid hierarchical social schemes, mostly related to intra-group competition in food access priority (van Schaik and van Noordwijk, 1986; van Schaik, 1989; Barton *et al.*, 1996; Sussman and Garber, 2007).

9.2 Materials and methods

We analyzed all occurrences data of animal interactions separating them in three categories: associative (H, KC), affiliative (G, GO, LK, MG, MT, P, SG), agonistic behaviors (BIT, CH, CU, DS) (see Appendix I). We calculated the interaction rate for each category, for each groups and for each dyad, during the “gestation” and the “lactation” period. We also calculated the interaction rate between sexes for each group in different seasons. We used daily interaction rates to analyze differences between groups and sites (Mann Whitney U Test), while interaction rates between dyads were used to compare “gestation” and “lactation” period (Wilcoxon T Test).

We analyzed sexual dominance in each group by the comparison of associative, affiliative and agonistic interactions for each dyad: differences between sexes were evaluated via multiple Chi-Square Tests. Dominance relationships among animals were determined on the basis of ‘decided’ interactions, defined as interactions in which one opponent showed only submissive behavior, while the other did not. Following Pereira and McGlynn (1997), we defined a relationship between an adult male and female as ‘special’ if their frequency of association and affiliative interaction was higher than expected by chance and the frequency of conflicts was lower than expected by chance. In contrast to Pereira and McGlynn (1997), we could not include agonistic support as an additional criterion because third party aggression was not observed in either study group. According to our definition of a special relationship, all the above criteria had to be met and the bonding had to be reciprocal, that is, the frequency of interaction of animal A with animal B had to be higher than expected by chance and vice versa. For every male–female dyad, we tested whether the frequency of interactions was higher than X+SD considering the observed-expected values (Ostner and Kappeler, 1999 modified in this study).

To account for proximity-dependent, unequally distributed opportunities for interactions, we used standardized residuals of affiliative and agonistic interactions. We calculated the sum of differences between the observed and proximity-corrected expected number of affiliative and agonistic interactions in each member of the group whit the others (considering dyads), and corrected it for the absolute frequencies of interaction by dividing by the square root of the expected values (Everitt 1977; see also Kappeler 1993a).

To implement the knowledge on relative dominance within the group, we used three ranking methods and we calculated the mean rank for each individual, for females and for males.

For the first ranking method (AttFr, Attack/win frequency), the frequency with which an individual, i, attacks or wins from an opponent, j, x_{ij}, is summed per individual ($\Sigma_j\ w_{ij}$) over the phase of the run-time in which the hierarchy is 'stable' (Hemelrijk and Gygax, 2004). A higher frequency is supposed to indicate a higher dominance-rank (Zumpe and Michael, 1986). Second, the average individual dominance index (ADI, Average Dominant Index) is calculated as follows. The dominance index per pair of individuals, w_{ij}, is the number of times an individual has beaten (or attacked) a certain opponent divided by the total number of fights in which the pair was involved with each other, thus $w_{ij} = x_{ij}/(x_{ij}+x_{ji})$. If a pair of individuals were not involved in a fight with each other, it was excluded from the analysis. The average dominance index of an individual is the average of all its dominance indices with all its interaction partners, thus $1/N\ \Sigma_j$ wij . A higher value indicates a higher dominance in the group. This index is a simplified version of the dominance index by Zumpe and Michael (1986). Zumpe and Michael calculated the average of the sum of the two percentages of attack and of submission received per pair and they averaged these per individual. Third, the David's score is a sophisticated dominance index (Gammell *et al.*, 2003). Like in the dominance index, per dyad the ratio of winning (losing) is calculated, w_{ij}, and these ratios are summed per row (called 'w') and summed per column (called ‘l’). Further, as an indication of the power of the victim in each pair, each ratio is weighted by the summed winning ratio of the loser and these products are summed per row-individual (called ‘w2’). A higher value indicates that ego itself wins more often and/or that the winning tendency of egos victims is high. Similarly, ratios are summed per column (called ‘l’) and the product with the total winning ratio of each opponent is calculated and summed per column (called ‘l2’). The David’s score is the sum of the measures of winning in the rows minus those in the columns (DS=w+w2−l−l2).

9.3 Results

We found multimale-multifemale groups of *Eulemur collaris* at both sites, with the exception of group AB in which one female only was present. However, field assistants reported the presence of two other females until 2009, when one of them died and the other left the group. Average group size and changes in group composition were described in chapter 3. Details are shown in Table 9.1. Changes in group compositions happened on September, during the gestation period. At the end of the study, male:female ratio was 6:7 in group A, 7:4 in group B, 3:1 in group AB and 3:3 in group C. First born at Mandena was Dodò, on September 22th, while Olivia was born on October 4th. At Sainte Luce, we were not present at the moment of the birth, but we can argue that all infants were born between the 31st of September and the 10th of October whit synchronicity.

Table 9.1: Composition of the study groups.

NAME	CODE	GENDER	AGE	BIRTH YEAR	KINSHIP
Sainte Luce - Group A					
Ala	AL	F	AD		Mother of Zaza, Kana and Tsara
Boko Boko	Bo	M	IN	2011	Son of Volana, twin of Hariva
Chefo Be	Ch	M	AD		
Fana	FA	F	AD		Mother of Lena
Hariva	HA	F	IN	2011	Daughter of Volana, twin of Boko Boko
Kana	KA	F	IN	2011	Daughter of Ala, twin of Tsara
Lena	LE	F	IN	2011	Daughter of Fana
Masoandro	Ma	M	AD		
Rivotra	Ri	M	AD		
Sotro	So	M	AD		
Tsara	TS	F	IN	2011	Daughter of Ala, twin of Kana
Volana	VO	F	AD		Mother of Boko Boko and Hariva
Zaza	Za	M	JUV	2010	Son of Ala
Sainte Luce - Group B					
Alina	ALI	F	AD		Mother of Biby and Velo
Bibi	Bi	M	JUV	2010	Son of Alina
Fotsy*	Fo	M	AD		
Haso	Ha	M	IN	2011	Son of Lanitra
Kintana	KI	F	SA-AD	2009	Daughter of Lanitra, mother of Tantely
Lanitra	LA	F	AD		Mother of Kintana, Mamy, Shielo, Haso
Mamy	MAM	F	JUV	2010	Son of Kintana
Nify	Ni	M	AD		
Omby	Om	M	AD		
Rano*	RA	F	AD		
Shielo	Sh	M	SA-AD	2009	Son of Lanitra
Tantely	Ta	M	IN	2011	Son of Kintana
Velo	Ve	M	IN	2011	Son of Alina
Mandena - Group AB					
Abelardo	Ab	M	AD		
Barabarà	BA	F	AD		Mother of Octavio and Dodò
Dodò	Do	M	IN	2011	Son of Barabarà
Octavio	Oc	M	SA-AD	2009	Son of Barabarà
Mandena - Group C					
Apollo	Ap	M	SA-AD	2009	Son of Mamiska
Eddy[e]	Ed	M	AD		
Filippo	Fi	M	AD		
Lita	LI	F	JUV	2010	Daughter of Mamiska
Mamiska	MA	F	AD		Mother of Apollo, Lita, Olivia, Tina
Olivia	OL	F	IN	2011	Daughter of Mamiska
Tina[l]	TI	F	SA-AD	2009	Daughter of Mamiska

F: female; M: male; AD: adult; SA: sub-adult; JUV: juvenile; IN: infant; *: left group B on September 2011. [e]: joined group C on September 2011; [l]: left group C on September 2011

Eulemur collaris between July 2011 and January 2012 showed a daily rate of associative interactions (as n° of interactions per hour of observation) of (median (quartile range)) 1.60 (1.00-2.81), followed by affiliative (1.21 (0.71-2.09)) and agonistic (0.09 (0.00-0.32)) interactions. Mandena groups showed more interactions between adults in every category (table 9.2). Differences between groups living in the same site were found at Sainte Luce (group B showed more agonistic interactions between adults as compared to group A: $U_{25,25=}171$, p=0.006) and at Mandena (group C showed more agonistic interactions between adults compared to group AB: $U_{28,23}=198$, p=0.018).

	Associative (n°/hour)	**Affiliative (n°/hour)**	**Agonistic (n°/hour)**
Group A	**1.16**	**0.89**	**0.00**
	0.61-1.60	0.58-1.54	0.00-0.09
Group B	**1.23**	**0.69**	**0.09**
	0.92-1.66	0.44-0.96	0.00-0.35
STL	**1.23**	**0.72**	**0.04**
	0.87-1.61	0.51-1.25	0.00-0.18
Group AB	**2.07**	**1.71**	**0.08**
	1.84-3.40	1.13-2.40	0.00-0.34
Group C	**1.64**	**2.03**	**0.20**
	1.02-3.34	1.21-3.04	0.17-0.51
MDN	**2.06**	**1.77**	**0.18**
	1.35-3.34	1.15-2.72	0.00-0.41
U	638**	496**	916*
p-level	0.000	0.000	0.015

Table 9.2: Daily rate of *Eulemur collaris* interactions at Mandena and Sainte Luce. Daily rate as n° of interaction per hour of diurnal observation during the study period. Bottom: results of Mann-Whitney test between daily rate at Sainte Luce and Mandena. *p<0.05, **p<0.01

During the study period we passed from “gestation period”, including July, August and September, to “lactation period”, from

October to January. During the lactation period, social interactions between adults were higher, especially at Sainte Luce (table 9.3).

		Gestation (n°/hour*100)	Lactation (n°/hour*100)	N	T	p-level
Sainte Luce	**Associative**	**2.38**	**4.47**	72	164**	0.000
		0.79-2.78	2.55-8.29			
	Affiliative	**1.59**	**3.82**	72	416**	0.000
		0.79-2.78	1.91-5.75			
	Agonistic	**0.00**	**0.00**	72	45*	0.025
		0.00-0.00	0.00-0.00			
Mandena	**Associative**	**16.56**	**29.76**	12	10*	0.023
		9.11-38.54	16.22-72.66			
	Affiliative	**24.43**	**41.55**	12	12*	0.034
		16.56-37.41	20.94-65.63			
	Agonistic	**0.00**	**0.00**	12	3	0.225
		0.00-1.55	0.00-4.37			

Table 9.3: Differences in social interactions between "gestation" and "lactation" period in *Eulemur collaris* at Mandena and Sainte Luce. Total rate of interaction between dyads per hour of observation during the study period. Values are in medians (in bold) and quartiles. On the right: results of Wilcoxon T test between dyads interactions during "gestation" and "lactation". *p<0.05, **p<0.01

During the study period, females were statistically dominant over males at both study sites (see Table 9.4 and 9.5). Group A was the only group were females did not have more aggressive interaction over males than *vice versa*, but affiliative and associative interaction started more frequently from males over females (Table 9.4). In the other groups present at Mandena and Sainte Luce, females were dominant over males considering every interaction type. But not each male was subordinated to females. In fact, we noted male-female preferences at both sites, with dominant males and females and preferred dyads. In Group B Omby was subordinate of Lanitra, but was also the preferred male for the other two females: Alina and Kintana.

Table 9.4: Sexual dominance at Sainte Luce.

	Associative				Affiliative				Agonistic			
	Total		Obs-Exp		Total		Obs-Exp		Total		Obs-Exp	
	FM	MF	F	M	FM	MF	F	M	FM	MF	F	M
Sainte Luce - Group B												
ALI-Fo	2	2	1.00	1.00	2	2	0.97	0.97	0	0	0	0
ALI-Ni	10	17	-7.30	-0.30	4	6	-5.73	-3.73	0	0	-0.14	-0.14
ALI-Om^{P}	9	28	-0.92	18.08	10	21	3.86	14.86	0	0	-1.05	-1.05
ALI-Sh	1	26	-13.89	11.11	6	11	0.16	5.16	5	0	4.27	-0.73
KI-Fo	0	0	-1.22	-1.22	0	0	-1.30	-1.30	0	0	-0.36	-0.36
KI-Ni	17	21	-1.79	2.21	8	20	-4.86	7.14	0	1	-0.63	0.37
KI-Om^{P}	8	29	-1.86	19.14	9	26	0.80	17.80	0	2	-0.99	1.01
KI-Sh	3	20	-10.97	6.03	2	8	-5.64	0.36	3	0	2.56	-0.44
LA-Fo	1	0	-0.10	-1.10	1	1	-0.26	-0.26	0	0	-0.11	-0.11
LA-Ni^{P}	20	55	1.39	36.39	14	40	1.69	27.69	1	1	-0.06	-0.06
LA-Om	0	2	-10.50	-8.50	0	0	-7.84	-7.84	18	2	10.99	-5.01
LA-Sh	8	21	-7.61	5.39	4	12	-3.33	4.67	7	0	2.20	-4.8
RA-Fo	1	0	0.95	-0.05	0	0	0	0	0	0	0	0
RA-Ni	0	4	-0.98	3.02	0	0	0	0	0	0	0	0
RA-Om	0	2	-0.58	1.42	0	0	0	0	0	0	0	0
RA-Sh	0	0	-0.90	-0.90	0	0	0	0	0	0	0	0
TOT	**80**	**227**	**-55.29**	**94.17**	**60**	**133**	**-21.48**	**65.52**	**34**	**6**	**16.69**	**-11.31**
X^2			239.33**				183.59**				74.13**	
p-level			<0.001				<0.001				<0.001	
							F>>M					
Sainte Luce - Group A												
AL-Ch	4	5	-3.09	-2.09	3	7	-3.49	0.51	0	0	0	0
AL-Ma	2	7	-9.00	-4.00	5	7	-6.06	-4.06	0	0	0	0
AL-Ri^{P}	12	31	1.30	20.30	10	25	0.43	15.43	0	0	-0.2	-0.2
AL-So	2	10	-9.23	-1.23	1	4	-9.77	-6.77	0	0	0	0
FA-Ch	12	14	2.43	4.43	9	11	-0.35	1.65	1	0	0.9	-0.1
FA-Ma	5	8	-2.24	0.76	7	11	-0.97	3.03	0	0	-0.2	-0.2
FA-Ri	7	9	-6.98	-4.98	5	6	-8.69	-7.69	1	5	-0.7	3.3
FA-So^{P}	18	34	3.59	19.59	16	40	0.57	24.57	0	0	-0.2	-0.2
VO-Ch	4	7	-2.57	0.43	3	9	-3.42	2.58	0	0	-0.2	-0.2
VO-Ma	0	5	-5.09	-0.09	0	1	-5.47	-4.47	1	0	0.6	-0.4
VO-Ri^{P}	14	22	4.11	12.11	16	31	6.56	21.56	0	0	-0.2	-0.2
VO-So	2	7	-8.35	-3.35	4	5	-6.63	-5.63	2	0	1.6	-0.4
TOT	**82**	**159**	**-35.12**	**41.88**	**79**	**157**	**-37.30**	**40.70**	**5**	**5**	**1.4**	**1.4**
X^2			123.88**				168.17**				24.99	
p-level			<0.001				<0.001				0.351	
							F>M					

Female dominance is significant when the conflicts won by females *vs.* males and the associative or affiliative interactions started by males on females are statistically more frequent than expected if in dyads male and female has the same role; *vice versa* for male dominance. Multiple Chi-square tests on female-male dyads were used at both sites. *p<0.05, **p<0.001; ^{P}: preferred dyad for females. FM: action started by females on males; MF: action started by males on females; F: observed-expected values for females; M: observed- expected values for males.

Lanitra's preferred male was Nify. Shielo was subordinated to Alina, Kintana and Lanitra, while Fotsy and Rano left the group in September and showed no particular preferences during the study period. Kintana was the only female which received more aggressions by males (Nify and Omby). In group A Rivotra was the preferred male for Ala and Volana, while Sotro was the preferred male for Fana. Moreover, Fana was the only female subordinated to a male, Rivotra. At Mandena, group size was smaller and the structure was similar, whit a dominant pair (Barabarà and Abelardo in group AB, Mamiska and Filippo in group C) and subordinated young males (Octavio in group AB, Apollo in group C) (Table 9.5).

Table 9.5: Sexual dominance at Mandena.

	Associative				**Affiliative**				**Agonistic**			
	Total		Obs-Exp		Total		Obs-Exp		Total		Obs-Exp	
	FM	MF	F	M	FM	MF	F	M	FM	MF	F	M
Mandena - Group AB												
BA-Ab^P	103	187	13.81	97.81	66	125	-9.02	49.98	0	0	0	0
BA-Oc	50	297	-96.57	150.43	47	186	-43.37	95.63	60	0	30	-30
TOT	**153**	**484**	**-82.76**	**248.24**	**113**	**367**	**-52.39**	**145.61**	**60**	**0**	**30**	**-30**
X^2			327.43**				156.39**				60.00**	
p-level			<0.001				<0.001				<0.001	
							F>>M					
Mandena - Group C												
MA-Ap	15	61	-22.96	23.04	9	50	-33.79	7.21	70	0	41.93	-28.07
MA-Ed	0	0	-7.73	-7.73	0	0	-13.34	-13.34	0	0	-6.21	-6.21
MA-Fi^P	56	101	15.37	60.37	63	120	17.62	74.62	0	2	-0.26	1.74
TI-Ap	6	4	-0.42	-2.42	1	3	-4.18	-2.18	0	0	0	0
TI-Fi	9	11	1.39	3.39	3	6	-2.47	0.53	0	0	0	0
TOT	**86**	**177**	**-14.35**	**76.65**	**76**	**179**	**-36.16**	**66.84**	**70**	**2**	**35.46**	**-32.54**
X^2			141.58**				189.59**				114.99**	
p-level			<0.001				<0.001				<0.001	
							F>>M					

Female dominance is significant when the conflicts won by females *vs.* males and the associative or affiliative interactions started by males on females are statistically more frequent than expected if in dyads male and female has the same role; *vice versa* for male dominance. Multiple Chi-square tests on female-male dyads were used at both sites. *p<0.05, **p<0.001; ^{P}: preferred dyad for females. FM: action started by females on males; MF: action started by males on females; F: observed-expected values for females; M: observed- expected values for males.

However, in the dominant pair the male searched more the female than *vice versa* in each group. In group C Tina left the group on September, joining a solitary male (personal observation), while Eddy joined group C in the same period. Eddy remained far from Mamiska for the most time of the study period due to the aggressive reaction of Filippo when Eddy was near her.

Relations between males and females changed over time: during the gestation period a possible special relationship (table 9.6) between males and females was found only in group C between Filippo and Mamiska, while during the lactation period relationships between females and males became stronger, especially at Sainte Luce. In fact, in group A we found a possible special relationship between Ala and Rivotra, between Volana and Rivotra, and between Sotro and Fana. In group B we found a possible special relationship between Lanitra and Nify, a preference for Omby in Alina, and a preference for Kintana in Omby. In group AB we found no special relationships. In group C we found a possible special relationship between Mamiska and Filippo also during the lactation period. Inter-sexual interactions at Sainte Luce and Mandena are shown in table 9.7 and 9.8. In group B male-male and female-female associative interactions were more frequent than expected if the members of dyads had different sex, principally due to Shielo and Kintana. Male-male agonistic interactions were less than expected. In group A male-male and female-female associative and affiliative interactions were more frequent than expected. In group AB associative and affiliative interactions between Octavio and Abelardo were higher than expected.

Table 9.6: Male-female relationship during "gestation" and "lactation".

	Gestation season								Lactation season							
	Associative			Affiliative		Agonistic		Relation type	Associative			Affiliative		Agonistic		Relation type
	FM	MF	Focal	FM	MF	FM	MF		FM	MF	Focal	FM	MF	FM	MF	
Sainte Luce - Group A																
AL-Ch																
AL-Ma																
AL-Ri									+	+	+		+			(S)
AL-So																
FA-Ch						+										
FA-Ma																
FA-Ri															+	
FA-So									+	+	+		+			(S)
VO-Ch																
VO-Ma																
VO-Ri				+					+		+	+	+			(S)
VO-So																
Sainte Luce – Group B																
ALI-Ni																
ALI-Om									+			+	+			FP
ALI-Sh																
KI-Ni			+	+												
KI-Om										+		+	+			MP
KI-Sh																
LA-Ni		+	+			+				+	+	+	+			(S)
LA-Om														+		
LA-Sh						+								+		
Mandena – Group AB																
BA-Ab																
BA-Oc	+					+								+		
Mandena – Group C																
MA-Fi		+	+	+	+			(S)	+		+	+	+			(S)
MA-Ap						+								+		
MA-Ed																

A special relationship is defined by above average reciprocal frequencies of association and affiliative behaviour and below average frequencies of conflicts. Dyads that fulfill all these criteria are indicated by "S". Dyads with "(S)" may reflect a special relationship, as six out of seven criteria were fulfilled. Focal is considered as the frequency of instantaneous in which the members of the dyads rested together: +:frequency above X+SD. Association/affiliation: +: frequency above X+SD of (observed – expected) for each dyad. Conflict: +: frequency of agonistic interactions above X+SD. First sign: first animal's perspective; second sign: second animal's perspective. Female acronyms: capital letters; male acronyms: initial capitals and lowercase letters. MP: male preference over females; FP: female preference over males.

Table 9.7: Inter-Sexual interactions at Sainte Luce.

	Associative				Affiliative				Agonistic			
	Total		Obs-Exp		Total		Obs-Exp		Total		Obs-Exp	
	ab	ba	A	b	ab	Ba	a	b	ab	ba	a	b
Sainte Luce - Group B												
ALI-KI	14	25	0.61	11.61	8	7	0.19	-0.81	0	0	-0.27	-0.27
ALI-LA	12	14	-0.08	1.92	7	5	-0.56	-2.56	0	0	-0.14	-0.14
ALI-RA	0	1	-0.56	0.44	0	0	0	0	0	0	0	0
KI-LA	27	14	11.91	-1.09	11	13	2.03	4.03	0	7	-3.08	3.92
KI-RA	1	0	0.24	-0.76	0	0	0	0	0	0	0	0
LA-RA	0	0	-0.63	-0.63	0	0	0	0	0	0	0	0
Fo-Ni	0	4	-1.49	2.51	2	2	0.55	0.55	2	0	1.89	-0.11
Fo-Om	2	1	1.17	0.17	1	1	0.09	0.09	2	0	1.16	-0.84
Fo-Sh	1	0	-0.22	-1.22	1	1	0.12	0.12	0	0	-0.58	-0.58
Ni-Om	2	7	-8.71	-3.71	2	2	-5.13	-5.13	3	0	1.64	-1.36
Ni-Sh	9	42	-5.57	27.43	12	13	4.69	5.69	1	0	0.13	-0.87
Om-Sh	5	11	-0.85	5.85	4	2	-0.48	-2.48	0	0	-0.58	-0.58
Exp-Obs			**22.95**				**2.32**				**0.02**	
X^2 F-F			22.88*				3.26				8.88	
p-level			0.018				0.987				0.633	
Exp-Obs			**14.66**				**-1.31**				**-0.69**	
X^2 M-M			75.44**				16.70				41.88**	
p-level			<0.001				0.117				<0.001	
Sainte Luce - Group A												
AL-FA	13	20	0.09	7.09	16	19	5.31	8.31	0	1	-0.1	0.9
AL-VO	11	11	2.97	2.97	9	9	1.79	1.79	0	0	-0.2	-0.2
FA-VO	24	12	11.98	-0.02	14	13	3.36	2.36	0	3	-1.6	1.4
Ch-Ma	8	10	4.18	6.18	7	8	2.60	3.60	0	0	0	0
Ch-Ri	6	4	-1.35	-3.35	6	7	-1.35	-0.35	0	0	-0.2	-0.2
Ch-So	10	10	2.47	2.47	13	12	4.66	3.66	0	0	0	0
Ma-Ri	2	3	-3.46	-2.46	2	1	-4.27	-5.27	0	1	-0.4	0.6
Ma-So	9	12	3.44	6.44	16	16	8.89	8.89	0	0	0	0
Ri-So	12	15	1.35	4.35	13	15	1.20	3.20	0	0	-0.4	-0.4
Exp-Obs			**25.07**				**22.91**				**0.2**	
X^2 F-F			18.03*				11.56*				4.14	
p-level			0.003				0.041				0.529	
Exp-Obs			**20.28**				**25.47**				**-1**	
X^2 M-M			32.86**				39.50**				2,50	
p-level			<0.001				<0.001				0.996	

Multiple Chi-square tests on male-male and female-female dyads were used to show if relationships between lemurs of the same sex were stronger than expected if the members of dyads had different sex. *p<0.05, **p<0.001

ab: action started by first member of the dyad (a) on the second member of the dyad (b); ba: action started by b on a; a: observed-expected values for a; b: observed- expected values for b.

In group C male-male interactions were higher than expected, especially for Apollo and Eddy. Affiliative interactions between Mamiska and Tina were higher than expected.

Table 9.8: Inter-Sexual interactions at Mandena.

	Associative				**Affiliative**				**Agonistic**			
	Total		Obs-Exp		Total		Obs-Exp		Total		Obs-Exp	
	ab	ba	A	b	ab	Ba	a	b	ab	ba	a	b
Mandena - Group AB												
Ab-Oc	42	216	-61.19	112.81	149	181	53.28	85.28	12	0	6	-6
Exp-Obs			**51.61**				**138.55**				**0.00**	
X^2 M-M			159.60**				105.62**				12**	
p-level			<0.001				<0.001				<0.001	
Mandena - Group C												
MA-TI	9	9	1.93	1.93	9	11	5.33	7.33	0	0	0	0
Ap-Ed	30	22	22.30	14.30	60	54	41.59	35.59	0	1	-0.40	0.60
Ap-Fi	60	30	24.64	-5.36	88	87	31.82	30.82	0	6	-10.03	-4.03
Ed-Fi	1	2	-7.78	-6.78	2	2	-17.42	-17.42	0	17	-2.21	14.79
Exp-Obs			**3.86**				**12.65**				**0.00**	
X^2 F-F			1.05				22.34**				0.00	
p-level			0.305				<0.001				1.000	
Exp-Obs			**41.33**				**104.96**				**-1.28**	
X^2 M-M			121.34**				228.88**				113.93**	
p-level			<0.001				<0.001				<0.001	

Multiple Chi-square tests on male-male and female-female dyads were used to show if relationships between lemurs of the same sex were stronger than expected if the members of dyads had different sex. *p<0.05, **p<0.001

ab: action started by first member of the dyad (a) on the second member of the dyad (b); ba: action started by b on a; a: observed-expected values for a; b: observed- expected values for b.

Overall, Lanitra was the dominant female in group B with the highest standardized residual of agonistic interactions (i.e. she was the one that won more conflicts within the group, with the highest value of agonistic done-agonistic received), and the lowest standardized residual of associative and affiliative interactions (i.e. she was the one more searched within the group, with the highest value of associative/affiliative received-associative/affiliative done) (Figure 9.1). Fotsy was probably the dominant male since he left the group. After this event Nify became the dominant male. Shielo was the youngest adult male and he had the highest standardized residual of associative and affiliative interactions, and the lowest standardized residual of agonistic interactions.

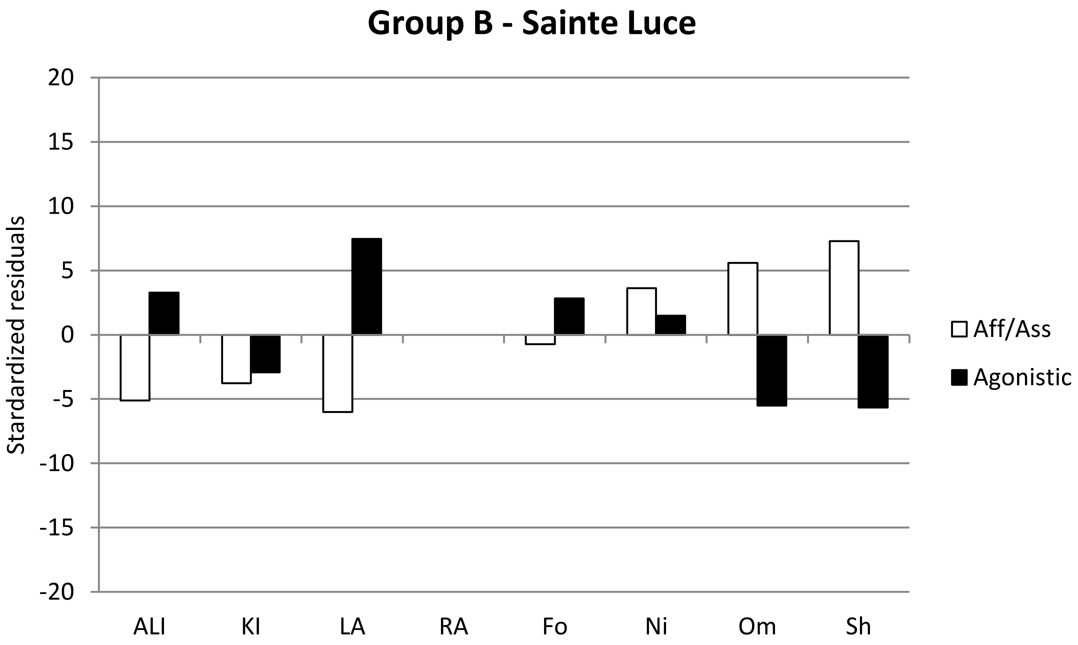


Fig. 9.1: Total standardized residuals for affiliative/associative and agonistic interactions in members of group B in Sainte Luce. Female acronyms: capital letters; male acronyms: initial capital and lowercase letters. Lanitra was the dominant female; Fotsy since he left the group on September and Nify after this event were the dominant males.

Kintana was the youngest female and she had the highest standardized residual of associative and affiliative interactions (Rano excluded, whose value was zero) and the lowest standardized residual of agonistic interactions between females. Omby was the lemur with the second lowest standardized residual of agonistic interactions principally due to Lanitra. Alina was higher in rank compared to Kintana, having a higher standardized residual of agonistic interactions. In group A differences in standardized residuals were lower than in group B (Figure 9.2). Rivotra and Volana were the dominant male and female as their standardized residuals of agonistic interactions were higher than all the others. Male standardized residuals of affiliative and associative interactions were positive, while those of females were negative.

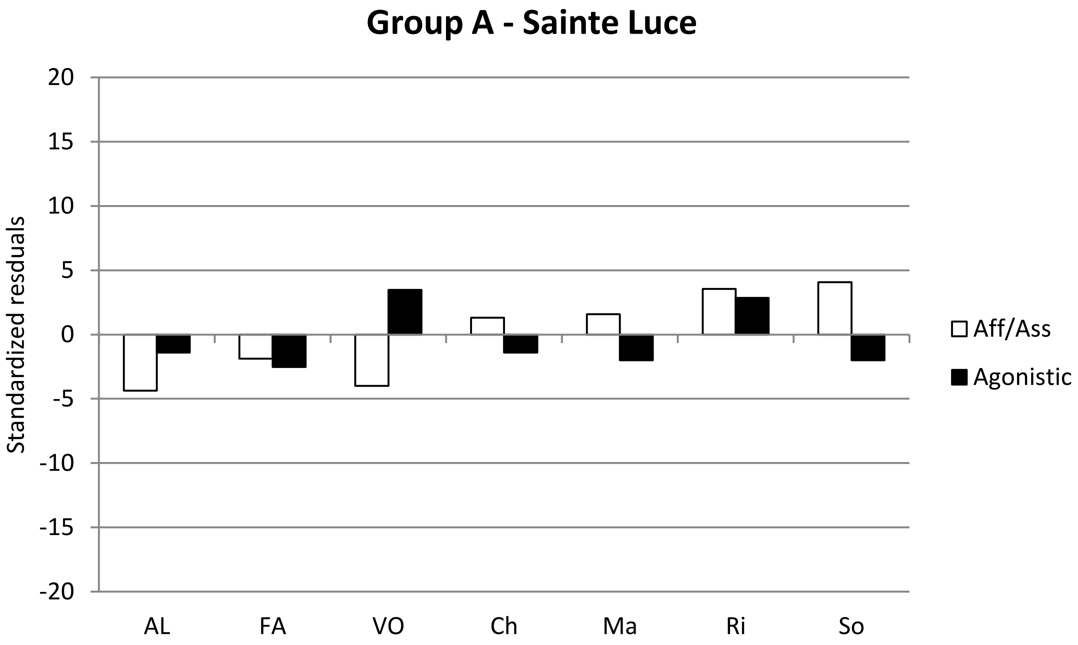


Fig. 9.2: Total standardized residuals for affiliative/associative and agonistic interactions in members of group A at Sainte Luce. Female acronyms: capital letters; male acronyms: initial capital and lowercase letters. Volana was the dominant female; Rivotra was the dominant male.

In group C Mamiska was the dominant female with the highest standardized residual of agonistic interactions and the lowest standardized residual on affiliative and associative interactions (figure 9.3). Filippo was the dominant male with the highest standardized residual of agonistic interactions. Apollo, the youngest adult male, had the highest standardized residual of affiliative and associative interactions, and the lowest standardized residual of agonistic interactions. Eddy had a negative standardized residual of agonistic interactions and of affiliative and associative interactions.

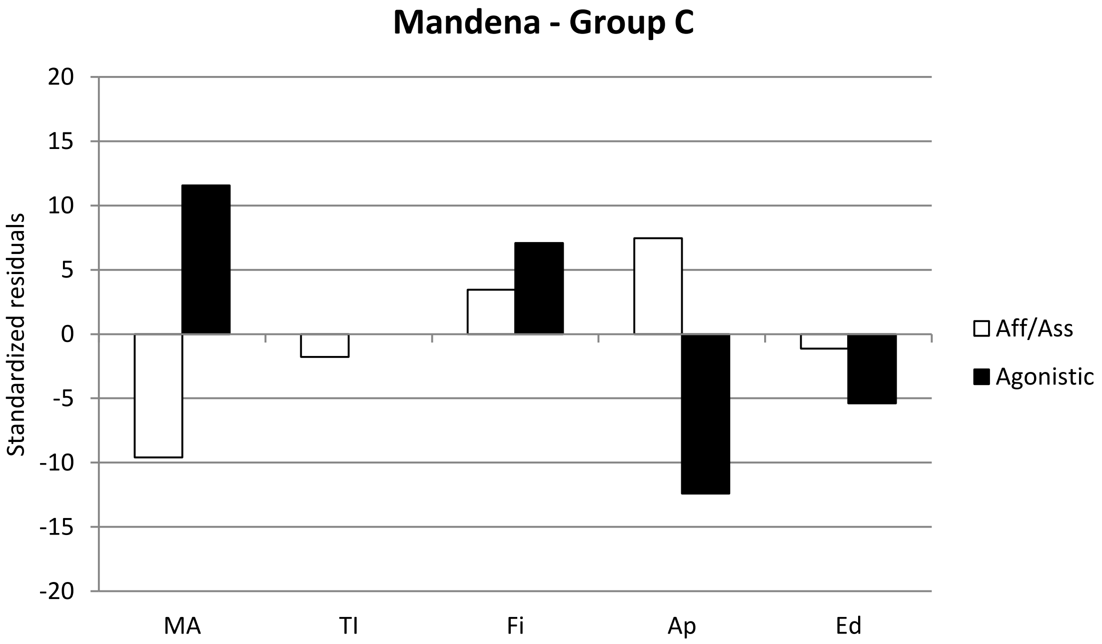


Fig. 9.3: Total standardized residuals for affiliative/associative and agonistic interactions in members of group C at Mandena. Female acronyms: capital letters; male acronyms: initial capital and lowercase letters. Mamiska was the dominant female; Filippo was the dominant male.

In group AB we had the highest difference in standardized residuals (figure 9.4). Barabarà was the dominant female and Abelardo the dominant male. Octavio was the youngest adult whit the highest standardized residual of affiliative and associative interactions, and the lowest standardized residual of agonistic interactions.

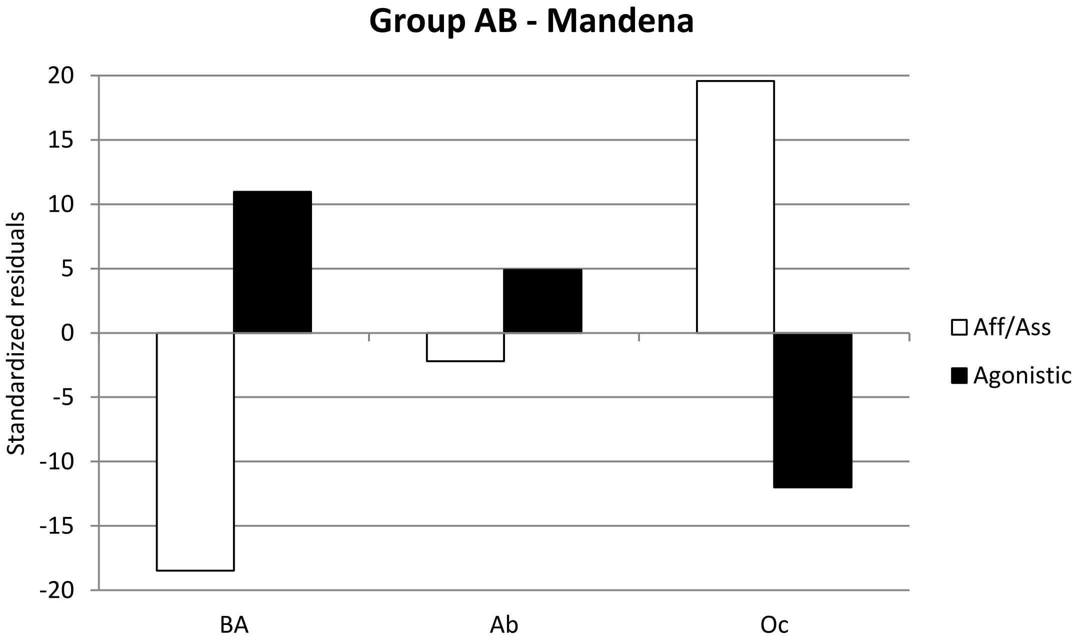


Fig. 9.4: Total standardized residuals for affiliative/associative and agonistic interactions in members of group AB at Mandena. Female acronyms: capital letters; male acronyms: initial capital and lowercase letters. Barabarà was the dominant female; Abelardo was the dominant male.

Finally, we used three indices based on aggressive interactions only to see the dominance within the group (Table 9.9). In group A, Volana was the highest in rank, followed by Rivotra (the highest male in rank), Fana and Sotro. Mean ranks of females were higher compared to mean ranks of males. In group B, Lanitra was the highest ranking, followed by Fotsy (the highest ranking male), Nify and Alina. Mean ranks of females were higher compared to mean ranks of males. In group AB Barabarà was the highest ranking, followed by Abelardo. In group C Filippo was the highest ranking, followed by Mamiska. This was the only case in which a male had the highest rank within a group. However, mean ranks of females

(Mamiska) was higher as compared to mean ranks of males, due to the fact that Apollo was clearly subordinated.

	Gender	AttFr	Rank$_{AttFr}$	ADI	Rank$_{ADI}$	DS	Rank$_{DS}$	Rank$_{Total}$	Rank$_{F}$	Rank$_{M}$
Sainte Luce - Group A										
Ala	F	0	2.5	0	2.5	-2.83	1.5	2.17		
Chefo Be	M	0	2.5	0	2.5	-2.83	1.5	2.17		
Fana	F	3	5	0.54	5	0.5	5	5		
Masoandro	M	0	2.5	0	2.5	-2.17	3	2.67		
Rivotra	M	6	6.5	0.92	6	3.17	6	6.17		
Sotro	M	0	2.5	0	2.5	-1	4	3		
Volana	F	6	6.5	1	7	5.17	7	6.83		
									4.67	3.50
Sainte Luce - Group B										
Alina	F	5	5	1	6.5	1	4	5.17		
Fotsy*	M	4	3.5	1	6.5	6.6	7	5.67		
Kintana	F	3	2	0.25	2	-7	2	2		
Lanitra	F	33	7	0.85	5	5.5	5.5	5.83		
Nify	M	6	6	0.7	4	5.5	5.5	5.17		
Omby	M	4	3.5	0.28	3	-2.5	3	3.17		
Rano*	F	NA	NA	NA	NA	NA	NA	NA		
Shielo	M	0	1	0	1	-9.1	1	1		
									4.33	3.75
Mandena - Group AB										
Abelardo	M	12	2	1	2.5	1	2.5	2.33		
Barabarà	F	60	3	1	2.5	1	2.5	2.67		
Octavio	M	0	1	0	1	-2	1	1		
									2.67	1.67
Mandena - Group C										
Apollo	M	0	1	0	1	-5	1	1		
Eddy[e]	M	1	2	0.5	2.5	0	2.5	2.33		
Filippo	M	25	3	1	4	5	4	3.67		
Mamiska	F	70	4	0.5	2.5	0	2.5	3		
Tina[l]	F	NA	NA	NA	NA	NA	NA	NA		
									3	2.33

Table 9.9: Dominance within the groups at Mandena and Sainte Luce. AttFr: Attack/win frequency; ADI: Average Dominant Index; DS: David's score. Rank$_{Total}$: mean rank between ranks obtained using the AttFr, ADI and DS index; Rank$_{F}$: mean total rank between females total ranks; Rank$_{M}$: mean total rank between males total ranks. *: left group B on September 2011. [e]: joined group C on September 2011; [l]: left group C on September 2011. NA: index not available (i.e. no aggressive interactions received or done).

9.4 Discussion

Eulemur collaris showed a multimale-multifemale social structure at both sites as the other brown lemurs. In fact, brown lemurs are known to live in multimale-multifemale social systems with group size ranging from 4 to 17 individuals (Sussman, 1974; Harrington, 1975; Overdorff, 1993; Freed, 1996; Vasey, 1997; Johnson, 2002). *E. f. rufus* is primarily characterized by female philopatry and male dispersal, although females may also migrate from natal groups (Ostner and Kappeler, 2004). During our study period we had two females (Tina, group C and Rano, group B) and one male (Fotsy, group B) that left the group, meaning that probably in *Eulemur collaris* there is no female philopatry. Long term studies may clarify this aspect of sociality. We found even sex ratios, or perhaps a slight bias in the number of males, which seems to be the norm across the brown lemur complex (Overdorff *et al.*, 1999; Kappeler, 2000; Johnson, 2002; Ostner, 2002). Such a proportionally higher number of males is unusual among polygynous primates and may be maintained by equal birth and mortality rates for males and females (Overdorff *et al.*, 1999; Kappeler, 2000). Moreover, estrus synchrony may limit male potential for monopolization of females, reducing incentives for males to exclude others from the group (Ostner and Kappeler, 2004). The ultimate causes for even or male-biased sex ratios remain obscure. Overdorff *et al.* (1999) suggest that increased numbers of males may result from the relatively greater energetic demands of females. Males may also perform some group services such as increased vigilance or aid in intergroup conflicts (Overdorff *et al.*, 1999).

We found evidence for female dominance at both sites, with some differences between groups. In every group, females received more grooming and males in general were more responsible for maintaining proximity. This is in line whit other studies on polygynous brown lemurs (e.g. *E. coronatus*; Marolf *et al.*, 2007). In monogamous brown lemurs (e.g. *E. rubriventer*; Marolf *et al.*, 2007) there is no sex difference in grooming, and females seem to be responsible for maintaining proximity. Additionally, *E. rubriventer* has lower rates of intersexual aggressions compared to *E. coronatus* (Marolf *et al.*, 2007). In *E. collaris* we found in general more intersexual than intrasexual aggressions. Our findings on female dominance may be influenced by the fact that our study period corresponds to gestation and lactation periods. In fact, most studies of lemurs indicate that aggression occurs mostly during feeding. Therefore, it has been proposed that female feeding priority is part of a behavioral strategy to maximize foraging efficiency, particularly during gestation and lactation periods (Jolly, 1984; Richard, 1987).

Overall, lemurs at Mandena showed a greater rate of interactions per hour despite the smaller group size. Interaction rates were lower compared to other studies in captivity (e.g. Kappeler, 1989; Marolf *et al.*, 2007). In particular, wild populations of brown lemurs have been characterized by low rates of agonistic behavior (Kaufman, 1996). Additionally, during lactation, interactions between individuals were higher than during gestation. We noted that during lactation the greatest part of agonistic interactions in Mandena was by adult females over sub-adult males (Mamiska over Apollo, Barabarà over Octavio). These agonistic interactions were mostly ‘cuff’ behaviors, performed when the sub-adult male tried to get in contact with the infant, or tried to play whit the mother, especially during the first two months of infants life (October-November). Moreover, we noted a higher rate of ‘play’ behaviors at Mandena. At Sainte Luce this behavior was less evident, especially in Group A. In group B we had some evidence of agonistic behavior made by adult females over sub-adult males (Kintana, Alina and Lanitra over Shielo). Differences in agonistic rate between Mandena and Sainte Luce can be due to this particular behavior. In fact, we must expect to find a higher agonistic rate in larger groups as feeding competition increases with the number of animals in the group (Kubzdela, 1997). Even if in Mandena we could have a higher feeding competition as the habitat quality is lower, we can observe that the major part of agonistic behavior in Mandena was not a consequence of feeding competition. In fact, we noted that most agonistic behaviors at Mandena occured during resting, while at Sainte Luce we noted more agonistic behaviors during feeding (pers. obs.).

Relationships between individuals changed over the biological cycle: during gestation male-female relationships were less strict, while during lactation male-female dyads became closer. In this thesis we omitted data during the other two periods, the non-reproductive and the mating seasons (from February to June), but the whole data will be the subject of a future publication. The mating season in particular is fundamental in determining bonded male–female pairs (van Schaik and Kappeler, 1993). We found possible special relationships between male-female dyads during lactation. Females may increase benefits such as higher foraging efficiency from coalitions with individual males, thus reducing the impetus to dominate all males, while males may pursue a strategy of special relationships with individual females for increasing mating opportunities (due, in part at least, to concealed ovulation in these females) (Pereira and McGlynn, 1997). Special relationships established during the mating season may occur during the lactation period, as the probability of paternity is high. Another possible social structure in brown lemurs concerns the presence of one central male, able to monopolize social interactions with females to varying degrees, and several peripheral males (Ostner and Kappeler, 1999). We must evaluate the relationships during the mating season to avoid the presence of one central and several peripheral males in our groups, but no evidence was present during our study period (also considering the more complex groups at Sainte Luce).

In Mandena, social structure was simpler, due to the small group size. Group AB in particular had one clearly subordinate male (Octavio) and two dominant individuals (Barabarà and Abelardo) that never showed agonistic behavior one to the other. Group C was more complex as Eddy joined this group on September. In fact, we had one clearly subordinate male (Apollo), one dominant female (Mamiska) which received two times agonistic interactions by

Filippo (the dominant male, which had the highest rank in the group), and Eddy. Eddy remained mostly in contact with Apollo, and never went in contact with Mamiska, due to the fact that Filippo chased him when he tried to enter in proximity with Mamiska. Moreover, Eddy never fed on the same tree of Mamiska, and rested mostly with Apollo.

At Sainte Luce, the social structure was clearly more complex. In group A, Volana was the dominant female and Rivotra the dominant male. But this was not evident in every period, due to the fact that agonistic interactions in this group were very rare. Males were more responsible for proximity and females received more grooming, but there were no differences concerning agonistic behavior between males and females. In group A we found three possible special relationships during lactation: between Fana and Sotro, Volana and Rivotra, Ala and Rivotra. Visualizing the spatial proximity pattern (i.e. the time spent resting together for each dyad), we can see that the most evident difference between gestation and lactation period was the lack of a strong association between Fana and Rivotra, and between Sotro and Rivotra (figure 9.5). Fana in particular seemed to be more linked to Sotro during lactation, also having a possible special relationship with him. Chefo be and Masoandro seemed to be peripheral males. Ala, even if she was low in rank using dominance indices, was in strong association with Rivotra and Volana, especially during lactation, and formed a possible special relationship with Rivotra during lactation. Female-female associations remained strong during the entire study period (excepted for Volana-Ala during gestation).

Group A was the study group with the lowest within group agonistic rate.

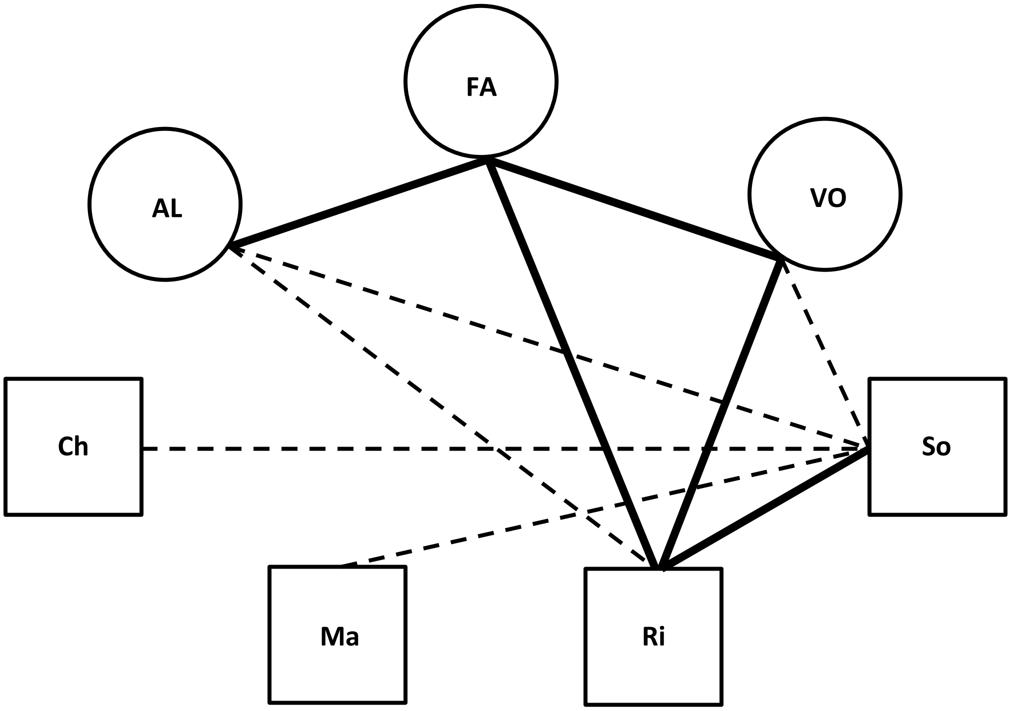
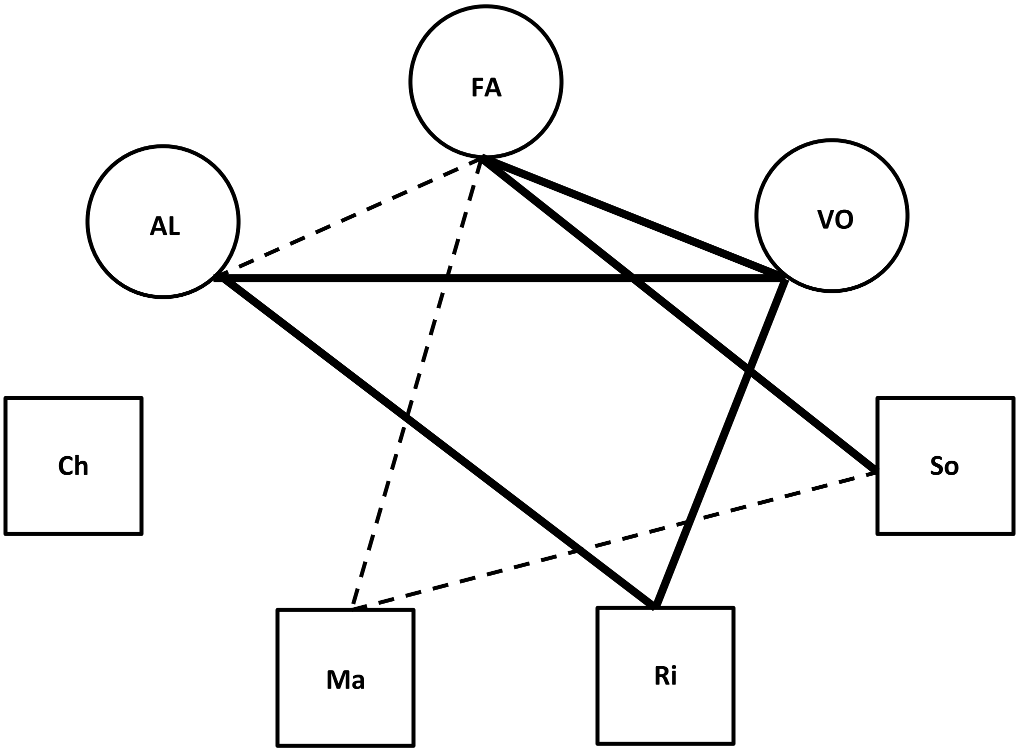


Fig. 9.5. Spatial proximity patterns in group A during gestation (above) and lactation (below). Fat lines refer to proximity values in the highest 25 percentile of observed dyads, and dashed lines refer to values in the next highest 25 percentile (50-75%). Adult females are represented by circles; adult male by squares.



In group B, aggressive interactions occurred more frequently than in group A, and dominance indices gave clearer results. Lanitra was the dominant female, but also Alina was high ranking. Fotsy was the dominant male until he left the group on September, and after this event Nify became the dominant male, forming a possible special relationship with Lanitra. Kintana, and in particular Shielo, were the subordinated sub-adults. Omby was subordinated to Lanitra, but remained linked with the other two females (Alina and Kintana). Visualizing the spatial proximity pattern (i.e. the time spent resting together for each dyad), we can see that the most evident difference between gestation and lactation period was the lack of a strong association between Nify and Kintana (figure 9.6). Shielo rested more with Lanitra and Nify during the lactation period. Omby remained out of the dominant group formed by Lanitra and Nify, but Alina and Kintana remained in association whit him. Female-female associations remained strong during the entire study period.

In conclusion, *Eulemur collaris* seemed to follow the social flexibility typical of the brown lemur complex. We found multimale-multifemale groups and equal sex ratios. We found evidences of female dominance in both sites and female-female strong association at Sainte Luce. However, we also found evidence of special relationships and dyadic preferences. Moreover, social structure seemed to change seasonally, depending on the reproductive cycle. Thus, it will be fundamental to join our data with the data collected from February 2011 to July 2011 in order to have one full year of data.

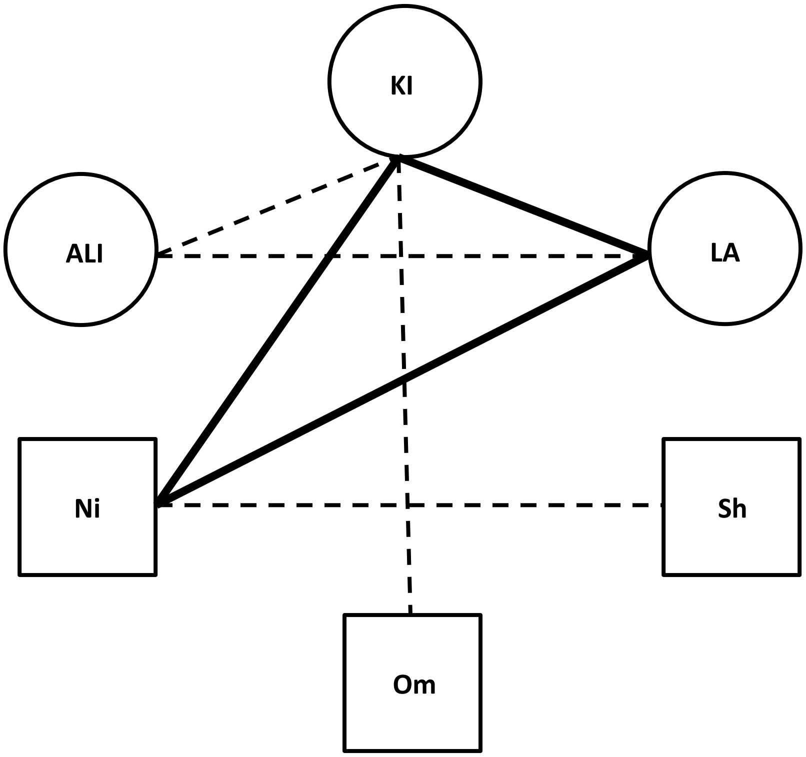
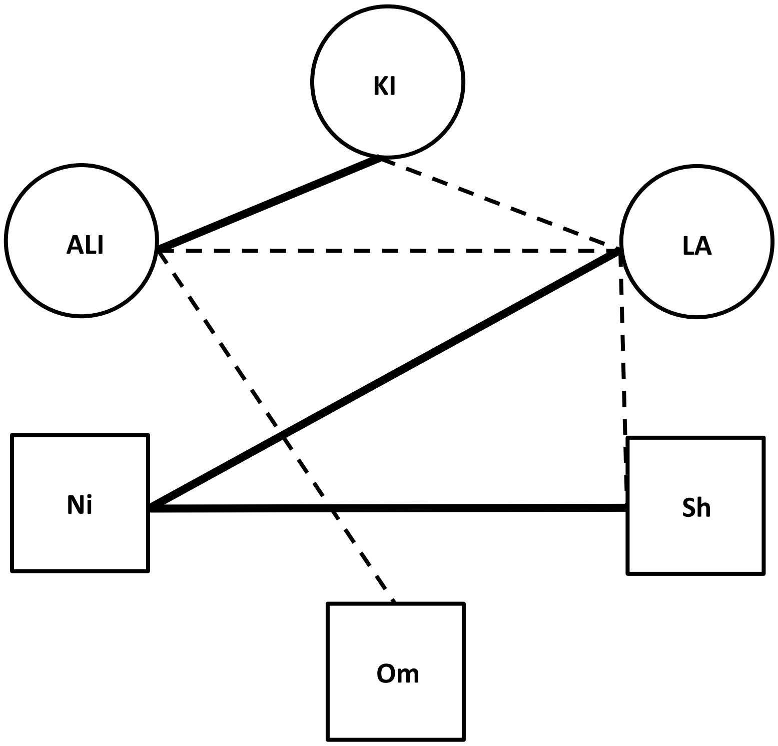


Fig. 9.6. Spatial proximity patterns in group B during gestation (above) and lactation (below). Fat lines refer to proximity values in the highest 25 percentile of observed dyads, and dashed lines refer to values in the next highest 25 percentile (50-75%). Adult females are represented by circles; adult male by squares.



CHAPTER 10

GENERAL CONCLUSIONS

Eulemur collaris seemed to be able to cope with habitat degradation, showing a great flexibility over the study period. We investigated ecological, social and also physiological aspects, finding a wide range of strategies used by this lemur.

In the more degraded forest of Mandena, the first response to habitat degradation was the reduction in group size. Moreover, lemurs at Mandena used a wide range of energy-saving behaviors over the study period. In fact, they were found to have low daily ranges and distance traveled, higher time spent resting during the day and higher time spent in energy-saving postures during resting. Probably, Mandena cannot support more than the actual individuals of red collared brown lemur, considering the extension of the home ranges. Lemurs at Mandena integrated in great quantity their diet whit 'bad' fruits, generally discarded and considered marginal fruits in a more intact forest. Thus, *Eulemur collaris* living in a degraded forest have to assume a high quantity of non-digested fibers (Acid Detergent Fibers), and a high quantity of secondary compounds which are known to bind proteins and reduce their digestibility (tannins). Moreover, at Mandena predation risk seemed to be higher. It will be interesting to integrate our eco-ethological data with the data on stress degree evaluated via glucocorticoids levels. We found slight evidence of flexibility in physiological mechanisms (heterothermy) during lean and cool periods. Thus, it will be interesting to clarify this aspect with further studies on skin temperature of *Eulemur collaris*.

In conclusioni, due to its high behavioral and ecological flexibility, *Eulemur collaris* is able to cope with modified environmental conditions. The really alarming consideration on these results is that a species with such a high flexibility is nevertheless listed as ‘Vulnerable’ on the ‘Red List of Threatened Species’ (IUCN 2008). Furthermore, the new IUCN congress decided to ‘elevate’ *Eulemur collaris* to the ‘Endangered’ category.

Appendix I. Ethogram of *Eulemur collaris*, including codes and descriptions of actions, postures and food items

ACTION	CODE	DESCRIPTION
FEEDING	F	Bite, chew and swallow a food item
HUDDLING	H	Remain inactive in close body contact with one or more conspecifics
MOVING	M	Get around on trees or on the ground
RESTING	R	Remain inactive and motionless, no contact with conspecifics
SOCIAL INTERACTIONS:		Every action determined by the contact with other individuals
Affiliative (intra-group)		
GENITAL OTHER	GO	Rubbing genitals on a conspecific's body
GROOMING	G	Smoothing, repeatedly, a conspecific's hair, using the toothcomb or the tongue
HEAD RUB	HB	Rubbing the top of the head on a conspecific or on a substrate
KEEP CONTACT	KC	Approach and/or sit next to another individual while remaining in contact
LACTATING	LC	Female nursing an infant
LICK	LK	Licking hairless parts of a conspecific (palms, eyelids and nostrils)
MOUNT	MT	Moving rhythmically over the back of the partner, with the face in the same direction
MUTUAL GROOMING	MG	Sharing "grooming" simultaneously or interchanging in rapid succession with one or more conspecifics
PLAY	P	Chase, fight a conspecific, and vice versa, with no signs of aggression (vocalizations, attack displays)
SNIFF GENITALS	SG	Put the nose to less than 3 cm from the anogenital region of a conspecific, sniff and/or lick it
Agonistic		
BITE	BIT	Bite a conspecific
CHASE	CH	Chase a fleeing conspecific
CUFF	CU	Hit or try to hit a conspecific with the hand
DISPLACE	DS	Move toward a conspecific who immediately leaves its position
OTHERS:		
AGGRESSIVE INTERACTION	AI	Aggressive display exhibited during inter-group encounters: vocalizations, agonistic behaviors
ALARM CALL 1	AC1	Alarm for winged predator: the animals come down to the ground vocalizing and looking up
ALARM CALL 2	AC2	Alarm for ground-predator: animals vocalize, looking down and swinging their tails as pendulums

Appendix I (continued**)**

ALARM CALL 3	AC3	Alarm for other groups: animals vocalize, looking around and swinging their tails as pendulums
DEFECATE	DE	Expel the stool
DRINK	DK	Drink water from the leaves, in tree holes or in pools
FRIENDLY INTERACTIONS	FI	Affiliative behaviors exhibited during inter-group encounters
GENITAL MARK	GM	Rubbing genitals on an arboreal substrate
NEUTRAL INTERACTION	NI	Neutral behaviors exhibited during inter-group encounters: animals continue to carry on their activities
SCAN	SC	Rapid head rotation, lateral or up/ down, to find a possible threat

POSTURE	**CODE**	**DESCRIPTION**
CURLED, WITH TAIL	1*	The animal rests curled up on itself, with the tail close to the body
CURLED, WITHOUT TAIL	2*	The animal rests curled up on itself, with its tail hanging
SITTING	3	The animal rests on its haunches on a support
VENTRAL RECLINING	4*	The animal rests in a ventral lying position
DORSAL RECLINING	5*	The animal rests in a dorsal lying position
QUADRUPEDAL STANDING	6	The animal stays on its four limbs

* = thermoregulatory posture

FOOD ITEM	**CODE**	**DESCRIPTION**
RIPE FRUITS	RF	Fruit with the seed already developed
UNRIPE FRUITS	UF	Fruit with the seed not yet developed, usually green
FLOWERS	FL	The bloom or blossom of a plant, usually of a different color, shape, and texture from the foliage
YOUNG LEAVES	YL	Newly formed leaves, tender, light green or reddish
MATURE LEAVES	ML	Leaves of old formation, leathery, green or dark green
INVERTEBRATES	I	Small animals, especially arthropods, like insects, millipedes, spiders, etc.
MUSHROOMS	M	Wood mushrooms, flat, cream-colored below, orange above
PETIOLES	PE	The slender stalk by which a leaf is attached to the stem.
RESIN	RE	Solid or semisolid organic substance exuded by plants, transparent or translucent and yellowish to brown
ROOTS	RO	The basal portion of a plant.
STEMS	S	The stalk that supports a leaf, flower or fruit.

Appendix II. Plant species used by *Eulemur collaris* between July 2011 and January 2012 in Mandena (M) and Sainte Luce (SL).

VERNACULAR NAME	SCIENTIFIC NAME	FAMILY	ITEM	SITE
Ambora	*Tambourissa purpurea*	Monimiaceae	UF,RF	M,SL
Amboza	*Dypsis scottiana*	Arecaceae	RF	M
Ampoly	*Vepris elliotii*	Rutaceae	UF,RF	M,SL
Belataka	*Crataeva obovata*	Brassicaceae	RF	SL
Belavenoka	*Noronhia sp.*	Oleaceae	UF,RF	SL
Belavenoka marécage	*Noronhia sp.*	Oleaceae	UF,RF	SL
Beronono	*Trilepisium sp.*	Moraceae	FL,UF,RF	SL
Falinandro kely	*Dracaena reflexa*	Conavallariaceae	FL,RF	M,SL
Fandramana	*Aphloia theaeformis*	Flacourtiaceae	RF	M
Fandrana	*Pandanus sp.*	Pandanaceae	RO	M
Fandranabo	*Pandanus sp.*	Pandanaceae	FL,UF,RF	M,SL
Fandranala (Vakoa)	*Pandanus sp.*	Pandanaceae	RF	M
Fantsikaitramainty	*Canthium sp.*	Rubiaceae	RF	SL
Fantsikaitry	*Pyrostria sp.*	Rubiaceae	UF,RF	M,SL
Fantsikaitry marécage	*Gaertnera sp.*	Rubiaceae	RF	M
Farisaty	*Burasaia madagascariensis*	Menispermaceae	RF	M,SL
Fotondahy	*Schizolaena elongata*	Sarcolaneaceae	RF	M
Goava	*Psidium guayava*	Myrtaceae	RF	M
Harandrato	*Intsia bijuga*	Fabaceae	YL	SL
Harongana	*Harungana madagascariensis*	Clusiaceae	RF	M
Haziny	*Garcinia aphanophlebia*	Clusiaceae	RF	M
Haziny tomat	*Garcinia sp.*	Clusiaceae	YL,FL	SL
Haziny voany be	*Symphonia sp.*	Clusiaceae	FL	SL
Hazomainty	*Diospyros sp.*	Ebenaceae	FL,RF	M,SL
Hazomamy marécage	*Apodytes dimidiata*	Icacinaceae	RF	SL
Hazombato	*Campylospermum obtusifolium*	Ochnaceae	RF	M
Hazondrano	*Mascarenhasia arborescens*	Apocynaceae	FL	M
Kafeanala	*Tarenna thouarsii*	Rubiaceae	RF	M,SL
Kambatrikambatry	*Drypetes madagascariensis*	Euphorbiaceae	RF	M,SL
Lahinampoly	*Olea sp.*	Oleaceae	UF,RF	SL
Lendemibe	*Anthocleista madagascariensis*	Loganiaceae	RF	M,SL
Lona	*Oncostenum subcuspidatum*	Myrsinaceae	RF	M
Mampay	*Cynometra cloiselii*	Fabaceae	YL,FL	M,SL
Manjambondy	*Clidenia hirta*		RF	M

Appendix II (continued)

Menahihy marécage	*Erythroxilum platicladum*	Erythroxylaceae	RF	M
Meramavo	*Sarcolaena eriophora*	Sarcolaenaceae	FL	M
Merana	*Sarcolaena multiflora*	Sarcolaenaceae	FL,RF	SL
Mokarana	*Macaranga perrieri*	Euphorbiaceae	RF	M,SL
Nanto	*Faucherea exandra*	Sapotaceae	RF	M,SL
Nofotrako anala	*Vitex chrysomalum*	Verbenaceae	FL,UF,RF	M,SL
Nofotrako marécage	*Vitex tristis*	Verbenaceae	FL,RF	M
Nofotrakoho marécage	*Clerodendrum arenarium*	Verbenaceae	FL	SL
Nonoka	*Ficus reflexa*	Moraceae	ML,RF	M
Ramy	*Canarium boivinii*	Burseraceae	UF,RF	M
Randramboay	*Euphorbia lophogona*	Euphorbiaceae	FL	SL
Ranjonakanga	*Secamone humbertii*	Asclepiadaceae	YL	M,SL
Ranovao	*Pothos scandens*	Araceae	YL,ML,RF	M,SL
Raotry	*Dypsis pinnatifrons*	Arecaceae	RF	M
Ravenala	*Ravenala madagascariensis*	Strelitziaceae	FL	M,SL
Roandria	*Campnosperma micranteium*	Anacardiaceae	RF	SL
Rotry mena	*Syzigium sp.*	Myrtaceae	RF	M,SL
Sanira	*Tinopsis conjugata*	Sapindaceae	RF	SL
Sarigavo	*Malleastrum mandenense*	Meliaceae	RF	M
Sikondrokondro	*Rhodocolea sp.*	Bignoniaceae	RF	M
Sisikandrongo	*Poupartia chapelieri*	Lauraceae	RF	SL
Sivory be	*Mammea sessiliflora*	Clusiaceae	UF,RF	M
Sizena	*Croton louvelii*	Euphorbiaceae	RF	M
Somotsoy	*Rhodocolea racemosa*	Bignoniaceae	RF	M
Taolana	*Rothmannia mandenensis*	Rubiaceae	FL,RF	M,SL
Tapinandro	*Homalium albiflorum var leucophleum*	Flacourtiaceae	RE	SL
Tavolo	*Tacca leontopetaloides*	Taccaceae	RF,S	SL
Tavolohazo marécage	*Cryptocarya sp.*	Lauraceae	ML,RF	M,SL
Tavolohazo	*Cryptocarya retusa*	Lauraceae	YL	SL
Tomizo	*Memecylon sabulosum*	Melastomataceae	RF	M
Tsilanitria	*Vaccinum ermirnense*	Ericaceae	RF	M
Tsilavimbinanto	*Rhopalocarpus coriaceus*	Sphaerosepalaceae	UF,RF	SL
Vahabatra marécage	*Cinnamosma madagascariensis var. namoronensis*	Canellaceae	RF	SL
Vahabatra	*Cinnamosma madagascariensis*	Canellaceae	UF,RF	SL
Vahiazo 1	*Dichaepetalum sp.*	Dichapetalaceae	YL	M,SL

Appendix II (continued)

Vahiazo A	*Secamone sp.*	Asclepiadaceae	YL	M
Vahiazo B	*Secamone sp.*	Asclepiadaceae	YL	M
Vahiboatsimatra	*Salacia madagascariensis*	Hippocrateaceae	YL	M,SL
Vahifandrikatana	*Smilax kraussandra*	Smilacaceae	YL	M,SL
Vahifotsy	*Jasminium kitchingii*	Oleaceae	YL	M,SL
Vahigoneny	*Secamone sp.*	Asclepiadaceae	YL	M
Vahilengo	*Morinda sp.*	Rubiaceae	YL,UF	M
Vahimara	*Baroniella camtocarpioides*		YL	M
Vahimbokatepoka	*Senecio sp.*	Asteraceae	YL	M
Mahimety	*Monathotaxus sp.*	Annonaceae	YL	M
Vahy 1	*Secamone sp.*	Asclepiadaceae	YL	SL
Vahy 2	*Senecio sp.*	Asteraceae	YL	SL
Varikanda	*Dillenia triquetra*	Dilleniaceae	FL,RF	M,SL
Velomihanto	*Bakerella ambergensis*	Loranthaceae	ML	M,SL
Velomihanto 1	*Bakerella clavata*	Loranthaceae	RF	SL
Voahento			RF	M
Voakarepoka	*Brexia madagascariensis*	Celastraceae	FL,RF	M
Voapaky lahy	*Uapaca ferruginea*	Euphorbiaceae	UF,RF	M,SL
Voapaky vavy	*Uapaca littoralis*	Euphorbiaceae	RF	M,SL
Voatsilana	*Schefflera rainaliana*	Araliaceae	RF	M,SL
Zambo			RF	SL
Zorafotsy	*Ludia antanosarum*	Flacourtiaceae	RF	M
Zoramena	*Scolopia orientalis*	Flacourtiaceae	UF,RF	SL

FL: flowers, ML: mature leaves, RE: resin, RF: ripe fruits, UF: unripe fruits, YL: young leaves, S: stem, RO: root. Site: where the food item was eaten. M: Mandena, SL: Sainte Luce. Numbers and letters in parenthesis identify different tree species with the same vernacular name, found in Sainte Luce and Mandena, respectively. Vernacular names and relatives scientific names were provided by QMM botanists and controlled in Randriatafika and Rabenantoandro, 2008.

Appendix III: Nutritional content of food items eaten by *Eulemur collaris* at the Sainte Luce (SL) and Mandena (M) between July 2011 and January 2012.

Vernacular Name	Site	Item	Fatt	CP	SP	SC	NDF	ADF	CT	PP	Ref.
Ambora	M,SL	RF	3.7	5.6	5.1	9.2	50.1	36.7	2.5*	3.0	Pr. s
Ambora	M,SL	UF	2.5	2.9	1.8	3.9	72.7*	55.4*	1.0	0.9	2002
Amboza	M	RF	2.0	4.1	3.3	10.7	51.2	33.6	NE	0.7	2004
Ampoly	M,SL	UF	5.2	8.8	1.5	5.2	44.2	32.2	0.0	0.5	2002
Ampoly	M,SL	RF	17.7*	6.7	2.2	16.9	38.1	25.8	NE	0.4	2004
Belataka	SL	RF	1.4	8.8	2.0	10.8	57.8*	38.2	0.2	0.4	2002
Belavenoka	SL	UF	0.5	4.6	0.9^{-}	12.3	32.5	16.6	0.3	3.2	Pr. s
Belavenoka	SL	RF	0.3	5.4	0.7^{-}	19.5	23.3^{-}	5.5^{-}	0.1	2.7	2002
Belavenoka marécage	SL	UF	1.4	4.7	1.5	10.3	42.3	29.9	0.2	2.9	Subs.
Belavenoka marécage	SL	RF	1.3	5.5	1.5	18.5	32.2	14.6^{-}	0.1	2.5	Pr. s
Beronono	SL	RF	3.8	7.6	1.9	2.6	26.6	20.8	0.0	0.9	Pr. s
Beronono	SL	UF	2.9	7.7	2.3	2.3	32.2	24.3	0.0	1.2	Subs.
Beronono	SL	FL	1.3	11.0	4.3	15.4	41.2	29.5	0.9	2.5	Pr. s
Falinandro kely	M,SL	RF	1.0	6.7	0.7^{-}	10.9	41.9	21.9	NE	0.5	2004
Falinandro kely	SL	FL	1.2	13.2	6.7	25.4	31.4	17.8	0.5	2.2	Subs.
Fandramana	M	RF	2.4	4.1	2.5	8.9	15.0^{-}	9.9^{-}	0.0	3.5	Pr. s
Fandrana	M	RO	1.0	5.0	3.8	5.2	34.7	25.2	NE	3.6	2004
Fandranabo	SL	RF	0.4	2.8	1.6	12.4	67.7*	55.2*	0.0	0.6	Pr. s
Fandranabo	M,SL	UF	1.7	4.0	1.1^{-}	6.6	68.9*	56.1*	NE	0.5	2004
Fandranabo	M	FL	1.4	13.1	5.2	8.9	11.4	7.0	0.2	4.0	Subs.
Fandranala (vakoa)	M	RF	1.3	2.5	1.8	13.0	62.4*	48.2*	NE	0.8	2004
Fantsikaitramainty	SL	RF	4.9	5.6	4.3	18.2	27.8	20.1	0.2	1.7	2002
Fantsikaitry	M	UF	0.8	2.9	5.1	14.2	17.5^{-}	14.1^{-}	0.0	1.1	Pr. s
Fantsikaitry	M,SL	RF	1.3	5.4	0.9^{-}	34.0*	35.6	26.9	0.0	1.4	2002
Fantsikaitry marécage	M	RF	2.7	6.8	2.2	10.4	62.7*	43.1*	0.0	0.5	2002
Faritsaty	M,SL	RF	8.8	9.1	2.9	17.9	42.9	32.1	NE	0.6	2004
Fotondahy	M	RF	2.2	6.2	9.7*	26.6	18.2^{-}	13.7^{-}	0.0	1.8	2002
Goava	M	RF	2.8	4.0	2.3	10.4	52.5	38.9	NE	0.8	2004
Harandrato	SL	YL	2.4	36.2*	8.6*	7.3	12.8^{-}	5.8^{-}	0.2	2.4	2002
Harongana	M	RF	3.7	6.1	5.8*	17.3	46.7	42.3*	0.0	0.5	Pr. s
Haziny	M	RF	11.1*	5.1	2.5	43.3*	20.0^{-}	16.7	0.0	1.2	2002
Haziny Tomat	SL	FL	2.3	6.2	4.3	9.2	36.5	27.6	0.6	1.5	Subs.
Haziny Tomat	SL	YL	4.9	5.8	3.3	12.5	30.3	22.9	1.2	2.1	2002
Haziny voany be	SL	FL	7.4	5.9	4.0	7.2	33.6	23.4	0.5	1.3	2002
Hazomainty	M,SL	RF	0.6	3.1	7.8*	6.5	51.8	27.7	0.6	3.1	2002

Appendix III (continued)

Hazomainty	SL	FL	0.3	9.3	3.9	9.5	20.8^{-}	15.2	0.0	2.5	2002
Hazomamy marécage	SL	RF	2.9	6.9	1.5	64.1*	17.8^{-}	9.8^{-}	0.0	0.5	2002
Hazombato	M	RF	38.9*	6.1	4.7	8.0	31.2	22.7	0.5	1.4	2002
Hazondrano	M	FL	1.3	4.8	1.2	3.5	53.0	43.0	0.1	1.9	Subs.
Kafeanala	M,SL	RF	5.0	4.9	2.2	18.9	36.4	28.0	0.0	0.5	Pr. s
Kambatrikambatry	M,SL	RF	2.8	2.7	1.4	18.2	23.3^{-}	18.6	0.0	11.4*	2002
Lahinampoly	SL	UF	5.1	8.4	1.4	5.2	44.6	32.7	0.0	0.6	Subs.
Lahinampoly	SL	RF	17.4	6.5	2.1	15.2	38.2	26.1	0.0	0.5	Subs.
Lendemibe	M,SL	RF	3.9	2.3	1.3	26.3	55.7*	45.9*	0.2	1.7	2002
Lona	M	RF	6.0	3.4	2.7	40.8*	16.6^{-}	11.0^{-}	NE	3.0	2004
Mampay	M,SL	YL	0.3	16.1*	11.2*	10.1	29.1	20.2	4.1*	5.7*	Pr. s
Mampay	M,SL	FL	1.3	15.6	6.0	16.3	39.5	28.6	1.4	3.0	2002
Mangavoa	M,SL	RF	3.6	4.4	0.9^{-}	49.9*	23.2^{-}	17.0	0.3	0.4	2002
Manjambondy	M	RF	4.0	8.3	5.4	5.6	53.8	36.7	0.4	2.9	Subs.
Menahihy marécage	M	RF	13.4*	8.2	4.7	36.0*	16.3^{-}	11.0^{-}	2.6*	4.6*	Pr. s
Meramavo	M	FL	2.2	7.9	9.2*	8.7	23.3^{-}	17.7	0.5	13.0*	Pr. s
Merana	SL	RF	3.9	4.3	2.5	15.0	47.5	34.5	0.2	3.5	2002
Merana	SL	FL	1.3	4.4	3.4	46.6*	21.0^{-}	14.0^{-}	0.2	3.5	2002
Mokarana	M,SL	RF	4.5	5.4	6.4*	2.9	56.7*	42.3*	0.0	1.5	2002
Mushroom 1	M	All	1.4	10.3	2.9	3.8	59.5*	36.6	0.0	0.6	Pr. s
Mushroom harandrato	SL	All	1.0	4.7	1.6	1.8	79.2*	60.5*	0.0	0.1	Pr. s
Mushroom voantsila	SL	All	0.9	14.9	5.3	4.1	68.9*	33.1	0.1	0.5	Pr. s
Nanto	M,SL	RF	5.2	2.9	7.1*	21.3	43.7	25.1	3.5*	6.4*	2002
Nofotrako anala	SL	FL	1.6	8.3	5.4	23.4	43.8	29.0	3.5	5.4	Subs.
Nofotrako anala	SL	UF	1.7	4.3	1.8	19.3	53.0	38.2	1.0	1.5	Pr. s
Nofotrako anala	M,SL	RF	2.7	4.5	1.7	33.0*	46.2	32.8	1.0	1.7	2002
Nofotrako marécage	M	RF	2.0	3.0	0.7^{-}	19.8	39.0	27.3	NE	1.4	2004
Nofotrako marécage	M	FL	1.5	13.2	6.4*	22.6	18.4^{-}	11.5^{-}	5.4*	6.3*	Pr. s
Nofotrakoho marécage	SL	FL	1.2	4.8	1.2^{-}	3.0	63.3*	47.5*	0.1	1.9	2002
Nonoka	M	RF	5.6	7.3	5.0	2.8	51.6	40.5*	0.4	2.2	2002
Nonoka	M	ML	2.8	8.8	2.5	4.8	37.5	22.2	0.7	1.3	Pr. s
Ramy	M	UF	4.6	4.2	1.3	1.3	65.7*	52.8*	NE	0.6	2004
Ramy	M	RF	13.0*	9.2	2.0	2.2	47.5	38.6	0.0	0.4	2002
Randramboay	SL	FL	5.0	15.4	4.7	4.2	24.2	15.3	0.0	5.2*	Pr. s
Ranjonakanga	M,SL	YL	3.2	8.1	1.5	6.2	49.5	36.3	0.0	0.4	2002
Ranovao	M	L	3.2	15.6	2.7	5.1	46.8	36.0	0.0	0.3	Pr. s

Appendix III (continued)

Ranovao	M,SL	RF	2.0	16.0*	3.8	9.3	42.0	15.1	NE	0.4	2004
Raotry	M	RF	1.6	2.4	4.2	40.0*	26.9	12.7^{-}	0.0	1.8	2002
Ravenala	M,SL	FL	1.5	4.2	3.7	17.5	49.3	25.8	1.1	1.4	2002
Roandria	SL	RF	2.5	9.1	4.6	2.5	34.6	26.8	0.0	1.3	2002
Rotrymena	M,SL	RF	3.4	4.9	2.8	43.4*	24.1	19.1	1.1	2.5	2002
Sanira	SL	RF	8.3	6.9	8.1*	16.3	32.0	22.5	4.7*	7.6*	2002
Sarigavo	M	RF	2.6	11.3	3.7	25.9	24.0	15.4	6.7*	6.0*	2002
Sikondrokondro	M	RF	12.6*	8.5	1.9	11.8	45.3	31.4	NE	0.6	2004
Sisikandrongo	SL	RF	0.7	5.7	2.5	12.6	18.5^{-}	15.0	0.0	10.6*	2002
Sivory be	M	UF	27.9*	2.8	6.4*	27.9	15.7^{-}	11.7^{-}	NE	0.6	2004
Sivory be	M	RF	12.4*	5.7	3.4	32.7*	22.4^{-}	17.5	0.0	1.3	2002
Sizena	M	RF	8.0	8.1	5.7	5.9	42.0	21.7	NE	2.2	2004
Somotsoy	M	RF	13.1*	8.9	5.0	30.3*	27.7	16.3	NE	0.3	2004
Taolana	SL	FL	2.3	11.0	7.7*	15.3	21.5^{-}	14.3^{-}	3.2*	5.1*	2002
Taolana	M	RF	0.3	4.6	5.2	8.1	50.5	35.7	0.1	1.5	2002
Tapinandro	SL	RE	0.5	3.6	1.2	48.2	19.4	0.0	0.3	0.1	Subs.
Tavolo	SL	S	3.1	14.2	2.6	10.4	43.4	30.9	0.0	0.8	2002
Tavolo	SL	RF	1.4	8.8	2.2	48.3*	20.9^{-}	13.7^{-}	0.7	1.6	2002
Tavolohazo	SL	ML	7.3	7.8	2.5	5.9	60.0*	43.9*	0.2	1.7	2002
Tavolohazo marécage	M,SL	RF	12.8*	13.1	3.7	8.9	34.3	18.9	0.2	2.1	2002
Tavolohazo 5	SL	YL	2.0	8.9	2.3	2.1	65.1*	45.6*	0.1	0.5	Pr. s
Tomizo	M	RF	2.9	4.8	4.0	9.3	43.7	23.7	NE	2.0	2004
Tsilanitria	M	RF	1.4	1.8	1.2^{-}	50.4*	36.5	26.8	0.1	0.5	2002
Tsilavimbinanto	SL	UF	3.5	6.6	2.3	4.6	43.4	35.7	0.2	2.6	Subs.
Tsilavimbinanto	SL	RF	5.3	7.6	2.2	9.0	35.4	27.9	0.0	2.3	2002
Vahabatra	SL	RF	5.0	5.3	3.8	26.0	17.7^{-}	12.4^{-}	1.7	4.4*	2002
Vahabatra 1	SL	UF	1.0	6.7	2.2	30.3*	19.4^{-}	10.4^{-}	0.0	4.7*	Pr. s
Vahabatra 1	SL	RF	1.7	3.8	0.6^{-}	38.5*	30.6	22.4	0.1	0.9	2002
Vahiazo 1	M,SL	YL	1.7	16.4*	5.4	2.3	50.4	39.2*	0.0	0.6	Pr. s
Vahiazo A	M	YL	2.4	6.4	3.0	6.0	32.3	20.4	1.4	1.7	Pr. s
Vahiazo B	M	YL	4.6	9.3	2.6	4.9	41.3	28.3	0.5	0.7	Pr. s
Vahiboatsimatra	M,SL	YL	2.7	7.9	1.5	1.5	44.6	25.2	0.0	0.3	Pr. s
Vahifandrikatana	M,SL	YL	0.9	8.9	2.6	6.2	55.5*	38.3	0.0	0.5	Pr. s
Vahifotsy 1	M,SL	YL	1.0	8.9	1.1^{-}	10.6	48.9	29.7	0.0	0.5	Pr. s
Vahigoneny	M	YL	5.2	10.6	3.3	4.4	38.3	28.0	0.0	1.2	Pr. s
Vahilengo	M	UF	1.1	8.6	2.7	11.3	55.8*	42.4*	0.0	0.5	Pr. s
Vahilengo	M	YL	3.0	10.4	0.6^{-}	7.1	32.3	21.8	NE	2.3	2004

Appendix III (continued)

Vahimara	M	YL	3.8	21.1*	4.1	5.3	34.1	19.4	0.0	2.6	Pr. s
Vahimbokatepoka	M	YL	2.4	8.5	0.5¯	5.2	36.9	28.2	0.0	0.9	Pr. s
Vahimety	M	YL	0.2	14.8	5.8	10.1	53.9*	40.9*	1.0	4.1	Pr. s
Vahy 1	SL	YL	3.3	13.9	3.4	3.0	32.6	19.7	0.0	0.5	Pr. s
Vahy 2	SL	YL	1.5	13.4	1.9	2.6	29.6	21.6	0.0	0.5	Pr. s
Varikanda	M,SL	RF	3.1	6.5	5.3	2.9	50.3	32.5	0.3	0.9	2002
Varikanda	M,SL	FL	7.7	7.1	6.1	7.1	30.0	23.1	0.3	4.9	Subs.
Velomihanto	M,SL	ML	4.5	5.5	4.6	5.2	39.4	28.8	NE	4.3	2004
Velomihanto 1	SL	RF	2.3	16.0*	5.8*	9.3	42.0	25.6	0.0	0.4	Pr. s
Voahento	M	RF	8.2	18.6	4.6	4.7	35.4	21.2	0.1	0.4	Subs.
Voakarepoka	M	RF	0.4	1.8	0.6¯	3.8	52.0	35.1	0.0	0.2	Pr. s
Voakarepoka	M	FL	2.0	10.0	9.6*	6.1	23.0¯	16.7	0.0	2.3	Pr. s
Voapaky lahy	M,SL	RF	5.7	5.9	4.0	2.3	62.7*	51.0*	0.0	0.5	2002
Voapaky lahy	M	UF	7.0	6.0	3.5	1.9	68.0*	56.0*	0.0	0.7	Pr. s
Voapaky vavy	M,SL	RF	2.1	4.4	5.3	7.5	41.8	29.9	0.4	4.0	2002
Voatsilana	M	RF	5.7	6.9	2.7	61.8*	18.6¯	11.9¯	0.5	1.3	2002
Zambo	SL	RF	3.5	7.6	2.2	6.8	37.4	28.7	0.2	2.2	Subs.
Zorafotsy 1	M	RF	1.2	2.9	2.8	23.4	33.3	21.7	0.4	3.9	2002
Zoramena	SL	UF	1.2	3.6	2.6	21.2	28.7	19.3	0.6	4.3	Pr. s
Zoramena	SL	RF	0.8	3.1	2.5	33.4*	18.6¯	12.8¯	0.4	3.9	2002
Insects	M,SL	All	2.0	77.8*	11.5*	0.9¯	43.3	30.1	NE	1.8	2004

Site: where the food item was eaten. M: Mandena, SL: Sainte Luce, FL: flowers, L: leaves, ML: mature leaves, RF: ripe fruits, UF: unripe fruits, YL: young leaves, CP: crude proteins, SP: soluble proteins, SC: soluble carbohydrates, NDF: neutral detergent fibers, ADF: acid detergent fibers, CT: condensed tannins, PP: polyphenols. Some different trees species have the same vernacular name because local field assistants recognized them on the basis of morphological features (i.e. vahiazo means “liana of the tree”). *attribute higher than *X*±SD ¯attribute lower than *X*±SD.

References (Ref.): Pr. s: Present study; 2002: Donati, 2002; 2004: Unpub.data, 2004 (Donati). Subs.: substitute.

Appendix IV. Morphometric measures of captured lemurs.

DATA	5th of February 2011	7th of February 2011	24th of May 2011	26th of May 2011
GROUP	A	B	AB	C
SITE	Sainte Luce	Sainte Luce	Mandena	Mandena
NAME	FANA	NIFY	OCTAVIO	APOLLO
SEX	F	M	M	M
Weight (g)	1700	1950	2200	1950
Head length (cm)	11	14	14	11
Body length (cm)	30.5	32	33	33
Tail length (cm)	52	56	48	46
Thigh length (cm)	14	14	14	13
Leg length (cm)	14.5	15	16	14
Paw length (cm)	9.5	10	10.5	9.5
Arm length (cm)	9	12	11	9
Forearm length (cm)	10	10	12	11
Hand length (cm)	7	7	7	6.5
Canine length (cm)	9.8	14	8	8

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