# LEMURS OF THE KIRINDY FOREST

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## Résumé: Les lémuriens de la forêt de Kirindy

La forêt de Kirindy renferme une très riche communauté de primates et on y enregistre une des plus fortes densités de primates du monde. Les huit espèces connues à ce jour sont représentatives de tous les grands groupes de lémuriens, qui se caractérisent par de nombreux systèmes sociaux différents. Les lémuriens jouent un rôle important dans la dispersion des graines et certains ont une fonction de pollinisateurs. Cependant, la plus grande espèce, *Propithecus verreauxi*, est également un grand prédateur de semences. Les coupes de bois sélectives telles qu'elles sont pratiquées à ce jour n'ont pas d'effets négatifs sur les différentes espèces de lémuriens, car l'augmentation de la luminosité due aux vides laissés par les coupes permet aux arbres de compenser la perte de biomasse en augmentant leur production de feuilles et de fruits, et en produisant un feuillage de meilleure qualité.

## Abstract

The Kirindy Forest contains a very rich primate community with one of the highest primate densities of the world. The eight species recognized so far represent all the major guilds of lemurs with their many different social systems. Lemurs not only play an important role in seed dispersal and some may serve as pollinators, but also the largest species, *Propithecus verreauxi*, is an important seed predator. Selective logging, as practiced so far, has had no negative effects on the various lemur species. This is due to the fact that under the increased light levels found in the logging gaps, the trees can compensate for the loss in biomass by increasing both leaf and fruit production and by the devolopment of higher quality leaves.

## 1. Introduction

Within the forestry concession of the CFPF, called here the Kirindy Forest, lemurs reach one of the highest primate densities found anywhere in tropical forests, forming a substantial part of the local fauna. In this report, we will review aspects of their behavior and ecology, investigate some of their potential roles in this dry forest ecosystem, and summarize their short-term responses to selective logging.

Nowadays, at least eight species of lemurs are known to occur in the Kirindy Forest (Table 1). The five smallest species are all nocturnal and belong to the family of mouse and dwarf lemurs. The sixth nocturnal species, the weasel lemur (the genus *Lepilemur*) is of the genus most widely spread over all the different kinds of forest habitats in Madagascar. Rufous lemurs and white sifakas, the sole representatives of the true lemur and indri families at Kirindy are both group-living and partly or predominantly diurnal, respectively. Signs of the aye-aye (*Daubentonia madagascariensis*) have been found along the Route des Lémuriens (STERLING, 1994), but direct observations are still lacking.

At present, ecological and behavioral studies are under way on most of these species. The data accumulated so far for the Kirindy Forest are summarized here and supplemented with observations by CHARLES-DOMINIQUE et al. (1980) in the nearby Marosalaza Forest and by other researchers in other parts of the Malagasy dry deciduous forest.

Table 1: Aspects of the natural history of lemur species of the Kirindy Forest.

| Family and Species | Local name | Body mass [g] | Act.[1] | Gestation [days] | Litter size | Social sysem[2] | Food[3] |
|---|---|---|---|---|---|---|---|
| **Cheirogaleidae** | | | | | | | |
| *Microcebus myoxinus* | Tsidy<br>Tsitsidy<br>Telitelivahy | 30 | N | | | S | F, Fl, I |
| *Microcebus murinus* | Tsidy<br>Tsitsidy<br>Telitelivahy | 60 | N | 62 | 2+ | S | F, Fl, I |
| *Cheirogaleus medius* | Kelibehoho | 280 | N | 62 | 2 | | F, Fl, I |
| *Mirza coquereli* | Tanta | 300 | N | 89 | 2 | S | F,Fl,I,V |
| *Phaner furcifer* | Tanta | 450 | N | | I | P | F, Fl, G |
| **Lepilemuridae** | | | | | | | |
| *Lepilemur ruficaudatus* | Boenga | 750 | N | | 1 | S? | L, F, Fl |
| **Lemuridae** | | | | | | | |
| *Eulemur fulvus rufus* | Gidro<br>Varika | 2300 | C | 120 | 1(-2) | G | F, Fl, L |
| **Indridae** | | | | | | | |
| *Propithecus v. verreauxi* | Sifaka | 3600 | D | 155 | 1 | G | L, F, Fl |

[1] N = nocturnal, D = diurnal, C = cathemeral (active day and/or night)

[2] S = solitary, P = pairs, G = groups

[3] F = fruit, Fl = flowers and nectar, L = leaves, G = gum, I = insects, V = vertebrates

## 2. Social systems of the Kirindy Forest lemurs

Studies focussing on social organization, social behavior, and mating systems have only recently been initiated in the Kirindy Forest. Local populations of *Microcebus, Mirza, Lepilemur, Propithecus,* and *Eulemur* have been marked individually, permitting detailed long-term studies of individual life histories, population dynamics, and social behavior. Extended grid systems in two areas have provided the second prerequisite for these studies, especially in the case of nocturnal species, where radio-tracking is an essential aspect of most research projects.

A fundamental goal of studies investigating social systems is the collection of information on the spatial and temporal distribution of adult males and females of a population. Because the distribution of females is expected to be closely linked to ecological factors (TRIVERS, 1972), the study of social organization integrates both behavioral and ecological research. The distribution of males, on the other hand, is known to be largely determined by the distribution of receptive females (EMLEN and ORING, 1977). The resulting competition among males, as well as its behavioral and morphological consequences, provides a logical starting point for studies examining the relationship between social organization and mating systems. Group-living diurnal species offer an additional opportunity for the detailed examination of the underlying behavioral mechanisms. In addition to these theoretical foundations, some lemur research projects at Kirindy also build on working hypotheses generated by captive studies (e.g., SCHILLING et al., 1984; KAPPELER, 1990, 1993, 1996b; VAN SCHAIK and KAPPELER, 1993). In the following section, we will briefly review the available information on these topics for each of the lemurs of Kirindy.

*Microcebus myoxinus*

The pygmy mouse lemur (Fig. 1) has been re-discovered recently in Kirindy Forest (SCHMID and KAPPELER, 1994). It is the smallest known primate with an adult body mass of about 30 g. Very little is known about its behavior and ecology. As in the other mouse lemurs, it is nocturnal and solitary. Preliminary observations indicate that, compared to sympatric *M. murinus*, it may have larger home ranges and rely more on nests and liana tangles, rather than tree holes, as daytime resting sites (J. SCHMID and D. SCHWAB, pers. comm.). Weak sexual size dimorphism and relatively large testes are suggestive of a mating system characterized primarily by scramble competition (KAPPELER, unpubl. data).

Fig. 1: The two mouse lemurs: *Microcebus myoxinus* (left) and *M. murinus* (right); photos by JUG and S. SOMMER.

*Microcebus murinus*

The social organization of the grey mouse lemur (Fig. 1) has been previously examined in several short-term studies outside Kirindy (MARTIN, 1973; PAGES-FEUILLADE, 1988). These reports revealed that *M. murinus* is solitary during its nocturnal activity, while maintaining characteristic spatial relationships among individuals. Individual home ranges were found to overlap with those of other males and females, with male ranges being generally larger than those of females. Two size classes of males were observed in some areas, where the smaller males, who had a much smaller range overlap with female ranges, may be reproductively supressed (PERRET, 1992). Because grey mouse lemurs tend to nest in groups in tree holes or leaf nests during the day, information about the composition of these sleeping groups may provide important additional information on their social organization. In previous studies, females were found to commonly share a nest with several other females, whereas males typically nested alone or in pairs (MARTIN, 1972).

An important determinant of the temporal distribution of these mouse lemurs is their response to seasonal variation in ambient temperature and food availability. During the austral winter months, individuals may enter periods of inactvity ranging in duration from hours to weeks (PETTER-ROUSSEAUX, 1980; SCHMID, in press). Seasonal variation in activity can also be induced in captvity and is accompanied by dramatic changes in body mass. In all captive populations, females were on average heavier than the males (KAPPELER, 1991). Because the females also have larger canines than males (KAPPELER, 1996a), the mating system of this species is of particular interest.

Ranging and resting behavior of individually-marked grey mouse lemurs has now been continuously monitored for over a year in the Kirindy Forest. Preliminary results indicate that males show great range overlap, that adult females may remain inactive for several months, and that sleeping groups have more complicated dynamics than previously thought. Observations relevant to their mating system have revealed so far that males gain weight during the pre-mating season, resulting in male-biased sexual dimorphism during the mating season in October. Also sperm competition, as evidenced by the occurrence of sperm plugs and relatively large testes (FIETZ, 1995, in press; KAPPELER and SCHMID, unpubl. data), is obviously one mechanism of intrasexual selection. Paternity analyses, which should reveal any variations in male reproductive success, are in progress.

*Cheirogaleus medius*

Fat-tailed dwarf lemurs (Fig. 2) are nocturnal and supposed to be solitary. The most salient feature of their life history is the prolonged inactivity during the austral winter months (PETTER-ROUSSEAUX, 1980). In a brief mark-recapture study, individual *C. medius* were found to concentrate their activities on home ranges of less than 4 ha (HLADIK et al., 1980). Given the high estimated population density in that study area (350 individuals/km$^2$) and similar densities of several hundred individuals/km$^2$ estimated for the Kirindy Forest (GANZHORN, 1992), this information implies a high degree of range overlap. Fat-tailed dwarf lemurs sleep in tree holes during the day, either alone or in small groups. However, sleeping groups have only been censused during the long period of inactivity (in August), and it is not known whether they form similar associations during the rest of the year (PETTER et al., 1977). In Kirindy Forest, *C. medius* is inactive between May and October.

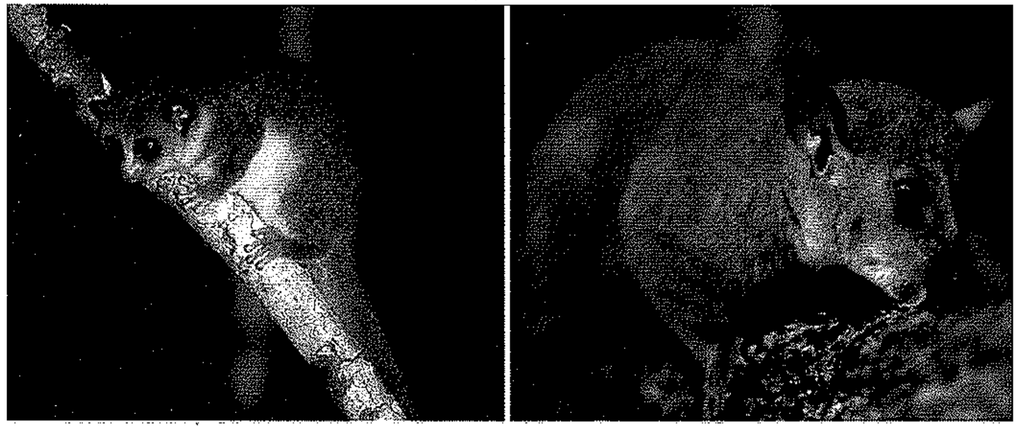

Fig. 2: Fat-tailed dwarf lemur (*Cheirogaleus medius*; left) and Coquerel's dwarf lemur (*Mirza coquereli*; right); photos by JUG and I. HERBINGER.

*Mirza coquereli*

Coquerel's dwarf lemur (Fig. 2) is nocturnal and solitary. In a brief radio-telemetry study of two males and two females during the dry season, PAGES (1978, 1980) found that adult *M. coquereli* females have non-overlapping home ranges and virtually never interact. Although male home ranges may overlap with those of more than one female, they are generally smaller. However, males tend to make longer excursions away from their core area. Male home ranges also do not overlap with each other and are actively defended against neighbors. The pattern of range overlap and interaction frequencies between males and females led PAGES (ibid.) to conclude that males and females may develop pair-bonds.

In 1993, a long-term study of the social organization and mating system of *M. coquereli* was initiated in N5 to verify PAGES' conclusions in the light of additional information gained from captive studies. Observations of one of the relatively largest testes found among prosimians (KAPPELER, 1996b) and the occurrence of female estrous calls (STANGER, 1993; STANGER et al., 1995) strongly suggested a non-monogamous mating system, whereas the lack of sexual size dimorphism (KAPPELER, 1991) supported PAGES' hypothesis. Radio-tracking during the mating season in October revealed that males range over much larger areas (up to 25 ha) than females and that male ranges overlap with those of several males and those of more than 10 females (KAPPELER, unpubl. data). After the mating season, male ranges were about four times smaller and similar in size to those of the females. These observations are clearly at variance with those of PAGES (1978, 1980) and are strongly suggestive of a mating system characterized by scramble competition polygyny. Seasonal male-biased size dimorphism and a large proportion of injured males during the mating season are indicative of an additional contest component of male-male competition (ibid.). Ongoing genetic analyses should reveal the distribution of paternity among the marked males, allowing an even more precise characterization of their mating system.

*Phaner furcifer*

The fork-marked lemur (Fig. 3) is best known for its impressive vocalizations at dusk that signal the onset of Kirindy night life. Detailed studies of this intriguing species have so far been hampered by the difficulties encountered in trapping them. The only study of *P. furcifer* revealed that males and females occupy home ranges which overlap little with those of neighbors of the same sex, whereas the home ranges of individual males and females were found to be perfectly superimposed throughout the year in three cases. These males and females were in close proximity and constant vocal contact throughout the night, frequently in the form of duetting, and the males also scent-marked the respective females with a throat gland. However, one male with a range overlapping those of two females, as well as a solitary male were also observed (CHARLES-DOMINIQUE and PETTER, 1980). These observations indicate that *P. furcifer* has a primarily monogamous mating system, which is unusual for nocturnal primates (VAN SCHAIK and KAPPELER, 1993).

*Lepilemur ruficaudatus*

Very little is known about the social organization of the brown weasel lemur (Fig. 5). So far, the species was considered to be solitary, but recent studies have shown that, at least during the dry season, males and females have overlapping home ranges and seem to live in pairs. Even though they might forage alone, resting periods are synchronized and the males and females may spend their resting periods or the whole day in the same or neigboring tree holes. Observations during their nocturnal activity require substantial enthusiasm for this species, as they often remain immobile for several hours, then jump a few meters, feed, and go back to rest. In total, their home range does not seem to be much larger than about 1 ha (ALBIGNAC, 1981; WARREN, 1994).

*Eulemur fulvus rufus*

Redfronted lemurs (Fig. 6) are group-living and cathemeral, i.e., they can be active during both day and night. This subspecies of *E. fulvus* found in the Kirindy Forest also occurs in the rainforests of southeastern Madagascar, providing a unique opportunity to compare the interactions between ecology and behavior within the same taxon. Studies in other regions have already suggested interesting differences between eastern and western redfronted lemurs: groups of 8-10 individuals had home ranges of just under 1 ha in the west (SUSSMAN, 1974), whereas the same-sized groups in the east ranged over 100 ha and more (OVERDORFF, 1993). At Kirindy, several groups of *E. fulvus* have been habituated and marked in CS7. Preliminary observations throughout the concession suggest a very flexible social organization. Observations of aggregations of between 30 and 100 individuals feeding in a single large fig tree (ROHNER, 1988), peaceful exchange of individuals between social units (C. VAN SCHAIK, pers. comm.), and aggressive inter-group encounters (KAPPELER, unpubl. data) make this species a very exciting subject for studies of social organization (GANZHORN, 1988).

*Propithecus verreauxi verreauxi*

Verreaux's sifaka (Fig. 6) are predominantly diurnal and live in groups of 2-13 individuals, with most groups containing 4-8 members (RICHARD, 1993). In April 1995, 25 members of six groups were captured and individually marked in CS7. These groups contained between three and seven individuals, with an average of 2.0 adult females and 1.2 adult males per group. Studies during the following dry season revealed that these groups range over 12-25 ha, with extensive range overlap between some groups and substantial range contraction after birth of the young (CARRAI and LUNARDINI, 1996; RALISOAMALALA, 1996). The mating system of sifakas is particularly interesting because their mating season is characterized by the brevity and synchrony of female estrous periods and male roaming behavior (RICHARD, 1992). Female estrous synchrony within and between groups and its consequences for male mating strategies were therefore the topic of a study during the first mating season of the marked population (S. RÜMENAP, unpubl.). Their first birth season has already revealed that more than one female per group may reproduce at the same time. Studies on anti-predator behavior, social structure, and communication are also planned or in progress.

## 3. Lemur ecology

### 3.1 Population densities and feeding behavior

Densities of the different lemur species, measured as encounter rates during standardized transect walks, vary widely between forest plots (Table 2). Population densities can be estimated based on encounter rates. For this, the distance perpendicular to the trail is estimated for the lemurs seen during transect walks. The mean of all detection distances is used to calculate the distance of detection per species and per forest bloc. Twice this detection distance (to account for detection on either side of the trail) multiplied by the length of the transect gives the area being censused. The number of lemurs seen divided by the area covered, yields an estimate of lemur density. For example: given the encounter rate of 2.6 individuals (ind.) of *L. ruficaudatus* in CN2 per 1000 m transect and a mean lateral detection distance of 9.0 m for this species, the density of this species in CN2 (individuals per km$^2$) is calculated as

$$2.6 \text{ ind.} / (1.0 * 2 * 0.009 \text{ km}^2) = 144 \text{ ind.} / \text{km}^2.$$

Although this procedure introduces errors, such as overestimation of population densities of species prefering edge habitats, it also corrects for the different detectability of different species in varying vegetation types and thus provides a first approximation of population density which can be compared with other studies (GANZHORN, 1992). Based on these calculations, the different lemur species can reach population densities of several hundred individuals per km$^2$ (Table 2).

Local population densities can vary seasonally in relation to food abundance. ROHNER (1988) describes observations of more than 100 individuals of *E. fulvus* feeding together in a big fig tree (*Ficus grevei*). These observations were limited to the months of October and November when the tree was fruiting. Several other causes linked to feeding behavior that are assumed to influence the distribution of lemurs have also been identified. All small nocturnal species (*Microcebus* spp., *C. medius*) feed on fruit, flowers, and insects. *M. coquereli* adds vertebrate prey when possible (PETTER et al., 1977; HLADIK et al. 1980; KAPPELER, unpubl.) and *P. furcifer* is specialized on gum produced by various large tree species (CHALES-DOMINIQUE and PETTER, 1980; HLADIK et al., 1980). *L. ruficaudatus* and *P. verreauxi* both feed on leaves, flowers and fruit; the former at night and the latter during the day. *E. fulvus* are more frugivorous than the other species, but they also eat substantial amounts of flowers and young leaves (Tables 1,3). Table 3 has to be considered as a preliminary summary as it lists only the most common food items recorded during unsystematic observations. Systematic observations should increase the number of different food items seen to be consumed, e.g., while Table 3 lists only 40 different food items for *P. verreauxi* for the whole dry season, a systematic study in this species from May to August identified more than 70 different items for these four months alone (CARRAI, 1996; RALISOAMALALA, 1996).

During the dry season, *M. murinus* uses parts of the forest with abundant secretions of the larvae of an Homopteran insect (*Flatidia coccinea*) more frequently than plots without these secretions (CORBIN and SCHMID, 1995). Similar to the positive link between *M. murinus* and insect secretions in N5, population densities of *P. furcifer* are correlated with the abundance of the tree species they use for gum feeding (Fig. 3). For these correlations, the number of food trees per km$^2$ has been weighed by their mean diameter at breast height, assuming that the DBH is correlated with production of food items. This may not be true for all tree species and individuals, but this is the best method currently available. In contrast to *M. murinus*, the abundance of potential food trees is not closely correlated with the density of *E. f. rufus*, *L. ruficaudatus*, or *P. v. verreauxi*. All these three species feed on a large variety of different types of food (leaves, flowers, fruits). Here it is not clear, whether we simply do not know all the relevant food species, whether the phenological variability is too high to allow simple generalizations, or whether ranging patterns and densities are influenced by factors other than food. In any case, the same food and habitat components might have different impacts on lemur behavior in different areas and are weighed differently by the different lemur species.

Table 2: Lemur populations in different forest plots of the CFPF forestry concession. Values are number of individuals seen per kilometer transect. Values are means ± SD of yearly transect counts during the wet seasons of 1988-1990 and 1992; N5 and N6 refer to data collected prior to logging; CN9 and LS11 were surveyed during the dry season of 1988. *Microcebus* spp. combines *M. murinus* and *M. myoxinus*; CN1, CS3, CS4 and LN4 are walking transects surveyed repeatedly by ROHNER (1988) between 1982 and 1987 during the day.

| **Forest plot** | **No of years** | ***Microcebus* spp.** | ***Cheirogaleus medius*** | ***Mirza coquereli*** | ***Phaner furcifer*** | ***Lepilemur ruficaudatus*** | ***Eulemur fulvus*** | ***Propithecus verreauxi*** |
|---|---|---|---|---|---|---|---|---|
| CN2 | 3 | 3.5±0.7 | 3.8±0.4 | 0.1±0.1 | 0.6±0.2 | 2.6±0.5 | 0.2±0.2 | 0.3±0.2 |
| CN5 | 4 | 0.2±0.1 | 3.5±0.7 | 0.2±0.0 | 0.4±0.2 | 2.7±0.3 | 0.3±0.1 | 0.4±0.2 |
| CN6 | 4 | 0.5±0.2 | 5.1±0.7 | 0.3±0.1 | 1.1±0.4 | 6.8±0.8 | 0.7±0.3 | 2.0±0.3 |
| CS5 | 3 | 0.2±0.1 | 3.7±1.2 | 0.4±0.1 | 0.8±0.1 | 2.9±0.4 | 2.1±1.2 | 2.2±0.9 |
| CS7 | 4 | 3.0±0.5 | 1.7±0.4 | 0.1±0.1 | 1.1±0.2 | 2.1±0.2 | 1.7±0.6 | 1.0±0.2 |
| CS8 | 1 | 5.0 | 0.3 | 0.0 | 0.6 | 0.3 | 0.0 | 0.0 |
| N5 | 3 | 0.1±0.1 | 3.6±1.1 | 0.1±0.1 | 0.8±0.3 | 3.2±1.0 | 1.2±0.3 | 0.9±0.5 |
| N6 | 1 | 0.5 | 3.6 | 0.0 | 1.1 | 8.1 | 3.8 | 1.7 |
| CN9 | 1 | 0.3 | | 0.6 | 0.1 | 1.4 | 0.4 | 2.6 |
| LS11 | 1 | 0.7 | | 0.2 | 0.7 | 5.0 | 1.2 | 1.9 |
| CN1 | | | | | | | 0.3 | 0.4 |
| CS3 | | | | | | | 1.4 | 0.9 |
| CS4 | | | | | | | 5.8 | 1.8 |
| LN4 | | | | | | | 2.8 | 2.6 |
| Mean detection distance | | 4.1 m | 6.0 m | 8.6 m | 7.2 m | 9.0 m | 17.7 m | 17.0 m |

Table 3: Food trees of lemurs in the Kirindy Forest during the wet and during the dry season. Items listed as wet season food were eaten between November and April. Items listed as dry season food were consumed between May and October. yL = young leaves, mL = mature leaves, L = leaves of unknown age, Fl = flowers, uFr = unripe fruit, Fr = ripe fruit, S = seeds, gum = tree exudates and gum; data from ROHNER (1988) and ROHNER and SORG, 1986, 1987) included. Too few vegetable food items are known for *Microcebus* spp.and *Mirza coquereli* to include these species in the present table. Plant taxonomy follows MABBERLY (1990).

| **Tree species** | ***Cheirogaleus medius*** | | ***Phaner furcifer*** | | ***Lepilemur ruficaudatus*** | | ***Eulemur fulvus*** | | ***Propithecus verreauxi*** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Wet season** | **Dry season** | **Wet season** | **Dry season** | **Wet season** | **Dry season** | **Wet season** | **Dry season** | **Wet season** | **Dry season** |
| **Anacardiaceae** | | | | | | | | | | |
| *Operculicarya gummifera* | Fr | | Gum | Gum | | | Fr | | Fr | |
| *Poupartia caffra* | | | | | | | | | | Fl, yL |
| *Poupartia silvatica* | Fr | | Gum | Gum | | | Fr | | Fr | Fl |
| *Poupartia* sp. | | | Gum | Gum | | | | | | |
| **Bignoniaceae** | | | | | | | | | | |
| *Fernandoa grevei* | | | | | L | L,Fl | | | | |
| *Phyllarthron bernierianum* | | | | | L | | Fr | | | |
| *Phylloctenium decaryanum* | Fr | | | | Fr, L | | | | | |
| *Stereospermum euphorioides* | | | | | Fr | | | | | |
| **Bombacaceae** | | | | | | | | | | |
| *Adansonia rubrostipa* | Fl | | Fl, Gum | Gum | Fl | uFr | Fl | uFr | Fl | uFr |
| *Adansonia za* | Fl, Gum | | Fl | Fl | Fl | Fl | Fl | Fr | Fl | Fl, Fr |
| **Burseraceae** | | | | | | | | | | |
| *Commiphora guillaumini* | | | Gum | Gum | | | | | Seed | Fl |
| *Commiphora mafaidoa* | | | | | | | | | | Fl |
| *Commiphora stellulata* | | | Gum | Gum | | | | | | |
| **Buxaceaea** | | | | | | | | | | |
| *Buxus madagascariensis* | | | | | Fr | | | | Fr | |
| **Celastraceae** | | | | | | | | | | |
| Astrocassine pleurostyloides | Fl, Fr | | Fl | | Fr, L | | | | Fr | |
| **Combretaceae** | | | | | | | | | | |
| *Terminalia ruffovestita* | | | | | L | | | | | |
| *Terminalia stellulata* | | | Gum | Gum | | | | | | |

| Tree species | *Cheirogaleus medius* | | *Phaner furcifer* | | *Lepilemur ruficaudatus* | | *Eulemur fulvus* | | *Propithecus verreauxi* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season |
| *Terminalia tricristata* | | | Gum | Gum | Fr, L | | | | Fl | |
| *Terminalia* sp. | | | Gum | Gum | Fr, S | L | Fr | | Fr | |
| **Ebenaceae** | | | | | | | | | | |
| *Diospyros aculeata* | Fr | | | | | | | | | |
| *Diospyros intricata* | | | | | | | | | | L |
| *Diospyros perrieri* | | | | | | | Fr | | Fr | |
| *Diospyros* sp. | | | | | Fr | L | | | L | L |
| **Erythroxylaceae** | | | | | | | | | | |
| *Erythroxylum platicladum* | Fr | | | | | | | | | |
| **Euphorbiaceae** | | | | | | | | | | |
| *Bridelia pervilleana* | | | | | Fr | | | | | |
| *Givotia madagascariensis* | | | | | | yL | Fr | yL | Fr | Fl, yL |
| *Phyllanthus decaryanus* | | | | | L | | | | | |
| *Phyllanthus* sp. | | | | | Fr | | | | | |
| **Lecthidaceae** | | | | | | | | | | |
| *Foetidia asymmetrica* | | | | | L | | | | L | L |
| **Leguminosae** | | | | | | | | | | |
| *Albizia boivini* | | | | | | | | | | L |
| *Albizia greveana* | | | | | | | | | Fl, yL | |
| *Albizia jaubertiana* | | | | | | | | | Fl, L | |
| *Albizia polyphylla* | | | | | | | | | | yL, L, Fl |
| *Albizia* sp. | | | | | L | | | | | Fl, yL, L |
| *Baudouinia fluggeiformis* | Fl | | | | Fr, L | L | | | L | L |
| *Colvillea racemosa* | | | Gum | Gum | Fl, L | Bark, L | | | Fl, L | Bark |
| *Cordyla madagascariensis* | | | | | | | uFr | Fr | uFr, L | Fl, yL, Fr |
| *Dalbergia greveana* | | | | | | | | | | L |
| *Dalbergia* sp. | | | | | uFr, L | L | | | L | L |
| *Dichrostachys* sp. | | | | | L | | | | | |
| *Tamarindus indica* | | | | | L | | | Fr | | Fr |

| Tree species | *Cheirogaleus medius* | | *Phaner furcifer* | | *Lepilemur ruficaudatus* | | *Eulemur fulvus* | | *Propithecus verreauxi* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season |
| *Delonix floribunda* | Fl | | | | | | | | | |
| **Loganiaceae** | | | | | | | | | | |
| *Strychnos decussata* | Fr | | | | Fr, L | L | Fr | | | |
| *Strychnos madagascariensis* | | | | | | | Fr | | Fr | |
| *Strychnos vacacoua* | | | | | | L | Fr | | Fr | |
| *Strychnos* sp. | | | | | | | | | Fr | |
| **Lythraceae** | | | | | | | | | | |
| *Capuronia madagascariensis* | Fr | | | | | | Fr | | Fr | |
| **Moraceae** | | | | | | | | | | |
| *Broussonetia greveana* | | | | | | | Fr | | Fr | |
| *Ficus* sp. | | | | | | | Fr | Fr | Fr | Fr |
| **Ochnaceae** | | | | | | | | | | |
| *Diporidium* sp. | Fr | | | | | | | yL | | |
| **Oleacea** | | | | | | | | | | |
| *Noronhia* sp. | | | | | L | | | | | |
| **Ptaeroxylaceae** | | | | | | | | | | |
| *Cedrelopsis grevei* | | | | | | | | | L | Fl |
| *Cedrelopsis* sp. | | | | | | L | | | L | |
| **Rhamnaceae** | | | | | | | | | | |
| *Berchemia discolor* | Fr | | | | Fr | | Fr | | Fr | |
| *Colubrina decipiens* | Fr | | | | Fr | | Fr | | Fl, Fr, L | yL |
| *Ziziphus mauritania* | | | | | | | | Fr | | Fr, L |
| **Rubiaceae** | | | | | | | | | | |
| *Breonia perrieri* | Fr | | | | Fr | | Fr | | Fr | |
| *Canthium* sp. | | | | | Fl, Fr, L | | | | L | |
| *Rothmannia tropophylla* | | | | | Fr | L | Fr | | | L |
| *Carphalea* sp. | | | Gum | Gum | | | | | | |
| **Rutaceae** | | | | | | | | | | |
| *Chloroxylon falcatum* | | | | | | | | | Fr | |

| Tree species | *Cheirogaleus medius* | | *Phaner furcifer* | | *Lepilemur ruficaudatus* | | *Eulemur fulvus* | | *Propithecus verreauxi* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season | Wet season | Dry season |
| **Sapindaceae** | | | | | | | | | | |
| *Camptolepis hygrophylla* | | | | | | | Fr | | Fr | |
| *Macphersonia gracilis* | | | | | L | | Fl | | | |
| **Sapotaceae** | | | | | | | | | | |
| *Capurodendron rubrocostatum* | | | | | | | Fr | | Fr | |
| *Capurodendron cf perrieri* | | | | | | | | | Fr | |
| **Tiliaceae** | | | | | | | | | | |
| *Grewia cyclea* | Fr | | | | | | Fr | Fr | Fr | Fr |
| *Grewia* sp. | Fl, Fr | | | | Fl, Fr, L | Fr, L | Fr | Fr | | Fr |
| **Verbenaceae** | | | | | | | | | | |
| *Clerodendrum* sp. | | | | | | | Fr | | Fr | |
| FROFKY | | | | | | yL | | | | |
| KARIMBOLA | | | | | | | Fr | yL | | |
| LENGO (Liana) | | | | | | | | | | L |
| MABIBOLANALA | | | | | | | | Fr | | Fr |
| VAPINDY (Liana) | | | | | | L | | | | |
| VOHEA | | | | | | | | | | Fr |
| VOAFOGNA | | | | | | | | | | L |

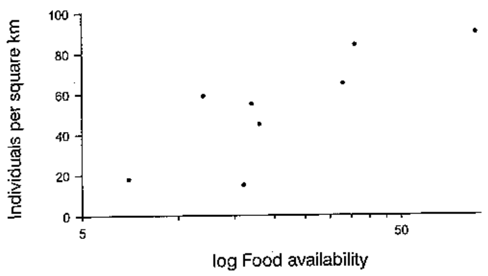

Fig. 3: Correlation between the abundance of *Phaner furcifer* and potential food trees used for gum feeding (photo by I. Herbinger).

### 3.2 Potential competition between lemur species

Among the different forest plots, there is a negative correlation between the abundance of *Microcebus* spp. and *C. medius* (Pearson's correlation: $r = 0.76$, $P < 0.05$, $n = 8$; Table 2). This might be a consequence of different habitat requirements of the species or could be a result of interspecific competition over limited resources. Aggressive encounters have been observed between *C. medius* and *M. coquereli* (*C. medius* won), but not as yet between *C. medius* and *Microcebus* spp..

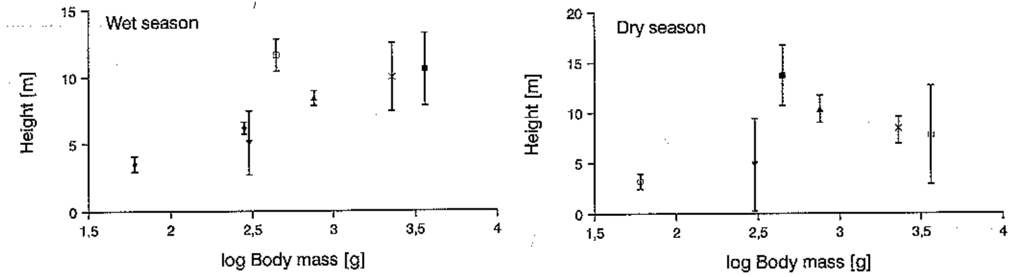

Fig. 4: Height at which the different lemur species can be found in the forest during the wet and dry seasons. Values are means ± 95 % confidence intervals. Different symbols mark different lemur species.

The different lemur species are active at different times of the day and forage at different heights in the forest. At least for the nocturnal species, these differences have been interpreted as the result of interspecific competition over limited resources (HLADIK et al., 1980). While the temporal aspect of niche differentiation might apply for feeding on insects, it is not applicable to resources such as fruit or leaves which cannot be renewed quickly. Once ripe fruits have been eaten from a scrub or tree at the beginning of the night, there simply will not be any more fruit left to eat later that night. Here, vertical separation of species might help to ameliorate potential competition (Fig. 4). In general, smaller lemur species forage more in the understory than the larger species. During the wet season, this results in significant differences in feeding height between species of the lemur community (ANOVA: $F=29.73$, $P < 0.001$, $R^2 = 0.22$). During the dry season, when food abundance is reduced and competition between species should be more intense, the separation of species by feeding height increases ($F = 14.01$, $P < 0.001$, $R^2 = 0.40$). *C.medius* has been omitted from the analysis of the wet season to allow better comparability between the wet and the dry season. The increased species separation based on feeding height during the time of food shortage is consistent with the idea that foraging at different height helps to reduce interspecific competition.

Among the more folivorous species (*L. ruficaudatus* and *P. verreauxi*), different discrimination against secondary plant chemicals, such as alkaloids and cyanogenic substances may also contribute to effective niche separation. *L. ruficaudatus* tolerates a fair number of food items containing alkaloids while *P. verreauxi* avoids most of these leaves (Fig. 5). These interspecific differences are obvious when these lemurs feed on leaves (differences with $P < 0.05$ are marked in Fig. 5), but they are not apparent with respect to fruit selection.

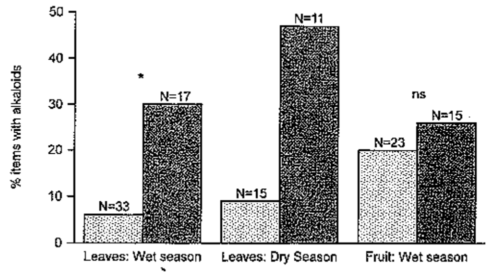

Fig. 5: Occurence of leaves and fruit with alkaloids in the diet of *Lepilemur ruficaudatus* (right) and *Propithecus verreauxi* (left) during the wet and dry seasons. N is the total number of food items analyzed (methods for chemical analyses as listed in GANZHORN, 1988); photo of *L. ruficaudatus* by JUG.

## 3.3 Some roles of lemurs in the dry forest ecosystem

### 3.3.1 Pollination

While several lemur species of the Malagasy rain forest, such as *Eulemur rubriventer*, *Varecia variegata*, or *Cheirogaleus major* have been found to pollinate plants (OVERDORFF, 1992; NILSSON et al., 1993; KRESS et al., 1994), evidence for the dry forests is still limited. SUSSMAN and TATTERSALL (1976) reported intensive nectar-feeding by *Eulemur mongoz* at Ampijoroa, which may have resulted in some pollination.

In the Kirindy Forest, BAUM's all-night observations of baobab flowers are the best documentation of potential pollination by lemurs, showing pollination of *Adansonia za* and *A. rubrostipa* by *P. furcifer* and *C. medius* (BAUM 1995a, 1996). While these two species might have contributed to pollination, the majority of flower visits especially by other lemur species is highly destructive. Thus, despite some occasional events of pollination by lemurs, the bulk of pollination in the dry deciduous forest seems to be carried out by butterflies and moths (WASSERTHAL, 1993; WALTHER, 1994).

### 3.3.2 Seed dispersal

Several lemur species may play a prominent role in seed dispersal, as Madagascar has comparatively few frugivorous birds that can disperse seeds (LANGRAND, 1990; BÖHNING-GAESE et al., 1995; GOODMAN and GANZHORN, submitted). In the Kirindy Forest, *E. fulvus* is known to disperse seeds of a fair number of tree species such as *Poupartia* spp., *Berchemia discolor*, *Terminalia* spp., *Ficus* spp., or *Tamarindus indica*, and can be assumed to disperse seeds of most of the fruits that they eat. In contrast, *P. verreauxi* normally destroys seeds when feeding on fruits (O'CONNOR et al., 1988; SCHARFE, 1991; SCHARFE and SCHLUND, 1996; RALISOAMALALA, 1996; DEW and WRIGHT, submitted; GOODMAN et al., in press; GANZHORN, unpubl.). *Microcebus* spp. and *C. medius* disperse many small-sized seeds. The behavior of *C. medius* is unique in this respect. This species spreads the seeds of mistletoes (e.g., *Viscum* sp.) during the end of the wet season by smearing its feces onto branches. This is quite unlike other primates which drop their feces on to the forest floor. In this manner, *C. medius* fills the role played by birds in other regions of the world (STILES, 1993).

Fig. 6: Red-fronted lemur (*Eulemur fulvus rufus*; left) and Verreauxi's Sifaka (*Propithecus v. verreauxi*; right); photos by S. SOMMER and JUG.

### 3.4 Predators and Prey

Apart from the relatively frequent observations of *M. coquereli* preying on vertebrates, the role of vertebrate prey in the diet of lemurs is poorly documented and probably rather low. In contrast, predators seem to have a major impact on lemur populations. Small species, such as *Microcebus* spp. are heavily preyed upon by owls (*Asio madagascariensis*), whereas large species, such as *P. verreauxi*, may lose almost one third of the number of animals born into the population each year through predation by *Cryptoprocta ferox* (GOODMAN et al., 1993; RASOLONANDRASANA, 1994; RASOLOARISON et al., 1995; Fig. 7).

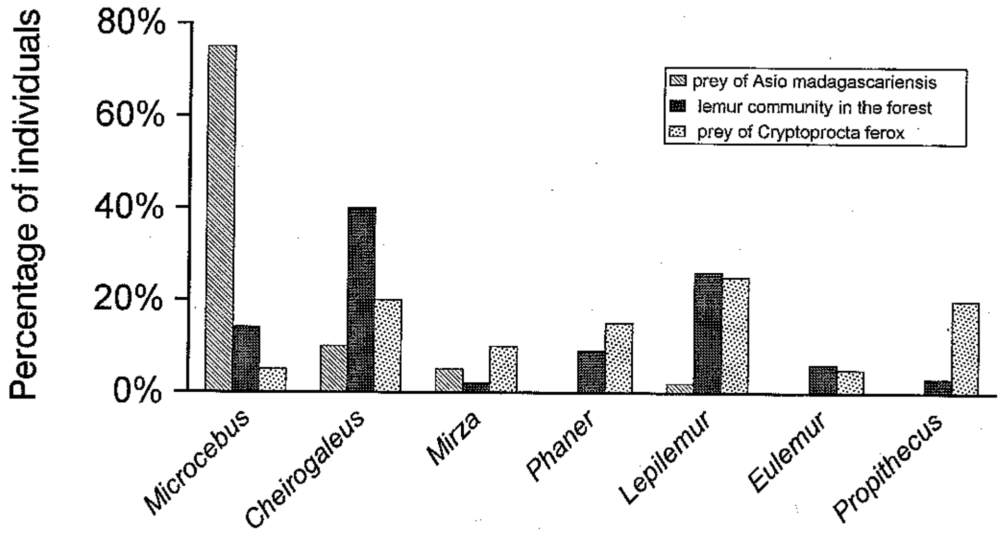

Fig. 7: Relative density of lemur species in the Kirindy Forest and their relative occurence in feces of *Cryptoprocta ferox* and in pellets of *Asio madagascariensis* during the dry season (data from RASOLOARISON et al., 1995).

## 4. Effects of logging on lemurs

Selective logging of the extent practiced by the CFPF did not have a major impact on the different lemur populations. There were, however, a few subtle effects which illustrate some basic factors influencing the abundance of lemurs. These processes have been described in detail elsewhere (GANZHORN, 1995b) and are only summarized here.

Semi-mechanized logging reduces forest cover by less than 10 % (DELEPORTE et al., 1996). The remaining trees receive more sunlight and compensate some of the loss of leaf biomass by increased growth and leaf production. Though the loss of leaf biomass is not compensated for completely, leaves which grow in the sun contain higher protein and sugar concentrations than leaves growing in the shade, and thus are of better nutritional quality than leaves from the shade. Also, trees and scrubs growing along logging trails and around treefall gaps show an increase in their fruit production (GANZHORN, 1995b; Fig. 8).

At low intensity logging, these reactions of potential food trees seemed actually to favour lemur populations. Sightings of all lemur species increased after logging compared to the pre-logging state. However, lemur populations started declining after logging was only slightly intensified. In some parts of forest plot N6, where the forest had been thinned more than in N5, especially the larger lemur species declined while higher numbers of the small species were encountered during transect walks (GANZHORN, 1994; 1995b; Fig. 9).

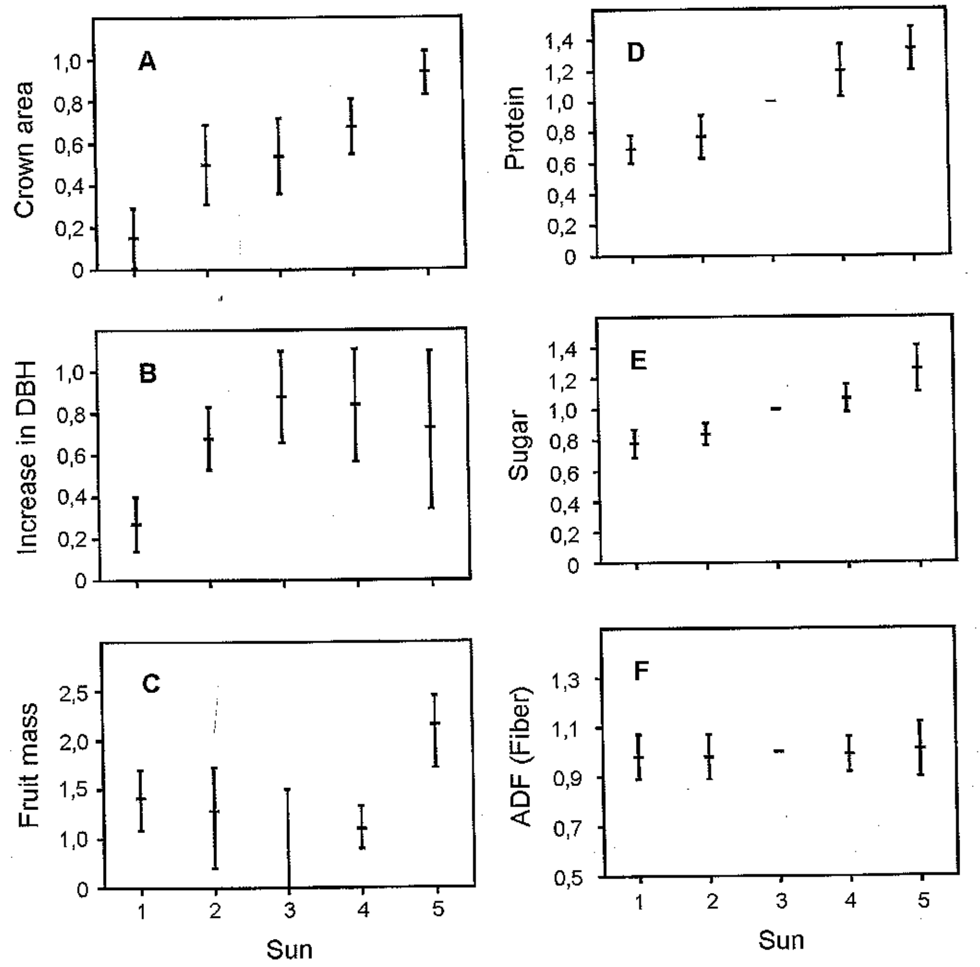

Fig. 8: Effects of solar exposure (1 = shade; 5 = sun) of tree crowns on leaf production (measured as crown extension); tree growth (measured as the increase in DBH); fruit production of *Astrocassine pleurostyloides*; relative protein, sugar, and fiber concentrations in leaves experiencing different solar exposures, growing on the same tree. The concentrations of the various chemicals were standardized to the concentration found at solar exposure level "3" (from GANZHORN, 1995b).

The reasons for the decline of some lemur species at higher logging intensities are not well understood. For some species, such as *Lepilemur* with their rather specialized locomotion of vertical clinging and leaping, the lack of stuctural support in a forest with many gaps might contribute to the decline (GANZHORN, 1993). Others, such as *P. furcifer*, who show a strong association with large-sized trees producing gum (Fig. 3), might simply suffer from the reduction of the number of their food trees. Despite this, no lemur species completely disappeared from the area of higher logging intensity.

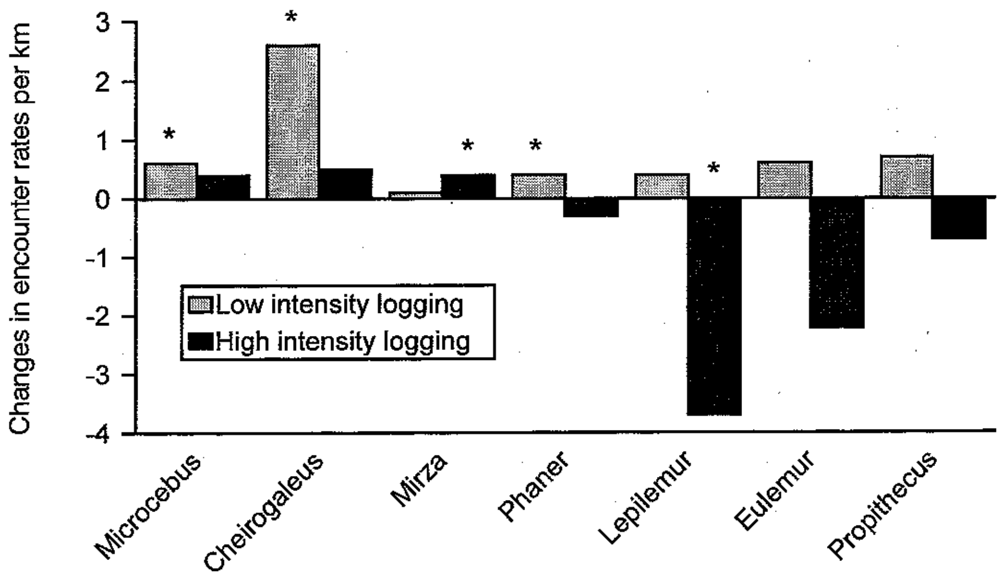

Fig. 9: Changes in lemur encounter rates after low and high intensity logging. Asterisks mark differences with $P < 0.05$ (from GANZHORN, 1994, 1995b). The pre-logging encounter rates are presented by the 0-line.

Thus, lemurs as well as many other primate species, seem to be able to tolerate some forms of logging (JOHNS and SKORUPA, 1987; GANZHORN, 1994, 1995b; FIMBEL, 1994; PLUMPTRE and REYNOLDS, 1994; GRIESER JOHNS and GRIESER JOHNS, 1995; FAIRGRIEVE, submitted). From the point of view of sustainable development, this result is encouraging. However, it should be kept in mind that minor changes in logging practices might change the reaction of the lemurs. Also it is well possible that all the species which are more sensitive to human impact have already become extinct and the only ones left are the disturbance-tolerant species.

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# ACTIVITY PATTERNS AND HOME RANGE USE OF TWO GROUPS OF *PROPITHECUS V. VERREAUXI* IN THE KIRINDY FOREST

V. CARRAI and A. LUNARDINI

**Résumé: Activités et habitata de deux groupes de *Propithecus v. verreauxi* dans la forêt de Kirindy.**

Cet article présente le premier compterendu sur les activités diurnes et le territoire exploité par *Propithecus v. verreauxi* (Sifaka) dans la forêt dense sèche de Kirindy dans l'ouest de Madagascar. Deux groupes de Sifaka ont été suivis pendant 416 heures à partir du débutet jusqu'à la moitié de la saison sèche (avril à août) en utilisant la méthode "focal animal sampling". Les données relatives à l'alimentation et à l'étendue du territoire ont été explotées. Les résultats obtenus montrent que le comportement des Sifakas de Kirindy présente des analogies plus marquées avec des Sifakas qui vivent dans une forêt mixte (sempervirente-décidue) du nord de l'île (Ampijoroa) plutôt qu'avec ceux vivant dans une forêt épineuse du sud de Madagascar (Hazafotsy). Toutefois, certaines caractéristiques du rapport avec le territoire semblent être plutôt liées aux variations saisonnières de la disponibilité des aliments.

## Abstract

This article presents the first account of the activity and ranging patterns of *Propithecus v. verreauxi* (Sifaka) in a dry deciduous forest of Western Madagascar (Kirindy, near Morondava). Two groups of Sifakas were observed for a total of 416 h during part of the 1995 dry season by focal animal sampling. Data on daily feeding and resting patterns, as well as on home range size and use were collected. The results showed that the behaviour of Sifakas in the Kirindy Forest was more similar to that found in *P. v. coquereli* in a northern mixed deciduous-evergreen forest (Ampijoroa) than to the one observed in *P. v. verreauxi* in a southern spiny forest [Hazafotsy; RICHARD (1978)]. This suggests that behavioural variation of *Propithecus verreauxi* reflects environmental constraints more than genetic differences on the subspecies level.

## 1. Introduction

The ecology and behaviour of *Propithecus verreauxi* have been extensively studied in different locations in Madagascar. RICHARD's work (1974, 1977, 1978,) contains detailed information on the habits of *Propithecus v. coquereli* in the forestry reserve at Ampijoroa (Northwestern Madagascar) and of *Propithecus v. verreauxi* near Hazafotsy, in the Réserve Nationale No. 11 (Southeastern Madagascar). Other surveys have been carried out on demography, group composition, social organization, and ranging behaviour of *Propithecus v. verrauxi* in the south of the island: at Berenty (JOLLY, 1966, 1972; RICHARD, 1978; JOLLY et al., 1982; SAITO, 1994), at Evasy and Ejeda (RICHARD, 1978), and at Beza Mahafaly (RICHARD, 1992; RICHARD et al., 1991). A census of the population of the same subspecies was also made at Antserananomby in western Madagascar (RICHARD, 1978). These studies showed a marked behavioural variation which could depend on ecological factors such as