



## Group Size, Home Range Use, and Seasonal Variation in the Ecology of *Eulemur mongoz*

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*We collected data during a 10-month study carried out on the mongoose lemur, Eulemur mongoz, at Anjamena in northwestern Madagascar, which provide baseline information on seasonal variation in the ecology, home range use and some aspects of the behavior of two neighboring groups. We monitored group size of nine groups in the study area and assessed them for seasonal variation. We present additional information collected during short-term surveys in other areas before and during the study for comparison. The study groups were small family units, and changes in group size were limited to births and emigrations of sexually mature progeny. In spite of clear seasonal changes in climate and vegetation, there is no variation in grouping patterns, so it is not possible to correlate variation in group size with seasonal variation of ecological variables. Comparison with ecological data from other field studies on lemurids reveals differences in food resource distribution in western forests versus other types of Malagasy forest. This distribution of food resources may predict home range size in mixed frugivorous-folivorous lemurs. Small home ranges, mainly in the West, could be correlated with a uniform distribution of food resources. Finally, we suggest that the dry season in the West may not present frugivorous-folivorous lemurs with major problems in finding an adequate food supply. This is supported by the lack of seasonal differences in ranging behavior of mongoose lemurs.*

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**KEY WORDS:** *Eulemur mongoz*; Lemuridae; group size; home range size; ecology.

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## INTRODUCTION

Lemur social structure is broadly characterized by three main grouping patterns: (1) a dispersed social system, often in the nocturnal species; (2) small family groups in diurnal, nocturnal, and cathemeral species; and (3) large groups consisting of multiple adult males and multiple adult females and their maturing offspring in diurnal and cathemeral species (Richard and Dewar, 1991; Tattersall, 1982; van Schaik and Kappeler, 1993). In contrast to other primate grouping patterns, behavioral plasticity is high in some species, e.g., *Eulemur mongoz*, *E. macaco*, *E. coronatus*, and *Varecia variegata*, and intraspecific and seasonal variation occurs in social structure (van Schaik and Kappeler, 1993).

Group size in primates may be correlated with two main ecological factors: the distribution of food resources and predation (Overdorff, 1996; Terborgh, 1983; van Schaik and Kappeler, 1993). Home range area, which is probably determined by the distribution of resources, is positively correlated with group size in primates (Clutton-Brock and Harvey, 1979). The effect of the distribution of food resources on grouping patterns has so far been assessed in detail in only two species of lemur (Overdorff, 1996): while it was suggested that maximum group size in the multimale, multifemale *Eulemur fulvus rufus* might be constrained by food supply, there is no link between food availability and group size in the socially monogamous *Eulemur rubriventer*. Links between predation and group size in Malagasy primates are difficult to assess, not least because predation pressure on the larger-bodied lemurs appears to be low compared to that in primates in Asian, African, and South American environments (Cheney and Wrangham, 1987). However, the documentation of antipredator behavior in a number of species and the recent extinction of a large eagle on Madagascar suggest that predation pressure may have been greater in the past and could have contributed to the extant grouping patterns observed in lemurs (Goodman, 1994; Goodman *et al.*, 1993). Home range size in the frugivorous and folivorous Lemuridae is highly variable and appears to be dependent on the type of forest habitat, e.g., seasonally dry forests, rain forest, and xerophytic vegetation, but seems not to be correlated with group size: *Lemur catta* and *Eulemur fulvus rufus*, which both occur in different types of forest, exhibit variation in home range size but consistency in group size (Overdorff, 1996; Sussman, 1974, 1991). van Schaik and Kappeler (1993) suggested that variability in grouping patterns in cathemeral (day- and night-active) lemurs may be related to the variation in the activity cycle: reports on grouping patterns and activity cycles in *Eulemur mongoz* point toward larger groups when they are diurnal and small pair-bonded groups when they are nocturnal.

The mongoose lemur (*Eulemur mongoz*: Lemuridae) is restricted to the subhumid seasonal forests of northwestern Madagascar and the Comoro Islands (Anjouan and Moheli) (Fig. 1). *Eulemur mongoz* is generally referred to as a pair-bonded species that lives in small family groups of 3 or 4 individuals (Albignac, 1981; Anonymous, 1992; Harrington, 1978, Kaudern, 1914, 1915; Tattersall, 1978), but there are also larger groups containing  $\leq 8$  individuals (Andriatsarafara, 1988a; Petter, 1962; Tattersall, 1978). Small family groups were observed at Ampijoroa during both seasons and both at night and during the day (Albignac, 1981; Harrington, 1978; Tattersall, 1978; personal observation), while Andriatsarafara (1988a) reports on larger, nocturnal groups during the dry season.

On the Comorian island of Anjouan (Fig. 1), in the cool, humid, less seasonal environment of the highlands, there were small, diurnal family groups (Anonymous, 1992; Tattersall, 1978), while in the seasonal Anjouan lowlands small family groups were predominantly nocturnal during the dry season and predominantly diurnal during the wet season (Clark, personal communication; Tattersall, 1978, personal communication).

In the seasonal environment of the Comorian island of Moheli (Fig. 1), some social groups contained  $>1$  adult-sized male or  $>1$  adult-sized female or both during the transitional period between the wet and dry seasons, (Tattersall, 1978). These groups may have been multimale or multifemale or both, but may also have been family groups with their subadult offspring. The mongoose lemurs on Moheli were predominantly diurnal during the dry season and predominantly nocturnal during the wet season (Tattersall, 1978). The mongoose lemur is also unusual in that it has been reported to form polyspecific associations with *Eulemur fulvus fulvus* and to be variably nocturnal or diurnal depending on the season (Andriatsarafara, 1988a; Harrington, 1978; Sussman and Tattersall, 1976; Tattersall, 1978). Its diet is highly nectarivorous during the dry season and frugivorous/folivorous during the wet season (Andriatsarafara, 1988b; Sussman and Tattersall, 1976).

Based on this information the mongoose lemur appears to be an ideal candidate for assessing the underlying mechanisms responsible for variability in group size: (1) variability in grouping patterns appears to be seasonally dependent; (2) variability in activity patterns appears to be seasonally dependent; (3) the presence of predation pressure can be inferred from the formation of polyspecific associations, as larger groups are selected for if predation pressure is high (Terborgh, 1983); and (4) dependence on limited resources during the dry season might impose constraints on group size (Overdorff, 1996).

During a 10-month study carried out at Anjamena (45°55'E, 16°03'S) in the riverine forests of the Mahavavy (Fig. 1), we collected data on the

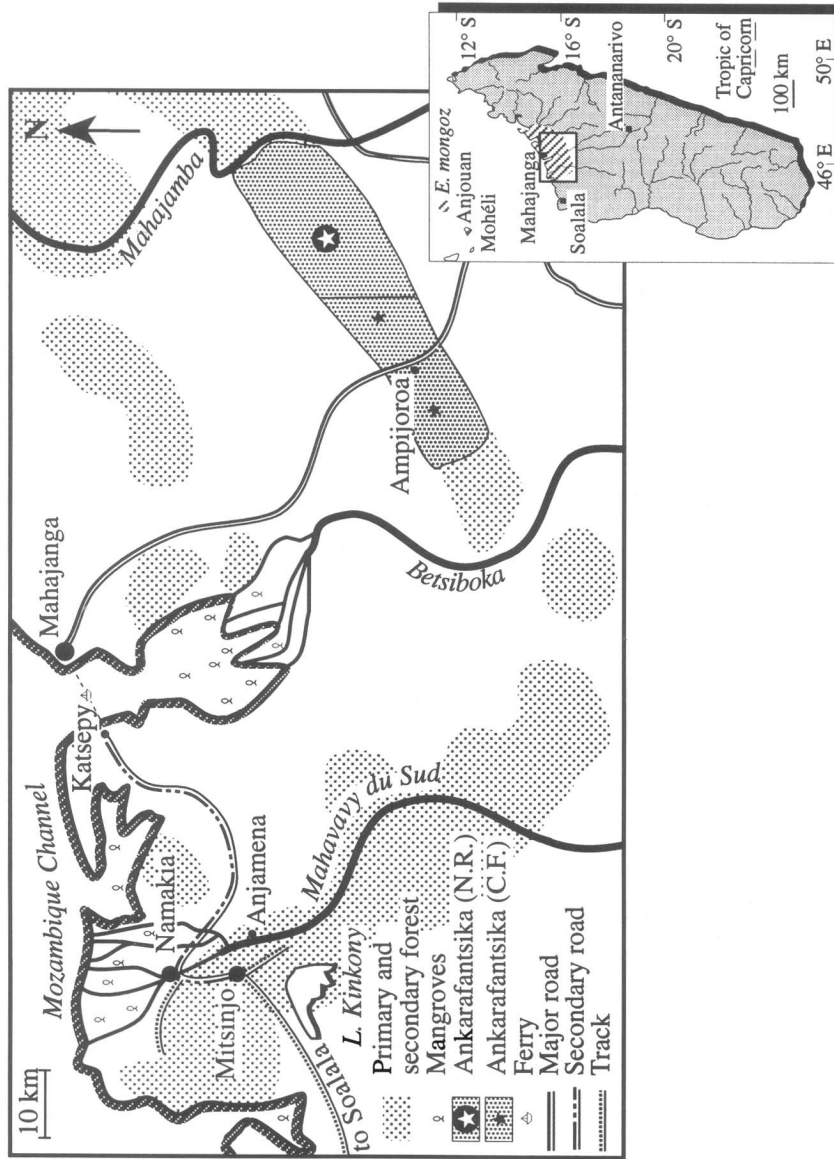


Fig. 1. Distribution of *Eulemur mongoz* (map) and location of field study site (inset). Adapted from Anonymus (1986), Nicoll and Langrand (1989) and Tattersall (1982). N.R., nature reserve; C.F., classified forest.

behavior and ecology of two neighboring groups of *Eulemur mongoz* (Curtis, 1997). We collected additional information from several other sites within the known range of *Eulemur mongoz* during a 3-month pilot phase and short excursions made during the focal study (Curtis *et al.*, unpublished data). Before our study, no long-term fieldwork had been conducted with mongoose lemurs. It is also the first study to be carried out throughout the entire diurnal and nocturnal active phases of a *Eulemur* species and revealed a cathemeral activity cycle throughout the entire year, with shifts toward more diurnal activity during the wet season and more nocturnal activity during the dry season (Curtis, 1997).

Our aims are as follows: (1) to document variation in group size; (2) to document and discuss seasonal variation in the ecology and certain aspects of the behavior of the mongoose lemur, more specifically of the climate, distribution of plant resources in time and space (phenology), population density, ranging behavior, interspecific interactions (competition/association with other animals), and predator pressure—such detailed documentation of the environment throughout the year is a prerequisite to the understanding of behavioral variability in lemurs; and (3) to relate variations in group size to seasonal variations of ecological variables.

## METHODS

We conducted the field study at Anjamena from September 1994 to September 1995 on two neighboring groups of *Eulemur mongoz*. Due to the proximity of the site to the Mahavavy River (Fig. 1) and consequent flooding, it was virtually impossible to work there during the peak wet season in January and February 1995.

### Vegetation and Climate

Characterization of the forest is based on 10 × 10-m quadrats ( $n = 15$ ) selected in the home range of each group using a table of random numbers. We catalogued species names of all trees with a DBH (diameter at breast height) >4 cm and estimated their heights and liana cover (Richard, 1978). We collected samples of all trees and lianas.

We assessed temporal variation in potential food resources by collecting phenological data on a monthly basis, recording the presence of immature and mature leaves, fruit, and flowers (Richard, 1978) for 19 species of trees and lianas in the home ranges of both study groups (Curtis, 1997). The sample size for each species ( $1 \leq n \leq 10$ ) is dependent on its

density within the home range. During January and February, these data were collected by A. Blaise whenever the water level and weather conditions permitted access to the study site.

We assessed the abiotic environment by measuring maximum and minimum daily temperature and total rainfall once per day at the camp. During January and February, all data were collected at Mitsinjo (Fig. 1) by O. D. Rabetsimalona. Mean daily temperature is the average of minimum and maximum values.

### Observations

We conducted 1–4 observations per month on two neighboring groups of mongoose lemurs (groups 1 and 4) throughout the entire active period. Each observation is split into a morning session and an afternoon or night session or both. During the 10-month study, we recorded a total of 26 complete activity periods for group 1 ( $n = 14$ ) and group 4 ( $n = 12$ ). Six of them are activity periods during the wet season (December–April) and the remaining 20 during the dry season (May–November). We conducted 1-min point-samples on one focal animal only throughout an observation session (Altmann, 1974). A total of 256 hr of observation was accumulated in this way, during which detailed information was collected on activity, feeding, posture, locomotion, vocalizations, and vertical and horizontal habitat utilization (Curtis, 1997). Of this information, we present only data on vertical and horizontal habitat utilization.

We employ 3 subgroups to describe the vertical habitat—different levels of the forest—and substrates used during the active phase of the 24-hr period. (1) Level: 0–3, extending from the ground up to the lowest areas of the canopy; level 4, representing the canopy; and level 5, the emergents. (2) Substrate diameter: large, 20–30 cm; medium, 10–20 cm; and small, 0–10 cm. (3) Substrate inclination: horizontal, 0–29°; oblique, 30–74°; and vertical, 75–90°.

The methods used to assess path length (PL) in a given activity period and home range use are more detailed for group 1 than for group 4. We split the home range of group 1 into  $10 \times 10$ -m quadrats and used a map of the home range during observations to mark the position of the group in a given quadrat at 1-min intervals. The map subsequently served to calculate home range use and PL for each activity cycle. We monitored the position of group 4 by marking trees with numbered tags at 15-min intervals. By superimposing  $10 \times 10$ -m quadrats on a map of the home range, we calculated home range size equivalent to that used for group 1 (home range size = sum of all quadrats in the home range). We calculated PL

based on the summed distances between numbered tags. We calculated home range use as follows: we scored each quadrat traversed by a line, as well as those quadrats  $\leq 0.6$  m from the line (corresponding to the accuracy with which the markers were placed; scale of the map, 1:1000), as having been used in a given observation. This means that the frequency at which a quadrat was used by the subjects corresponds only to the number of observations in which they used it. We also marked all dormitory trees (sleeping sites), locations of confrontations with neighboring groups, and feeding trees on the maps (Fig. 2).

Habituation of the study animals presented no problem and was fully accomplished during the preparatory phase of the study in September 1994. By the end of the preparatory phase, the mongoose lemurs would allow an observer to approach to  $\leq 4$  m without interrupting their activity.

### Population Density and Group Composition

Throughout the study, we collected information on group size for all groups in the study area and recorded the approximate location of their home ranges on a map (Fig. 2). We estimated absolute population density via these group counts and calculated it as follows: mean group size (MGS)

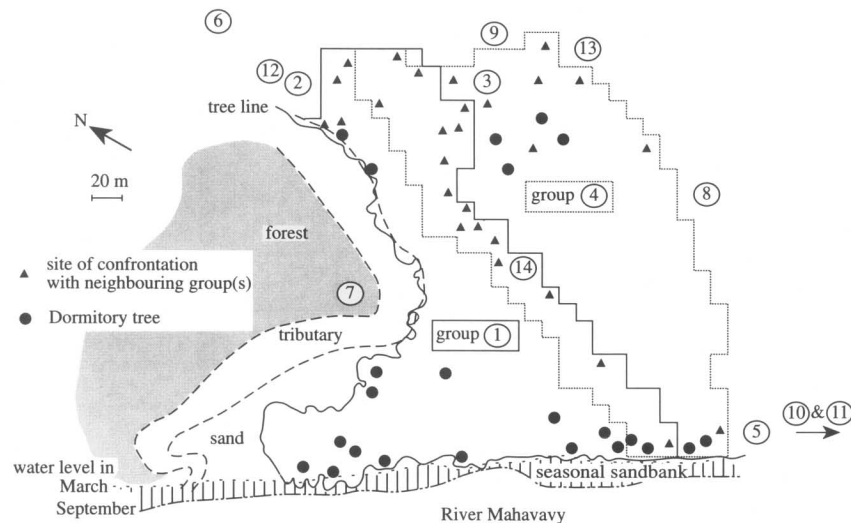


Fig. 2. Map of the study site and territories of the study groups at Anjamena.

divided by group density (GD), wherein GD is the mean home range size in the two study groups (Mutschler *et al.*, 1994).

Assessing group composition was facilitated by sexual dichromatism in the mongoose lemurs. However, while this aided distinction between the sexes, it was more difficult to assign animals to different age classes. We identified juveniles and young subadults by their smaller size. When close to sexual maturity, subadult animals of both sexes were generally difficult to distinguish from the adults. Subadult females could be reliably distinguished from adults only by the size of their external genitalia and by the lighter color of the surrounding hair. Subadult males were distinguished from adults by the absence of a triangular bald patch on the top of their heads. This patch is the result of head-rubbing and is found only in fully adult males. High cohesion between pair mates also helped to identify the adult animals in a group (Curtis, 1997).

## RESULTS

### Vegetation and Climate

The semideciduous, seasonally dry, secondary forest of Anjamena is dominated by *Tamarindus indica* (Caesalpiniaceae) and *Ziziphus jujuba* (Rhamnaceae). It is characterized by a closed canopy of 10–15 m, a subordinate tree and shrub layer of 2–10 m, and emergents reaching up to 28 m. Most trees support an abundant growth of lianas. Undergrowth is virtually nonexistent and the density of trees in the study area is low (840/ha). Considering only trees, species diversity is  $D_s = 0.84$  (Simpson's index of diversity) (Brower *et al.*, 1990).

$$D_s = 1 - (\sum n_i(n_i - 1)/N(N - 1))$$

wherein

$n_i$  = the abundance of species  $i$

$N = \sum n_i$

However, we identified only 68 species (31 families) of trees and lianas, of which 55 are represented in the sample plots and the remaining 13 are food resources used by the mongoose lemurs but not present in the plots (Appendix). There is no obvious difference in the habitat characteristics of the two territories: Calculation of Morisita's index of community similarity ( $I_M$ ) yielded a value of  $I_M = 0.97$ , indicating that species composition and the relative abundance of species are almost identical (Brower *et al.*, 1990).

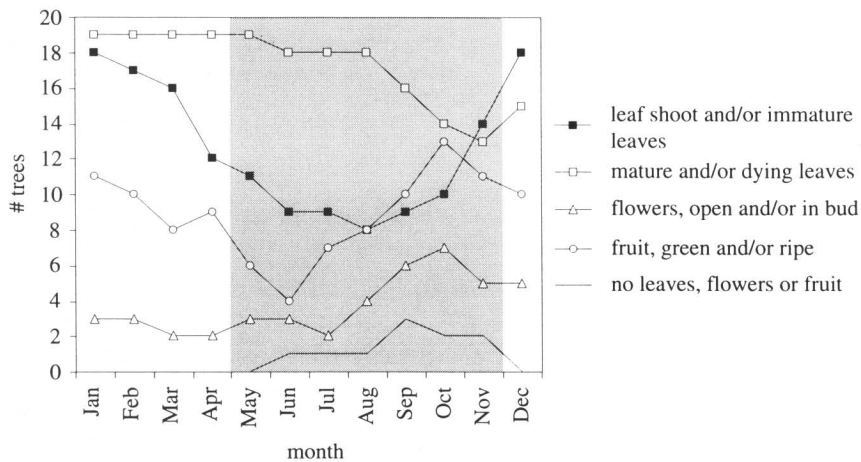


$$I_M = 2\sum n_i n_i / (D_{s1} + D_{s4}) N_1 N_4$$

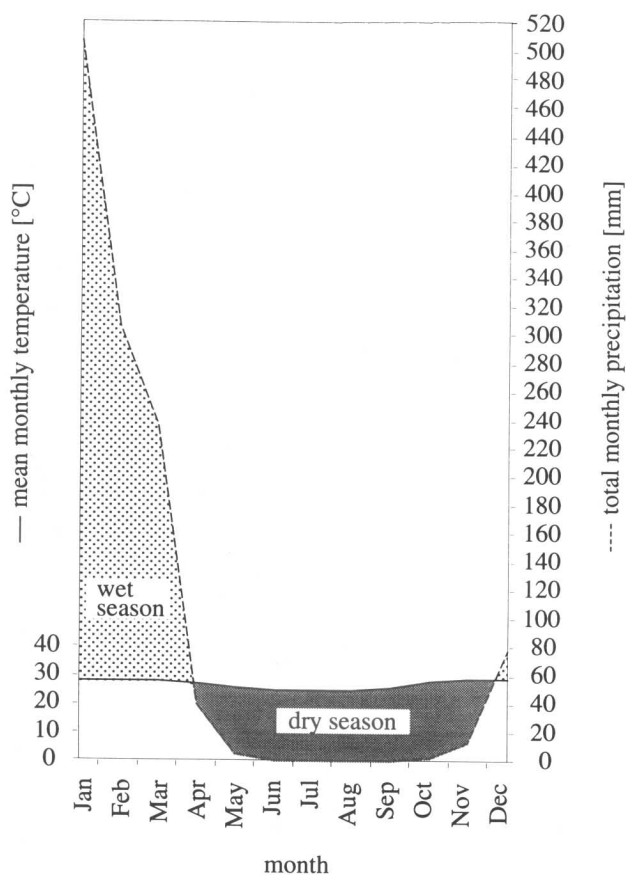
wherein  $n_i$  and  $N$  are defined in the formula for  $D_s$  (Simpson's index for diversity), 1 = home range 1, and 4 = home range 4.

Temporal changes in the vegetation throughout the study period are shown in Fig. 3. The semideciduous nature of the forest is evident in that leaves were present on some species of trees throughout the entire year. Immature leaf production peaked from December to March and was lowest from June to October. Flower production peaked once in October. Fruit production was highest in October and lowest in June. Some trees produced no leaves, flowers, or fruit throughout most of the dry season (June–November).

The climate in the study area is seasonal and clearly divided into a wet season (December–April) and a dry season (May–November) (Fig. 4). Total monthly rainfall is highest in January (507 mm). We recorded 1169 mm for the entire wet season, compared to only 20 mm for the entire dry season. Variation in mean monthly temperature was limited throughout the year, exhibiting a low of 25°C in June to August and a high of 29°C in November and December. The lowest mean minimum monthly temperature occurred in July and August (18°C) and the highest mean maximum monthly temperature was in November (36°C).



**Fig 3.** Availability of fruit, flowers, and leaves from October 1994 to September 1995. The gray area indicates the dry season.



**Fig. 4.** Climatograph emphasizing water availability at Anjamena from October 1994 to September 1995. The points where the temperature and rainfall graphs meet are points of equivalence for evapotranspiration and indicate the beginning and end of the dry season. Number of data points per month: Jan.  $n = 31$ ; Feb.  $n = 28$ ; Mar.  $n = 29$ ; Apr.  $n = 27$ ; May  $n = 28$ ; June  $n = 30$ ; July  $n = 22$ ; Aug.  $n = 30$ ; Sept.  $n = 20$ ; Oct.  $n = 25$ ; Nov.  $n = 29$ ; Dec.  $n = 18$ .

### Population Density and Group Composition

A total of 14 groups lived in the vicinity of the study site in an area approximating 30 ha (Fig. 2 and Table I). This is a high population density compared to Ampijoroa (Fig. 1), where we located only 5 groups in an area approximating 200 ha (mid-March to mid-April 1994). Based on 9 of

14 groups for which group size was known at the end of the study period (September 1995), absolute density at Anjamena is 1 animal/ha, calculated as follows (Mutschler *et al.*, 1994):

Group density (GD): 1 group/2.85 ha ( $n = 2$ )  
 Mean group size (MGS): 3 animals/group ( $n = 9$ )  
 Absolute density: MGS/GD = 1 animal/ha

Group composition of mongoose lemurs at Anjamena remained relatively constant throughout the study period. Both study groups were small, cohesive family units, containing 1 adult male, 1 adult female, and 1–4 offspring. Births occurred in October and November 1994. In groups 1 and 2, emigrations occurred between December and April (Table I).

#### Path Length and Home Range Use

Home range size differed only marginally between the two groups, with group 1 using 2.8 ha and group 4 using 2.9 ha (Fig. 2). Mean path length (PL) over the study period was  $1390 \pm 265$  m (minimum = 880 m; maximum = 1810 m;  $n = 14$ ) for group 1 and  $980 \pm 300$  m (minimum = 240 m; maximum = 1400 m;  $n = 12$ ) for group 4. The overlap in home ranges for the two neighboring groups was 0.85 ha, which represents 31% of the home range in group 1 and 30% in group 4. There was also extensive overlap with other neighboring groups, in particular, with group 3 (Fig. 2). Home ranges can also be referred to as territories, as they were actively defended (Curtis, 1997), and confrontations between groups occurred almost exclusively along

**Table I.** Group Composition in *Eulemur mongoz* for Groups for Which Group Size Was Known at Anjamena in September 1995

	Group									
	1	2	3	4	9	11	12 <sup>a</sup>	13	14	
Adult female	1	1	2 <sup>b</sup>	1	1	1	1	1		
Adult male	1	1	1	1	1	1	1	1		
Subadult female	1			1					1	
Subadult male						1			1	
Juvenile female	1			1		1		1	1	
Juvenile male		1								
Infant										
Total No. animals	4	3	3	4	2	4	2	3	3	
No. emigrations in 1995	2	1	0	0	0	?	0	?	?	

<sup>a</sup>New group founded in 1995.

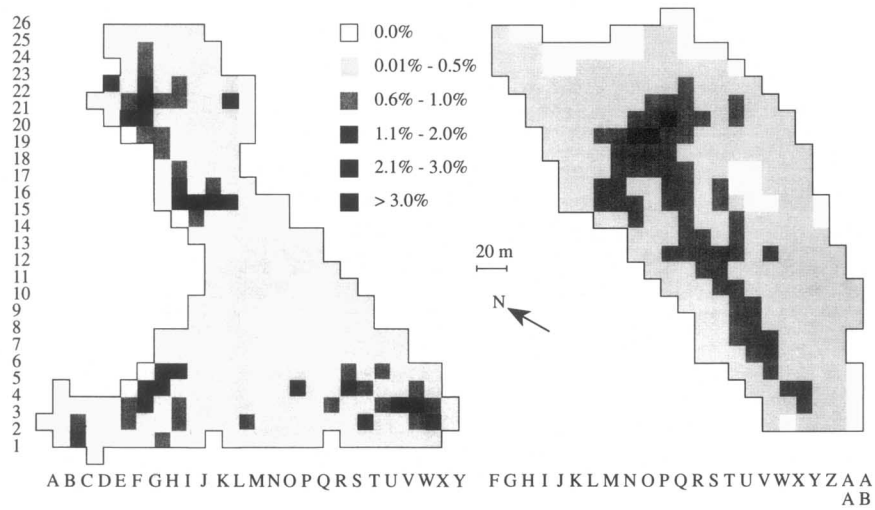
<sup>b</sup>One of the females appeared to be a hybrid (*Eulemur mongoz* × *E. fulvus rufus*).

the borders of their respective territories (Fig. 2). No clear seasonal difference is apparent in the mean PL or the mean number of quadrats used in an activity cycle (Table II).

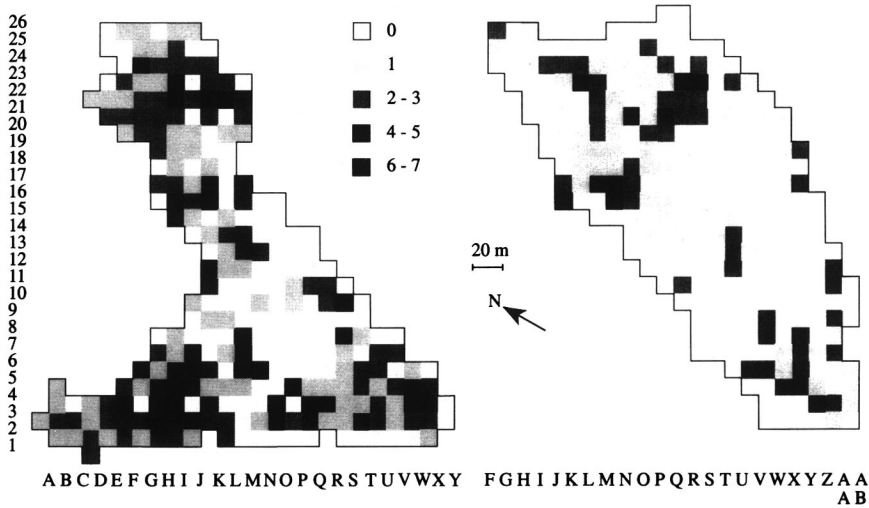
The intensity of quadrat use by the two groups throughout the study period in different areas of the home range is depicted in Fig. 5. In group 1 the intensity of quadrat use corresponds to the actual frequency at which a given quadrat was used during all observations, as the position of the group in a given quadrat was marked at 1-min intervals. In group 4, the intensity of quadrat use corresponds only to the number of observations during which it was used, as the position of the group was marked at 15-min intervals and the number of quadrats traversed was worked out subsequently. Quadrats scored as 0% are included in the home range, as they either were frequented during feeding observations (specific feeding observations were not included in this analysis) or were located in the center of the home range. Core areas are defined as the quadrats used at a frequency of >0.5%. In group 1, these areas cover 18% of the total home range, and in group 4 they account for 23%. Most dormitory trees are found within the core areas [group 1, 76% ( $n = 17$ ); group 4, 67% ( $n = 6$ )], as is a small proportion of territorial confrontation points [group 1, 15% ( $n = 20$ ); group 4, 25% ( $n = 24$ )] (Figs. 2 and 5). A third factor associated with quadrat use is the distribution of food resources within the home ranges (Fig. 6): the intensity of quadrat use is significantly associated with the number of known food species per quadrat [Kendall rank correlation; group 1,  $\tau = 0.418$  ( $Z = 10.402$ ),  $n = 279$ ,  $P < 0.001$ ; group 4,  $\tau = 0.198$  ( $Z = 5.022$ ),  $n = 290$ ,  $P < 0.001$ ]. There was no seasonal difference in

**Table II.** (a) Path Length (PL; m) in and (b) Mean Areas Within the Home Ranges Used by the Two Study Groups During the Wet and Dry Seasons

	Group 1		Group 4	
	Wet season	Dry season	Wet season	Dry season
a				
<i>n</i> observations	3	11	3	9
Mean	1580 ± 60	1330 ± 280	920 ± 380	990 ± 300
Minimum	1510	880	490	620
Maximum	1630	1810	1220	1400
b				
<i>n</i> observations	3	11	3	9
Mean	32 ± 4%	26 ± 5%	32 ± 11%	33 ± 12%
Minimum	27%	17%	20%	13%
Maximum	36%	35%	43%	56%



**Fig. 5.** Home range use by the two study groups. Intensity of quadrat use is ranked in 6 categories and represents the percentage of observation time for group 1 (left) and percentage of observations for group 4 (right).



**Fig. 6.** Distribution of food resources in the home ranges of the two study groups. The number of food species per quadrat is ranked in 5 categories for group 1 (left) and group 4 (right).

the intensity of quadrat use in either group and seasonal frequencies of quadrat use are significantly associated in both groups [group 1 (wet/dry) Wilcoxon signed ranks,  $Z = -1.054$ ,  $n = 279$ ,  $P = 0.292$ ;  $\tau = 0.867$  ( $Z =$

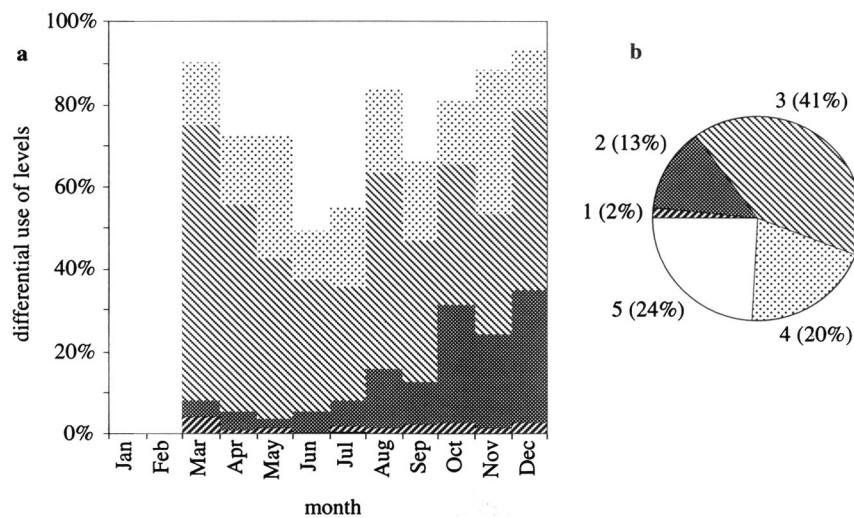
7.595),  $n = 279$ ,  $P < 0.001$ ; group 4 (wet/dry),  $Z = -0.309$ ,  $n = 290$ ,  $P = 0.757$ ;  $\tau = -0.521$  ( $Z = 13.233$ ),  $n = 290$ ,  $P < 0.001$ ].

### Vertical Habitat Utilization and Substrate Use

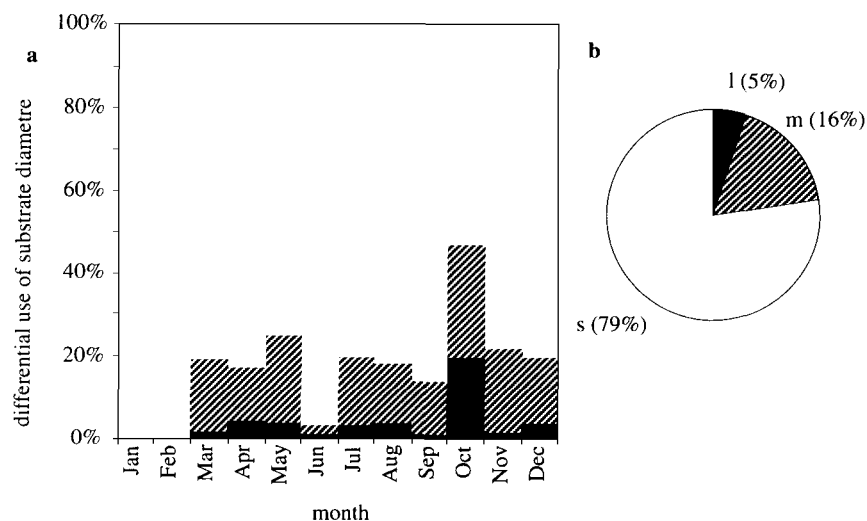
Over the 10-month study period, the subjects spent 24% ( $\pm 15\%$ ;  $n = 10$  months) of observation time at the highest level of the forest (5), 20  $\pm 7\%$  at level 4, 41  $\pm 12\%$  at level 3, 13  $\pm 11\%$  at level 2, only 2  $\pm 1\%$  at level 1, and  $< 1 \pm 0.1\%$  on the ground (0) (Fig. 7b).

The only levels that appear to vary in seasonal use are levels 3 and 5 (Fig. 7a). Given the significant intercorrelation between the two ( $\tau = -0.311$ ,  $n = 26$ ,  $P = 0.026$ ), we consider only level 5. However, the subjects did not use the highest strata of the forest—emergent trees—significantly more frequently during the dry season (Wilcoxon signed ranks:  $T^+ = 3$ ,  $T^- = 18$ ,  $n = 6$ ,  $P = 0.078$ , one-tailed).

The subjects used small substrates far more frequently during observations ( $79 \pm 11\%$ ;  $n = 10$ ). Medium-sized substrates accounted for 16  $\pm 7\%$  of observation time and large substrates for 5  $\pm 6\%$  (Fig. 8b). No seasonal preference was exhibited for a particular substrate diameter (Fig. 8a).



**Fig. 7.** The distribution of the use of different levels within the forest throughout the active phase of the 24-hr period in each month (a) and over the entire study period (b). No data were collected in January and February. Level 1, 0–2 m; level 2, 2–5 m; level 3, 5–10 m; level 4, 10–15 m; level 5, >15 m.



**Fig. 8.** The distribution of the use of different substrate diameters throughout the active phase of the 24-hr period in each month (a) and over the entire study period (b). No data were collected in January and February. l, 20–30 cm; m, 10–20 cm; s, 0–10 cm.

The subjects used horizontal substrates during the largest proportion of observation time ( $81 \pm 4\%$ ;  $n = 10$ ); oblique substrates account for  $17 \pm 3\%$  and vertical substrates for  $2 \pm 1\%$  (Fig. 9b). No seasonal preference is exhibited for any particular substrate angle (Fig. 9a).

### Interspecific Competition

*Eulemur mongoz* at Anjamena was predominantly frugivorous throughout the entire year but also fed on leaves, nectar, and flowers (Curtis, 1997). Potential competitors present throughout both seasons are other lemurs, birds, and possibly arboreal rodents. The crowned sifaka (*Propithecus verreauxi coronatus*), the rufous brown lemur (*Eulemur fulvus rufus*), the greater vasa parrot (*Coracopsis vasa*), and the Madagascar green pigeon (*Treron australis*) all exploited resources that are used by *Eulemur mongoz* (Table III). Several resources ( $n = 8$ : fruit, leaves, and flowers) were shared by *Eulemur mongoz* and *Propithecus verreauxi coronatus* (Table III). (Müller, 1997), but we saw no agonistic interaction between them. On one occasion, an adult *Propithecus* and a juvenile *Eulemur mongoz* fed together on a large fruit of *Bosqueia* sp. The most important potential competitor was probably *Eulemur fulvus rufus*, as it not only shared food resources ( $n = 7$ ; fruit and

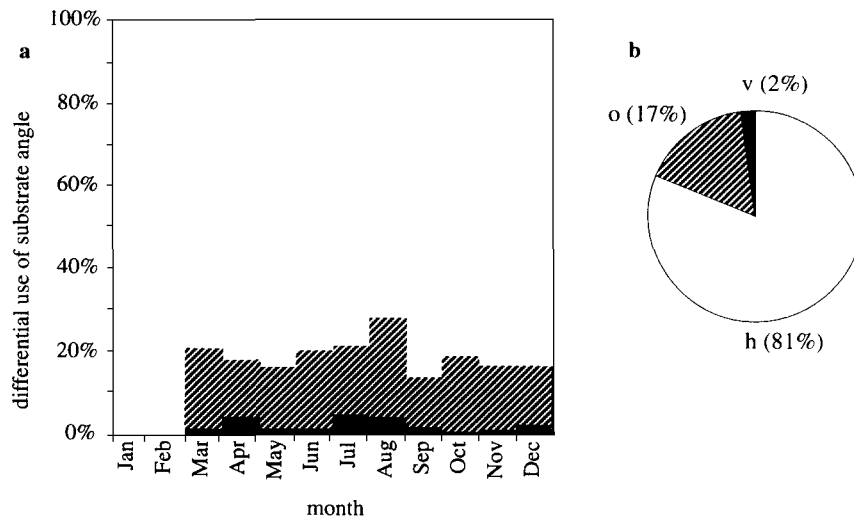


Fig. 9. The distribution of the use of different substrate angles throughout the active phase of the 24-hr period in each month (a) and over the entire study period (b). No data were collected in January and February. h, 0–29°; o, 30–74°; v, 75–90°.

leaves) with *Eulemur mongoz* but also exhibited a similar activity pattern (Table III) (Curtis, 1997). However, we saw only 7 interspecific confrontations involving feeding, 4 of which were agonistic, and both agonistic and nonagonistic interactions were evenly split between the two seasons.

During the wet season, two fruit bats (*Pteropus rufus*, *Rousettus madagascariensis*) and the fat-tailed dwarf lemur (*Cheirogaleus medius*) also shared resources with *Eulemur mongoz*; in April there was a confrontation between a juvenile *Eulemur mongoz* and *Pteropus rufus*.

### Predation

We observed no attempt or instance of nonhuman predation, though potential predators occur at Anjamena (Table IV). An infant (ca. 5 weeks old) was dead and still warm on the ground on the morning of the 11 November 1994. If this was a case of predation, the predator may have been disturbed by us. The cause of death was a large flesh wound to the head and a puncture below the left eye, which might have been inflicted by *Cryptoprocta ferox* (S. Goodman, personal communication), but possibly also by a dog. The nature of the wound was such that it was probably not inflicted by another lemur (S. Goodman, personal communication).



Table III. Potential Vertebrate Competitors for Food Resources at Anjamena

Class	Order	Species	Common food items
Mammalia	Chiroptera	<i>Pteropus rufus</i>	Fruit <i>Ficus cocculifolia</i> Nectar <i>Ziziphus jujuba</i>
		<i>Rousettus madagascariensis</i>	Fruit <i>Ficus cocculifolia</i> Nectar <i>Ziziphus jujuba</i>
	Rodentia	???	Fruit ???
	Primates	<i>Cheirogaleus medius</i>	Fruit <i>Rinorea</i> sp.
		<i>Propithecus verreauxi coronatus</i>	Fruit <i>Ficus cocculifolia</i> <i>Ziziphus jujuba</i> <i>Bosqueia</i> sp. Leaves <i>Diospyros megasepala</i> <i>Ficus cocculifolia</i> <i>Landolphia perrieri</i> <i>Ziziphus jujuba</i> <i>Rhynchosia bauckea</i>
		<i>Eulemur fulvus rufus</i>	Flowers <i>Ficus cocculifolia</i> Fruit <i>Ziziphus jujuba</i> <i>Bosqueia</i> sp. <i>Ficus soroceiodes</i> <i>Grewia lavanalensis</i> Leaves <i>Ficus cocculifolia</i>
Aves	Psittaciformes	<i>Coracopsis vasa</i>	Fruit <i>Ficus cocculifolia</i>
	Columbiformes	<i>Treron australis</i>	Fruit <i>Ficus cocculifolia</i>
	Cuculiformes	<i>Coua cristata</i>	Fruit ???
		<i>Coua ruficeps</i>	Fruit ???
	Passeriformes	<i>Copsychus albospecularis</i>	Fruit ???
		<i>Nectarinia souimanga</i>	Nectar ???
		<i>Nectarinia notata</i>	Nectar ???
		<i>Zosterops maderaspatana</i>	Fruit ???
		<i>Hypsipetes madagascariensis</i>	Nectar ??? Fruit ???

<sup>a</sup>Information on diet in *P. v. coronatus* taken from Müller (1997). Information on diet in birds taken from Langrand (1990).

Only 1 of 10 responses to potential predators occurred during the wet season. The adults gave warning calls if they saw a raptor ( $n = 8$ ), either overhead or perching nearby, but they also reacted to other large birds flying overhead, e.g., sacred ibis (*Threskiornis aethiopicus*). We observed one instance of mobbing; a Madagascar harrier-hawk (*Polyboroides ra-*

Table IV. Potential Nonhuman Predators at Anjamena

Class	Family	Species
Mammalia	Viverridae	<i>Cryptoprocta ferox</i> <i>Viverricula indica</i>
Reptilia	Boidae	<i>Sanzinia madagascariensis</i> <i>Acrantophis madagascariensis</i>
Aves	Falconidae	<i>Aviceda madagascariensis</i> <i>Milvus migrans</i> <i>Polyboroides radiatus</i> <i>Accipiter henstii</i> <i>Accipiter francesii</i> <i>Buteo brachypterus</i>

*diatus*) was eventually chased away by the group. On two occasions, mongoose lemurs spotted a colubrid snake on the ground and observed it intently, while grunting and tail-swinging.

## DISCUSSION

*Eulemur mongoz* is generally referred to as a pair-bonded species that lives in small family groups; however, the observed group size varies quite extensively and some authors have reported small family groups of 3 or 4 individuals (Albignac, 1981; Anonymous, 1992; Harrington, 1978; Kaudern, 1914, 1915; Tattersall, 1978), whereas in other cases there are larger groups containing  $\leq 8$  individuals (Andriatsarafara, 1988a; Petter, 1962; Tattersall, 1978). Variation in grouping patterns appears to be linked not only to the seasonal nature of mongoose lemur habitat, but also to the different temporal niches that they occupy during the wet (diurnal) and dry (nocturnal) seasons (Andriatsarafara, 1988a; Tattersall, 1978). The complex picture that emerges from these short-term studies does not, however, reveal a consistent pattern: family groups are evident at night and during the day, during the dry season, and during the wet season, in Madagascar and the Comorian islands of Moheli and Anjouan (Albignac, 1981; Anonymous, 1992; Clark, personal communication; Harrington, 1978; Tattersall, 1978, personal communication). Larger groups are apparent at night during the dry season in Madagascar and at night in Moheli (Andriatsarafara, 1988a; Tattersall, 1978).

Throughout the study at Anjamena, group composition remained relatively constant; changes in group size were limited to births and emigration of subadult individuals. Both main study groups were small, cohesive family units, containing 1 adult male, 1 adult female, and 1–4 offspring. Mean group size in the area is 3 animals per group ( $n = 9$ ). The activity pattern

was cathemeral throughout the entire year, but shifted toward predominantly diurnal activity during the wet season and predominantly nocturnal activity during the dry season (Curtis, 1997).

Unfortunately our study provides no comparative information as it was carried out in only one type of habitat. However, the results are confirmed by our observations at several different sites during the pilot phase and short-term excursions. At Ampijoroa (Fig. 1), during the transition between the wet and dry seasons—(mid-March to mid-April 1994)—we observed only small family groups and the mongoose lemurs were cathemeral. By mid-April they appeared to be almost exclusively nocturnal (Curtis and Zaramody, unpublished data).

Other sightings during the dry season at Katsepy, to the West of Mitsinjo, between Mitsinjo and Lac Kinkony, to the south and southeast of Lac Kinkony and south of Anjamena along both banks of the Mahavavy River (Fig. 1) also revealed small family groups. The mongoose lemurs always rested during the day and were active shortly before and shortly after dawn and dusk. The few nocturnal surveys revealed nocturnal activity (Curtis, Zaramody, and Müller, unpublished data).

In spite of the clear seasonal changes which we documented in both the climate and vegetation at Anjamena, there was no variation in grouping patterns. Therefore, we can make no correlation between variation in group size and the seasonal variation of ecological variables. However, we will discuss the activity pattern, predation, and home range size, all of which have been linked to group size (Clutton-Brock and Harvey, 1977, 1979; Overdorff, 1996; Terborgh, 1983; van Schaik and Kappeler, 1993) in the light of our data.

The activity pattern of mongoose lemurs is clearly affected by the seasonal nature of the environment at Anjamena. *Eulemur mongoz* is cathemeral throughout the entire year, exhibits a shift toward predominantly diurnal behavior during the warm wet season, and a shift toward predominantly nocturnal behavior during the cool dry season (Curtis, 1997). van Schaik and Kappeler (1993) suggested that as diurnal species tend to live in larger groups than nocturnal species, cathemeral species might be expected to live in small groups during the season when they were mainly nocturnal and in large groups during the season when they were mainly diurnal. At Anjamena, we observed no change in grouping patterns and there appears to be no reason to link grouping patterns in *Eulemur mongoz* in Madagascar to the variation in the activity cycle.

Predation could be a major factor influencing group size in primates (Terborgh, 1983; van Schaik, 1983; van Schaik and van Hooff, 1983). We observed no nonhuman predation at Anjamena, though several potential predators occur there. The dead infant mongoose lemur may have been a victim of predation. Infanticide is another possibility (van Schaik and Kap-

pelers, 1993), but the nature of the wound was such that it was probably not inflicted by another lemur (Goodman, personal communication). We observed antipredator behavior mainly during the dry season. If this behavior can be taken to indicate increased predator pressure, larger groups would be expected during the dry season, as the small group size in *Eulemur mongoz* would theoretically be favored if predation pressure were low (Cheney and Wrangham, 1987; Terborgh, 1983; van Schaik and van Hooff, 1983). Polyspecific associations, e.g., *Eulemur mongoz* and *Eulemur fulvus* at Ampijoroa (Harrington, 1978; personal observation), would constitute a mechanism to enlarge group size and provide increased protection from predators, but we observed none at Anjamena. Predation appears not to provide a satisfactory answer to the small group size in either of the monogamous lemurids—*Eulemur rubriventer*, *Eulemur mongoz*)—that have been studied (Overdorff, 1996; this study).

Home range size in *Eulemur mongoz* was small, covering areas of 2.8 and 2.9 ha in the two study groups. This is more than twice the sizes reported by Andriatsarafara (1988a) and Tattersall (1975) at Ampijoroa, but this is probably more a reflection of total observation time than of a real difference in home range size. The only lemurid with a smaller home range (0.75–1.0 ha) is *Eulemur fulvus rufus* in West Madagascar (Sussman, 1974). By comparison, average home range size in other Lemuridae that are either mainly frugivorous or mixed frugivore–folivores is often much higher. Species studied in seasonal forests in West Madagascar exhibited ranges from 5 to 9 ha (*Lemur catta*, *Eulemur fulvus fulvus*, *Eulemur macaco macaco*) (Colquhoun, 1993; Harrington, 1975; Sussman, 1974). *Lemur catta* at Berenty in the southern xerophytic vegetation zone of Madagascar exhibited large home ranges, with an average of 32 ha (Sussman, 1991). In the eastern forests, home ranges were also much larger, ranging from 19 ha in *Eulemur rubriventer* to between 23 and 26 ha in *Varecia variegata rubra* to 95–100 ha in *Eulemur fulvus rufus* and 197 ha in *Varecia variegata variegata* (Overdorff, 1993; Rigamonti, 1993; White, 1991). Home range area can be positively correlated with group size (Clutton-Brock and Harvey, 1979). However, the examples given above show that there must be other determinants of group size in lemurs. For instance, group sizes of *Lemur catta* and *Eulemur fulvus rufus* in different habitats did not vary but home range size did (Overdorff, 1996; Sussman, 1974, 1991).

Large home ranges in these lemurids occur in eastern rain-forest habitats and in the southern xerophytic vegetation zone of Madagascar (*Lemur catta*), whereas they have smaller home ranges in the seasonal forests of West Madagascar. This could imply a more abundant and perhaps uniform distribution of the main food resource (fruit) in seasonal western forests in comparison with the eastern rain forests and xerophytic forests. Distri-

bution of food resources may predict home range size, but given the consistency of group size in *Eulemur fulvus rufus* and *Lemur catta* in different types of forest, it does not appear to be an important determinant of group size in mixed frugivorous–folivorous lemurs. At Anjamena, food resources were distributed fairly evenly throughout the home ranges of *Eulemur mongoz*, supporting the idea that small home ranges could be correlated with a uniform distribution of food resources.

The seasonal nature of the western forests of Madagascar has often been cited as one of the main factors underlying many aspects of the behavior of the lemur living in them. The paucity of food resources during the difficult time of the year, i.e., the dry season, has been regarded as a possible factor in the timing of reproduction by Jolly (1984), Martin (1990), Meyers and Wright (1993), Richard and Dewar (1991), and Richard and Nicoll (1987) and as the factor responsible for a reduction in activity at this time of the year by Colquhoun (1993), Hladik (1988), Richard (1974), Sussman (1974), and Tattersall (1979). While this could be true for species that rely on foliage or insects as the major source of nutrients, it is questionable whether the more frugivorous species in these seasonal forests are affected to the same extent. Provided that the distribution of food resources is correlated with home range size (Clutton-Brock and Harvey, 1979), then our discussion of the variation in home range size demonstrates this point in that smaller home ranges occur in the more seasonal forests of the West than in the rain forests of the East. This implies that lemurs in the West need not range as far to find necessary resources as those in the East do. Perhaps the abundance of fruit in eastern rain forests of Madagascar is more seasonally variable than in the West. Our data provide further support for the idea that the dry season in the West may not present lemurs that are reliant on fruit for a large part of their sustenance with major problems (Curtis, 1997). At Anjamena, the environment was highly seasonal. This, however, is not reflected in the way the mongoose lemurs used their home ranges: there was no seasonal difference in path length, the intensity with which different areas of the home range were frequented, or the strata of the forest that were used. Furthermore, if resource availability was low during the dry season at Anjamena, then it might be expected that sympatric species with similar diets and activity patterns, e.g., *Eulemur mongoz* and *Eulemur fulvus rufus*, would compete more intensively with each other. This was not the case at Anjamena. Clearly much of what has been said in this last paragraph is highly speculative. However, it highlights the need for more detailed studies on lemur ecology in order to allow intra- and interspecific comparisons within and between different habitats.

Table A1. Vegetation at Anjamena and Plant Species Used for Collection of Phenological Data<sup>a</sup>

Family	Species	Malagasy	Plant
Anacardiaceae	<i>Sclerocarya caffra</i>	Sakoa	Tree
	<i>Sorindeia madagascariensis</i>	Voatsorindra	Tree p
Apocynaceae	<i>Landolphia perrieri</i>	Ditipira	Liana p
Asclepiadaceae	<i>Marsdenia verrucosa</i>	Bokalahy	Liana p
	<i>Cryptostegia madagascariensis</i>	Lombiry	Liana p
	<i>Leptadenia madagascariensis</i>	Vahy mavo	Liana p
Borraginaceae	<i>Ehretia</i> sp.	Tambitika	Tree
	Indet.	Tampotsy	Tree p
	<i>Cordia subcordata</i>	Tsimiranja	Tree p+
	<i>Cordia</i> sp.	Tsimiranja be	Tree
	<i>Cordia</i> sp.	Tsingomandambo lahy	Tree
Burseraceae	<i>Commiphora pervilleana</i>	Mantambelo	Tree
Caesalpinaceae	<i>Bauhinia</i> sp.	Kiloilo	Tree p+
	<i>Caesalpinia bonduie</i>	Katra	Liana p
	<i>Tamarindus indica</i>	Madiro	Tree p+
Capparidaceae	<i>Thylachium</i> sp.	Falianara	Tree p
Combretaceae	<i>Poivrea obscura</i>	Fatikakoholahy	Liana p+
	<i>Terminalia mantaly</i>	Mantaly	Tree p+
Connaraceae	<i>Cuestis</i> sp.	Katsongo	Liana p
Convolvulaceae	<i>Argyrea</i> sp.	Vahy marantsa	Liana p
	<i>Ipomoea</i> sp.	Vahy tsoanga	Liana p
Ebenaceae	<i>Diospyros megasepala</i>	Hazomafana	Tree p
Euphorbiaceae	<i>Alchorula</i> sp.	Kinamo/Sarigavo	Tree p+
	<i>Phyllanthus casticum</i>	Sanira	Tree p
	<i>Antidesma petiolare</i>	Taindalitra	Tree p+
	<i>Phyllanthus</i> sp.	Tainto	Tree
Fabaceae	<i>Mezoneuron hildebrandtii</i>	Tsirofota	Liana p
Flacourtiaceae	<i>Calantica grandiflora</i>	Hazoambo	Tree p+
	<i>Flacourtia ramontchi</i>	Lamoty/Tsingoma	Tree p
Flagellariaceae	<i>Flagellaria indica</i>	Viky	Liana p+
Icacinaceae	<i>Iodes</i> sp.	Vahy mbalala	Liana p
Leeaceae	<i>Leea guineensis</i>	Taindrakidraki	Tree p
Menispermaceae	<i>Anisocyclea fallax</i>	Vahy fotsy	Liana p
Mimosaceae	<i>Acacia</i> sp.	Robokida	Tree p
Moraceae	<i>Ficus cocculifolia</i>	Adabo	Tree p+
	<i>Ficus trichopoda</i>	Avy avy/Mandresy	Tree
	<i>Bosequia</i> sp.	Kiloilo lahy	Tree p
	<i>Ficus</i> sp.	Nonika	Tree p
	<i>Bosqueia</i> sp.	Tsitopa	Tree p+
	<i>Ficus</i> sp.	Vahy sary adabo	Liana p
	<i>Ficus soroceoides</i>	Vohory	Tree p+
Papilionaceae	<i>Mundulea</i> sp.	Fanamo	Liana p
	<i>Mucuna pruriens</i>	Tainkilotra	Liana
	<i>Mundulea</i> sp.	Vahy mandry	Liana p
	<i>Rhynchosia bauckea</i>	Vahy telo ravina	Liana p+
	<i>Abrus precatorius</i>	Voamaintilany	Tree
Passifloraceae	<i>Passiflora foetida</i>	Bonga piso	Liana
Rhamnaceae	<i>Zizyphus jujuba</i>	Mokonazy	Tree p+
Rubiaceae	<i>Paederia</i> sp.	Laingo be	Liana p
	<i>Paeleria farinosa</i>	Laingomaimbo	Liana p
	<i>Genipa</i> sp.	Tandridritra	Tree p

Table AI. Continued

Family	Species	Malagasy	Plant
	<i>Tricalysia</i> sp.	Taolanomby	Tree p+
	Indet.	Tsingomandambo	Tree
	Indet.	Voamay	Liana p
Sapindaceae	<i>Tina isoneura</i>	Soalafika	Tree p
	<i>Paullinia pinnata</i>	Vahy pisaka	Liana
Sterculiaceae	Indet.	Kabija lahy	Tree
	<i>Byttneria voolily</i>	Vahy tambitika	Liana p
	<i>Dombeya greveana</i>	Valoambaka	Tree p
Tiliaceae	<i>Grewia lavanalensis</i>	Sely	Tree p+
	<i>Grewia</i> sp.	Sely be	Tree p+
	<i>Grewia</i> sp.	Zorotanty	Tree p
Urticaceae	<i>Boehmeria platyphylla</i>	Magnary adabo	Tree p+
Verbenaceae	<i>Clerodendron</i> sp.	Hotika	Tree p
Violaceae	<i>Rinorea</i> sp.	Maintipototra	Tree p+
Vitaceae	<i>Cissus</i> sp.	Takifika	Liana p
	<i>Cissus</i> sp.	Takifika be	Liana p
Not determined	Not determined	Takifikala	Liana p

<sup>a</sup>p, present in sample plots; +, used in phenological sample. Determination of scientific names: J. Raharilala (PBZT). Local names were supplied by A. Blaise at Anjamena.

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