Cathemerality in the Mongoose Lemur, *Eulemur mongoz*

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Results of a 10 month study of the mongoose lemur (*Eulemur mongoz*) at Anjamena are presented. The activity pattern is documented in detail for both wet and dry seasons based on observations conducted over the entire 24 h period. *E. mongoz* was found to be cathemeral throughout the year but exhibited shifts towards more diurnal activity in the wet season and more nocturnal activity in the dry season. The cathemeral activity pattern in the mongoose lemur appears to be coordinated with sunrise, sunset, and day length and modulated by an inhibitory effect of low nocturnal light intensity in the forest during the wet season, resulting in mainly diurnal activity. Temperature and rainfall may also influence the activity pattern. Few advantages to food-related behavior appear to derive from this activity pattern, although resource accessibility may be enhanced by nocturnal behavior in the dry season, leading to reduction in interspecific competition. Cathemerality may also represent a behavioral thermoregulatory mechanism allowing the mongoose lemur to conserve energy by being active during the cool nights of the dry season. In addition, nocturnal behavior in the dry season probably allows avoidance of predation by raptors at the time of year when least protection is afforded by vegetation. Am. J. Primatol. 47:279–298, 1999.   © 1999 Wiley-Liss, Inc.

INTRODUCTION

Over the past few decades, it has become clear that activity patterns in the Malagasy lemurs can no longer be classified simply as diurnal or nocturnal, as several species exhibit both diurnal and nocturnal behavior [Tattersall, 1982, 1987; Richard & Dewar, 1991; van Schaik & Kappeler, 1993]. The need for a third term to describe activity patterns is further supported by evidence that some haplorhine primates are active both during the day and at night. Rare occasions of nocturnal activity have been reported in the usually diurnal howler

monkey (*Alouatta*) in Belize [Dahl & Hemingway, 1988] and in French Guyana [P. Kessler, personal communication] as well as in the generally diurnal lion-tailed macaque (*Macaca silenus*) in captivity [Harvey et al., 1994]. Diurnal activity has been reported for the usually nocturnal owl monkey (*Aotus trivirgatus*) in Paraguay [Wright, 1989, 1983].

The term *crepuscular* was initially introduced to describe the activity cycles of lemurs that could not be described as clearly diurnal or nocturnal [Petter, 1962; Albignac, 1981]. This term is still in use, although it has never been clearly defined and is confusing because many animals (insects, reptiles, birds, mammals) as well as plants exhibit peaks of activity at dawn and dusk [Aschoff, 1966; Hamner & Hoshizaki, 1974]. The term now generally employed to describe exploitation of both nocturnal and diurnal phases in lemurs is *cathemeral* (i.e., a pattern in which activity is distributed approximately evenly throughout the 24 h period or a pattern in which significant amounts of activity occur during both the light and dark phases of the 24 h cycle) [Tattersall, 1987].

The lemurs of Madagascar exhibit three different activity patterns: 1) Cheirogaleidae, *Lepilemur, Daubentonia,* and *Avahi* are nocturnal; 2) *Indri, Propithecus, Lemur,* and *Varecia* are almost exclusively diurnal; 3) *Eulemur* and *Hapalemur* are probably cathemeral [Tattersall, 1982, 1987; Richard & Dewar, 1991; van Schaik & Kappeler, 1993; van Schaik & Kappeler, 1996; this study]. The large-bodied subfossil lemurs were probably diurnal [Martin, 1972, 1990; Godfrey, 1988].

The mongoose lemur (*Eulemur mongoz;* Lemuridae) is restricted to the humid, seasonal forests of northwest Madagascar and the Comoro Islands (Anjouan and Mohéli) (Fig. 1). Its diet has been described as highly nectarivorous during the dry season and frugivorous/folivorous during the wet season [Sussman & Tattersall, 1976; Andriatsarafara, 1988]. It is unusual in that it has been reported to show a variable social structure, although in most cases monogamy, and to be variably nocturnal or diurnal. *E. mongoz* has been described as diurnal during the wet season and nocturnal during the dry season in Madagascar [Tattersall & Sussman, 1975; Sussman & Tattersall, 1976; Tattersall, 1978; Harrington, 1978; Andriatsarafara, 1988]. The same seasonal activity pattern was described in Mohéli and the Anjouan lowlands, whereas in the Anjouan highlands the mongoose lemur was found to be exclusively diurnal [Tattersall, 1976; unpublished report on the University of Bristol Comores '92 expedition]. There is no information from captivity that could clarify the issue of activity patterns in the mongoose lemur, as no studies have as yet been conducted over the 24 h period.

Three main hypotheses have been proposed to explain the cathemeral activity pattern in certain lemurs. 1) Cathemerality represents a transitional stage between nocturnality and diurnality, made possible by partial vacation of the diurnal phase of the 24 h cycle through the recent extinction of various large-bodied lemurs [Martin, 1972; Tattersall, 1982]. This hypothesis has been extended by van Schaik and Kappeler [1996], who suggest that the recent extinction of large diurnal raptors [Goodman, 1994] led to diurnal and cathemeral activity in the larger extant lemurs. 2) Cathemerality is a stable evolutionary strategy, possibly representing the ancestral activity pattern for the genus *Eulemur* [Tattersall, 1982]. 3) Cathemerality is a response to seasonality and diet. During periods of fruit scarcity, lemurs may shift their diet to include more leaf matter, thereby increasing the fiber intake. It is suggested that by extending activity across the 24 h cycle, interspersed with short rest periods rather than one long rest period, these small-bodied animals with simple digestive systems are more able to cope with a fibrous diet [Engqvist & Richard, 1991]. The first two of these hypotheses
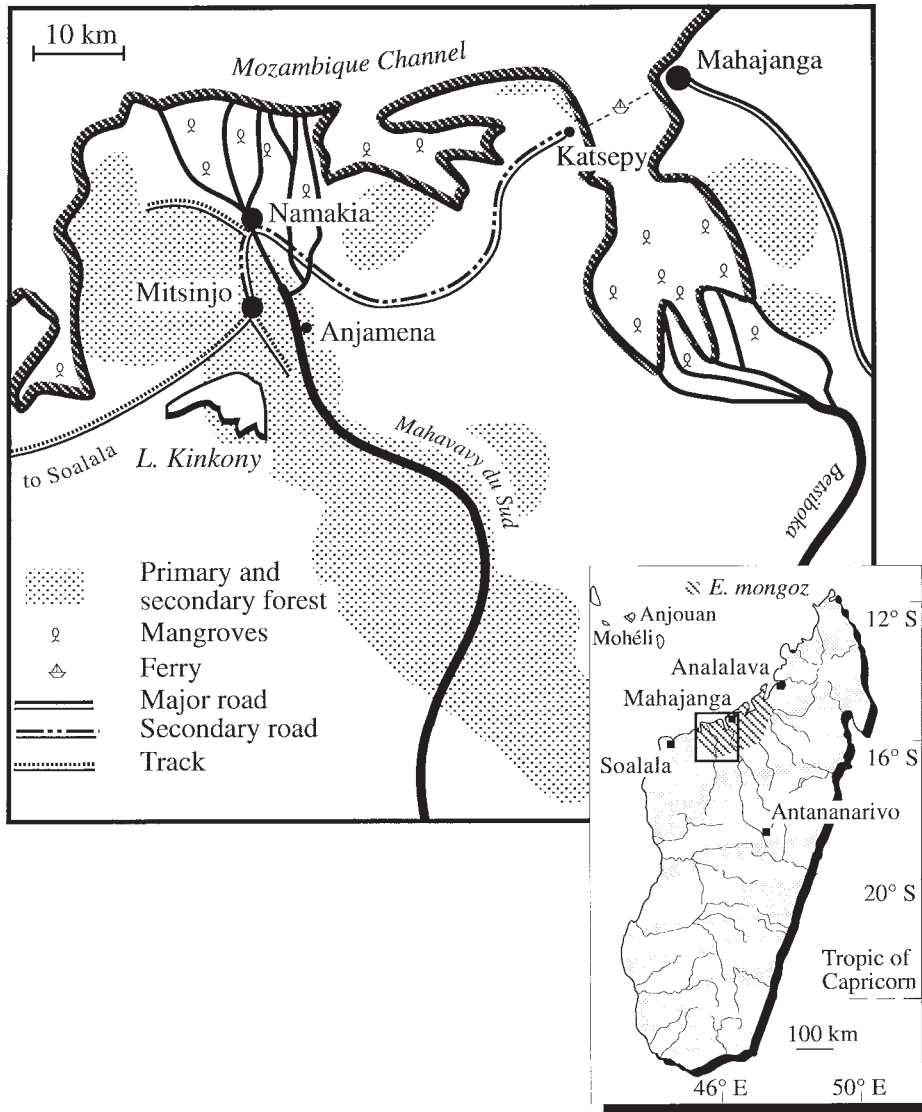
Fig. 1. Distribution of *Eulemur mongoz* (map) and location of field study site (enlarged section). Adapted from anonymous [1986], Nicoll and Langrand [1989], and Tattersall [1982].

are historical or evolutionary explanations and therefore difficult to test. At best, it was possible that the present study might contribute further information supporting or opposing one of the two. The third hypothesis is more ecologically based and therefore easier to test using information collected during a field study.

During a 10 month study carried out by the first two authors at Anjamena (45°55′E; 16°03′S) in the riverine forests of the Mahavavy, data were collected on the behavior and ecology of two neighboring groups of *E. mongoz* [Curtis, 1997]. Prior to this study, no long-term fieldwork had been conducted with mongoose lemurs. The present study is also the first to be carried out throughout the entire diurnal and nocturnal active phases of a *Eulemur* species in an attempt to

provide a more accurate description of cathemerality and to compare behavior and activity budgets during the two phases of the light–dark cycle. A detailed investigation of the activity pattern was carried out in the attempt to assess 1) the proximate role of environmental cues (Zeitgeber) in the activity pattern, 2) the functional relevance of cathemerality, and 3) seasonal shifts in the activity cycle. To this end, the following factors were investigated: climatological cues, the temporal distribution of food resources, diet and digestibility of food, thermoregulation, interspecific competition, and predation.

METHODS

Following a 3 month pilot study conducted from March–June 1994, the main field study at Anjamena was carried out from September 1994 to September 1995 on two neighboring groups of *E. mongoz*. Due to the proximity of the site to the river Mahavavy (Fig. 1) and consequent flooding, it was virtually impossible to work there during the peak wet season in January and February 1995.

Climate, Phenology, and Luminance

The abiotic environment was assessed by measuring maximum and minimum daily temperatures and total rainfall once a day, usually at the camp in Anjamena. During January and February, all data were collected at Mitsinjo (Fig. 1) by O.D. Rabetsimialona. Mean daily temperature was calculated by averaging minimum and maximum values. In addition, a qualitative description of cloud cover and wind was recorded. The categories used were *sunny* (<50% of sky overcast) or *cloudy* (>50% of sky overcast) and *windy* or *no wind* [Richard, 1978].

Temporal variation in potential food resources was assessed by phenological data collected on a monthly basis, recording the presence of immature and mature leaves, fruit, and flowers [Richard, 1978] on 19 species of trees and lianas in the home ranges of both study groups [Curtis, 1997]. The sample size for each plant species ($1 \leq n \leq 10$) was dependent on its density within the territory. During January and February, these data were collected by A. Blaise whenever the water level and weather conditions permitted access to the study site.

Seasonal light availability in the forest during daylight hours was assessed by measuring luminance both in the forest and in the open on sunny days in April (wet season) and in September (dry season) using a digital luxmeter (RD-1330; Roline, Taiwan) with a gelatine grey filter ($\times 10$) (Kodak, Stuttgart, Germany). Percentage transmittance (T) in the habitat was then calculated using the mean value for relative luminance (R_I) measured in ten randomly selected quadrats, where R_I = luminance at ground level in a given quadrat (l_d)/luminance in the open (l_o) and $T = 100 \times R_I$ [Brower et al., 1990]. Sunrise and sunset were recorded each day using a palmtop computer (Psion Series 3, London, England), which gives the times (± 2 min) based on the user-entered latitude and longitude of Anjamena ($45°55'E$; $16°03'S$).

A nocturnal illumination index, I, was calculated using an ad hoc Turbo C, v5.0, program (implemented by R.M. Thomas), which produced values of I normalized to the yearly maximum, I_{max}. This index was calculated for the 24 h period, as the moon sometimes rises and/or sets during daylight hours. The increment, dt, used in the integration was set at 0.01 day (dt = 0.24 h). The times for sunrise (SR), sunset (SS), moonrise (MR), and moonset (MS) and the phase of the moon (P) were calculated using Stephen L. Moshier's Ephemeris program, v5.1 [Moshier, 1991]. The following equation was used:

$$I = \int_a^b P \, dt$$

where:

$a < b$ [$dt = 0.24$ h]

MS after SS, a = SS; MR after SS, a = MR; MS before SR, b = MS;

MS before SR, b = SR

new moon, $P = 0$; and full moon, $P = 1$.

The nocturnal illumination index is based on the assumption that nights are clear. Therefore, an index for cloud cover (C) was introduced, using data collected for the 2 days either side of observation nights (both days cloudy: C = 0.75; both days cloudy and windy: C = 0.5; 1 day cloudy, 1 day sunny: C = 0.25; both days sunny: C = 0.00). The nocturnal illumination index was then transformed (I_C) to account for cloud cover: $I_C = I * (1 - C)$.

Observations

One to two observations per month were carried out on each of two neighboring groups of mongoose lemurs (group 1 and group 4) throughout the entire active period. To ensure that all daytime and nighttime activity was observed, we split each observation into a morning session and an afternoon and/or night session. The duration of these sessions was entirely dependent on the duration of the mongoose lemurs' activity and varied between 59 min and 11 h 55 min. The number of days separating the two sessions in each observation ranged from 0–9 (mean 3.3 days; n = 26). During the 10 month study, 26 complete activity periods were covered, divided between group 1 (n = 14) and group 4 (n = 12). Six of these were during the wet season (December–April) and 20 during the dry season (May–November). The number of days separating any two observations in a given month ranged from 1–8 (mean 4.5 days; n = 16). One-minute point sampling was used, and only one focal animal was observed throughout an observation session [Altmann, 1974]. A session began when the focal animal left a sleeping tree and ended when the focal animal entered a sleeping tree and no movement was seen or heard for 30 min. A total of 256 h 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].

The information relevant to the investigation of the activity cycle was observation time spent resting and time spent active—that is, the monthly and daily distribution of diurnal and nocturnal activity throughout the entire study period. Nocturnal activity was defined as activity taking place between sunset and sunrise, with diurnal activity covering the rest of the day. Data collected during observations were lumped into two main categories: resting (eyes half closed and/or animal curled up) and active (comprising all activities when the animal was fully alert). When the animal was not visible to the observer, data points were included in the two categories (active or resting) according to whether the animal could be heard to be active or not. Reliance on hearing the animals if they were not visible at night should not have created any sampling bias, as even when the mongoose lemurs were feeding quietly this was indicated by debris falling to the ground. Additional data points for the end of the nighttime rest period (n = 2) and for the beginning (n = 108) and end (n = 142) of the daytime rest period were collected predominantly on group 1, as many of its sleeping trees were located near the camp.

A further 73 h of observation were carried out on food-related behavior in the two study groups during daylight hours (n = 3–5 observations/month, 5–11 h/month). A group was followed and observations made only during food-related behavior. Absolute counts were made of all food items consumed by a focal animal [Curtis, 1997].

Although the use of radio-tracking equipment (Telonics, Mesa, Arizona; Holohil Systems Ltd., Carp, Ontario, Canada) was originally planned, this was delayed until the last 4 months of the study, as the recommended dosage of anesthetic agent (Ketasol; Gräub AG, Beru, Switzerland) proved to be insufficient for *E. mongoz* [Thalmann & Mutschler, personal communication] (15–40 mg/kg body weight for *Avahi;* effective dosage for *E. mongoz,* 100 mg/kg). Anesthesia was carried out using a blowpipe and darts supplied by Telinject (Oftringen, Switzerland). Radio collars were attached to the adult males of the two groups in June and were used only to locate the groups at the beginning of observations, thus avoiding any bias in observation quality. Nocturnal observations were conducted with the aid of a headlamp and a hand-held torch. Habituation of the study animals presented no problems 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 the observer to approach to within 3–4 m without interrupting their activity, and the use of torches at night did not appear to influence their behavior.

Quantification of Crude Fiber Intake

Quantification of food intake for each observation was carried out by making absolute counts of items consumed. The mean weight of each food item was assessed by weighing with an electronic balance (Neolab, Zurich, Switzerland) 10–20 representative items of the size consumed by the animals. The weight ingested per food item during observations in a given month was calculated by multiplying the absolute count with the mean weight for each food item. The sum of total food ingested during the 5–11 h of feeding observations conducted in a given month was assumed to be representative of the amount of food consumed per time unit for that month. Based on this assumption, the food intake for a day in each month was then extrapolated from the intake during feeding observation time; daily food intake (F_D) for each month was estimated by multiplying the ratio of mean daily time spent active (t_a) to feeding observation time (t_{fo}) by the weight of food ingested (F_{fo}) during feeding observations ($F_D = t_a/t_{fo} * F_{fo}$). Daily intake of crude fiber (insoluble carbohydrates) was then estimated following chemical analysis of its content in the food samples [Curtis, 1997].

Statistical Analysis

Results were plotted in histograms or pie charts and summarized using descriptive statistics prior to hypothesis testing. Once hypotheses had been formulated, nonparametric statistical tests were applied, as in many cases tests showed the requirements of parametric methods were not fulfilled (normality, homogeneity of variance, etc.) and sample sizes were small. The units of statistical analysis used throughout are either month (n = 10) or activity period (n = 26). The level of statistical significance was set at $P < 0.05$. Tests employed were Mann-Whitney U, Wilcoxon-Signed Ranks, and Kendall-Rank Correlation, carried out using the software Statview, v4.02 (Abacus Concepts, Inc., Berkeley, CA) and the annotation given in Siegel and Castellan [1988]. Unless otherwise indicated, two-tailed tests were employed.

RESULTS

Climate, Phenology and Luminance

The climate in the study area is seasonal and clearly divided into a wet season (December–April) and dry season (May–November) (Fig. 2). Total monthly rainfall was highest in January (507 mm). For the entire wet season, 1169 mm of rainfall was recorded, compared to only 20 mm for the entire dry season. Annual variation in mean monthly temperature was limited, exhibiting a low of 25°C in June through to August and a high of 29°C in November and December. However, the temperature fluctuated considerably over the 24 h period. The greatest differences between
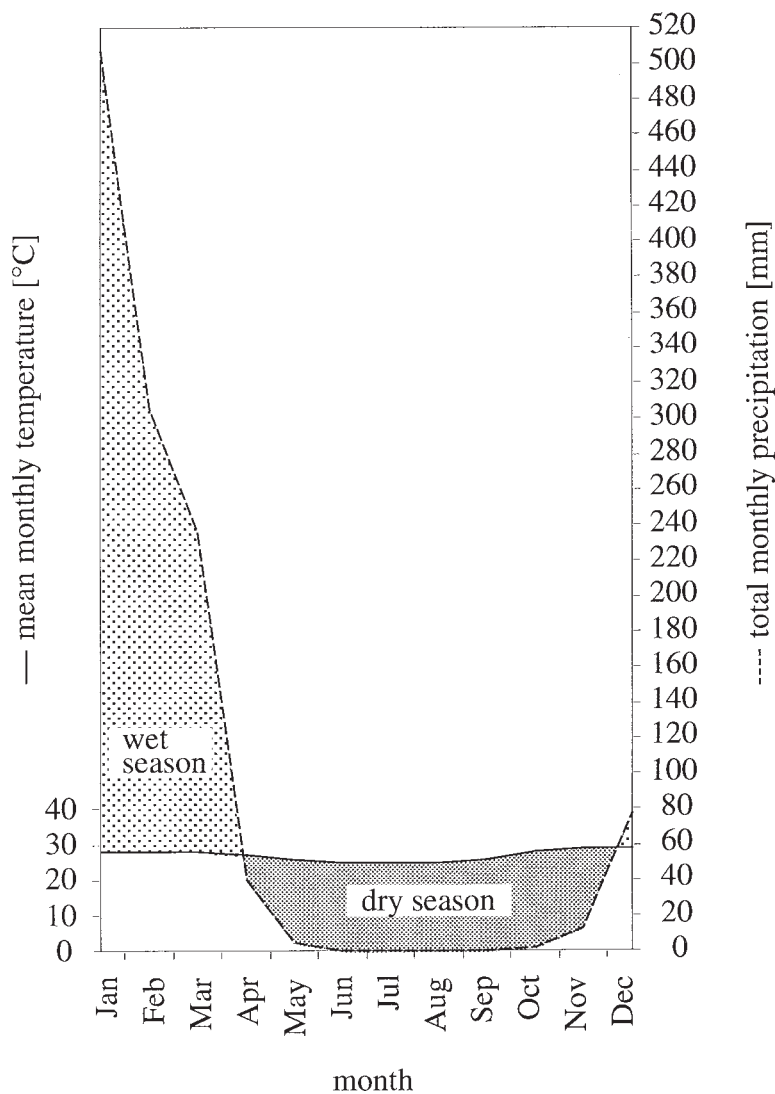

Fig. 2. Climatograph emphasizing water availability at Anjamena from October 1994 to September 1995. The points where the temperature and rainfall graphs meet are points of equivalence for evapotranspiration and indicate the beginning and end of the dry season. Number of data points per month: Jan, n = 31; Feb, n = 28; Mar, n = 29; Apr, n = 27; May, n = 28; Jun, n = 30; Jul, n = 22; Aug, n = 30; Sep, n = 20; Oct, n = 25; Nov, n = 29; Dec, n = 18. Reproduced from Curtis and Zaramody 1998 with permission from Plenum Press.

mean monthly values of maximum and minimum temperatures occurred during the dry season; differences were less extreme during the wet season. The lowest mean minimum monthly temperature was recorded in July and August (18°C) and the highest mean maximum monthly temperature in November (36°C).

Temporal changes in the vegetation throughout the study period are shown in Figure 3. Immature leaf production peaked from December–March and was lowest from June–October. Flower production peaked once in October. Fruit production was at its highest in October and lowest in June. Some trees produced neither leaves, flowers, nor fruit throughout most of the dry season (June–November).

Variation in day length was limited, as expected from the relative proximity of the study area to the equator (16°03′S). The longest days occurred in December and January (sunrise–sunset: 13 h 04 min) and the shortest in June (11 h 10 min). Light availability in the forest during the day was relatively low during both seasons, as expected for a forest with a closed canopy. Towards the end of the wet season (14 April 1995), the amount of light transmitted (T) through the canopy varied between 0.4% and 1.5% (mean 0.9%; SD 0.4%; n = 10 measurements; mean absolute light intensity 716 lux). During the dry season (11 September 1995), transmittance was greatly increased and varied between 1 and 16% (mean 6%; SD 4%; n = 10; mean absolute light intensity 5,155 lux). Nocturnal illumination was dependent on the phase of the moon and on night length. Light availability in the forest at night was highest in June and lowest in December.

Annual Variation in the Activity Cycle

The mongoose lemurs at Anjamena exhibited a cathemeral activity cycle [Tattersall, 1987] with a shift towards increased diurnal behavior during the wet season and an opposing shift towards increased nocturnal behavior during the dry season (Fig. 4).

Figure 5 provides a general picture of the activity pattern throughout the 24 h period during the two seasons. Activity in the wet season was clearly bimodal,
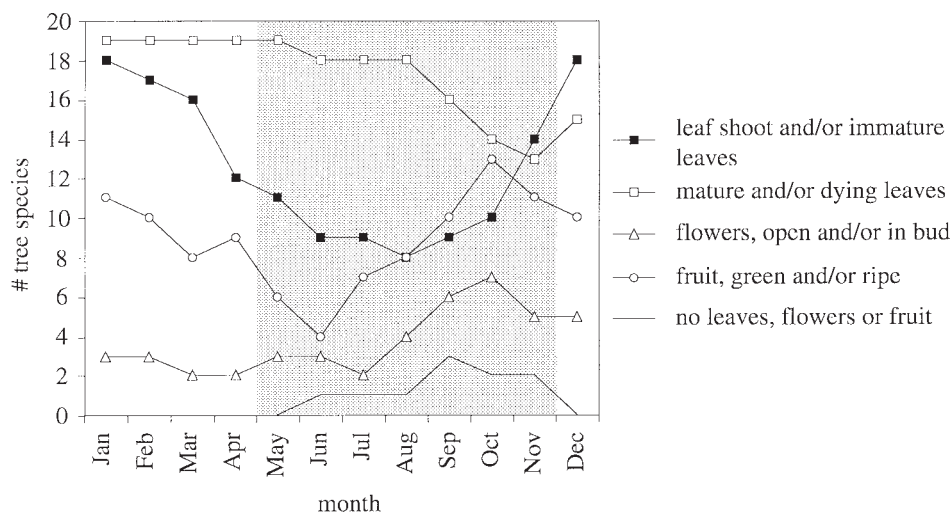

Fig. 3. Availability of fruits, flowers, and leaves from October 1994 to September 1995 based on data collected from one to ten trees in each of 19 tree species. The grey area indicates the dry season. Reproduced from Curtis and Zaramody 1998 with permission from Plenum Press.
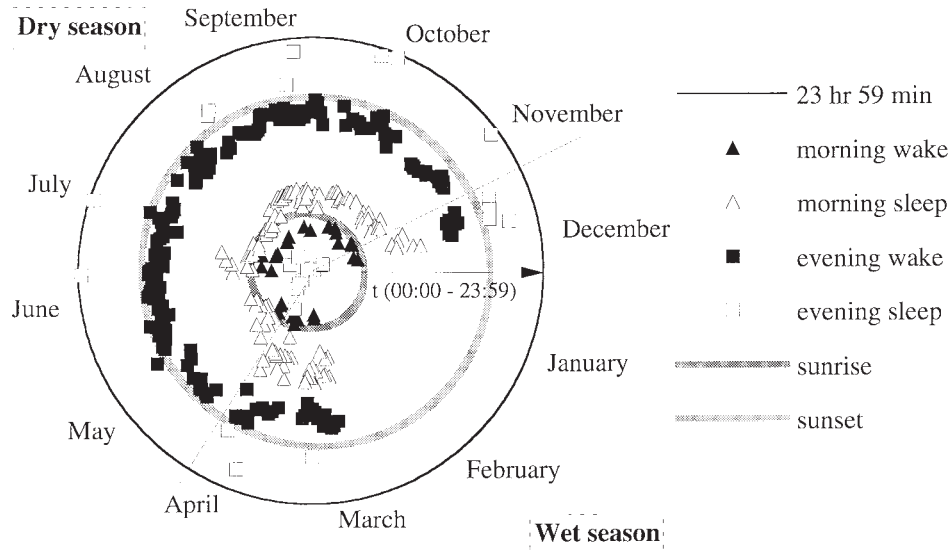
Fig. 4. Annual variation in the activity cycle in *E. mongoz* from October 1994 to September 1995. No data were collected for January and February. The year is depicted by the circumference of the circle, and the 24 h day is represented by the radius.

and the diurnal rest period was short, lasting only 3 h. Maximum activity was recorded during daylight hours, just after sunrise and just before sunset. With the exception of one out of six observations (activity between 23:00 and 04:00; mean hourly activity of 10 min), the nocturnal rest period was long, lasting about 6 h. Activity during the dry season showed a tendency towards a trimodal pattern. The two main peaks were found in the morning (just before sunrise), and in the afternoon and evening (at sunset). The third, smaller peak occurred during the night. The diurnal rest period was long, lasting about 6 h.

Table I shows the durations of diurnal and nocturnal activity in the wet and dry seasons. In spite of considerable variability within each season, significantly more diurnal activity was exhibited in the wet season, and significantly more nocturnal behavior occurred in the dry season (Mann-Whitney U (one-tailed); diurnal: $Z = -2.434$, $n_1 = 6$ activity periods, $n_2 = 20$ activity periods, $P = 0.008$, mean rank wet 20.167 > dry 11.500; nocturnal: $Z = -1.765$, $n_1 = 6$, $n_2 = 20$, $P = 0.038$, mean rank dry 14.950 > wet 8.667).

Figure 6 shows the distribution of diurnal and nocturnal activity over the year. The least diurnal activity occurred in May and June. It increased throughout the rest of the dry season and into the wet season and exhibited the highest value during March. Nocturnal activity was at a minimum in December and March and peaked in July; then it decreased from August to October and showed a secondary peak in November.

Abiotic Factors and the Activity Cycle

A number of environmental cues may mediate the seasonal shift in the activity pattern found in the mongoose lemur [Sussman & Tattersall, 1976; Tattersall, 1979; Schaaf & Stuart, 1983]. The most important of these is the day–night cycle of illumination [e.g., Aschoff, 1966; Hamner & Hoshizaki, 1974; Kavanau & Peters, 1976; Erkert, 1989].
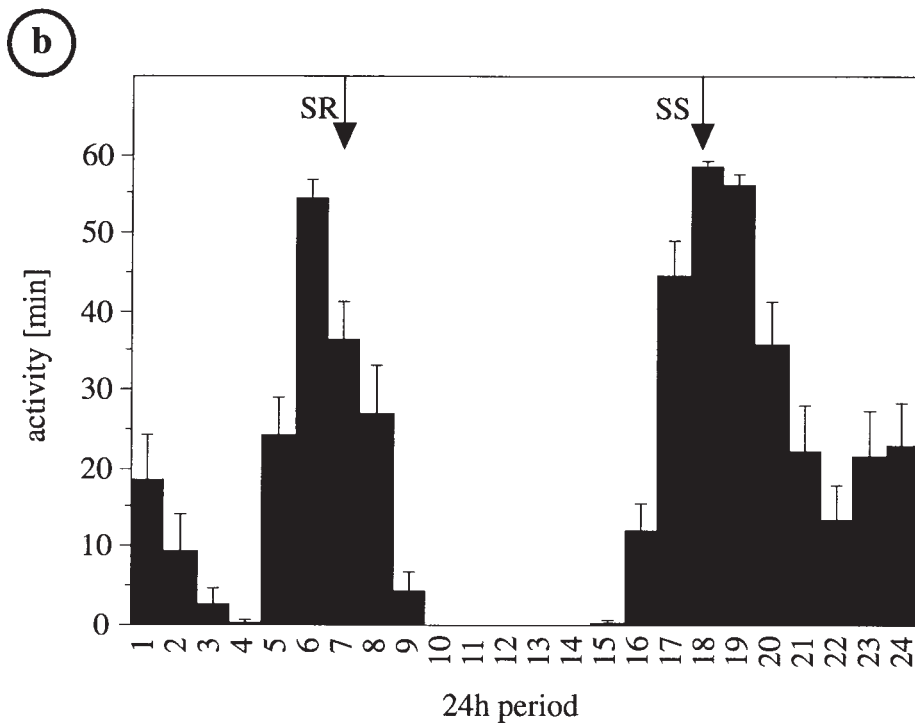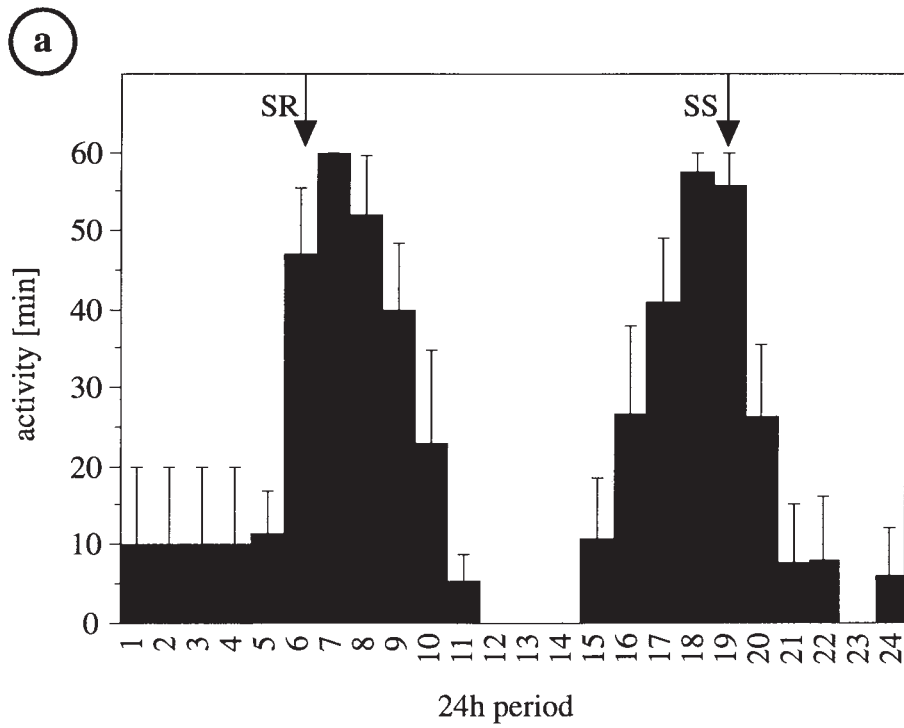
Figure 5.

TABLE I. Annual Variation in Time Spent in Nocturnal and Diurnal Activity

|	Diurnal activity		Nocturnal activity	
	Wet season	Dry season	Wet season	Dry season
Number of observations	6	20	6	20
Mean	5.7 h	3.3 h	3.9 h	6.3 h
SD	2.2 h	1.6 h	4.0 h	2.8 h
Minimum	2.2 h	0.7 h	0.9 h	1.4 h
Maximum	8.2 h	5.0 h	11.7 h	10.6 h

The role of day length in the distribution of activity in the diurnal and nocturnal phases is not considered alone but together with temperature and rainfall, as these factors all have a seasonal component and are intercorrelated. Therefore, it is not possible to assess their individual influence on the activity pattern. Instead, the mean monthly values for day length, temperature, and total monthly rainfall are combined by using the sum of their ranks in order to test for association with the activity pattern. Correlation between these abiotic factors and mean monthly diurnal and nocturnal activity is significant (Kendall Rank Correlation; diurnal: $\tau = 0.778$, n = 10 months, $P = 0.002$; nocturnal: $\tau = -0.600$, n = 10, $P = 0.016$). More diurnal behavior was exhibited when days were longer and temperatures and total rainfall were high, whereas nocturnality was preferred when days were short and temperatures and total rainfall were low.

Sunrise and sunset are the most important Zeitgeber and appear to be associated with the onset and cessation of activity in the mornings and evenings (Fig. 4). While day length was increasing (mid-June to mid-December), there was a definite negative relationship between sunrise and cessation of activity in the morning ($\tau = -0.337$; n = 87; $P < 0.001$). This implies that the earlier the sun rose, the later the animals ceased to be active in the morning. A strong positive association was found between cessation of activity in the evening and sunset ($\tau = 0.781$; n = 7; $P = 0.014$). This implies that the later the sun set, the later the animals ceased to be active. While day length was decreasing (mid-December to mid-June), a substantial negative relationship was found between the cessation of activity and sunrise in the morning ($\tau = -0.511$; n = 40; $P < 0.001$). There was a definite negative association between sunset and the onset of activity in the afternoon ($\tau = -0.351$; n = 57; $P < 0.001$). This implies that the later the sun rose, the earlier the animals ceased to be active, and the earlier the sun set, the later the animals commenced activity.

Nocturnal illumination was excluded from the analysis of the seasonal shift in the activity cycle, as its calculation is dependent on night length. However, activity cycles in other *Eulemur* species have been reported to be influenced by the phase of the moon [Harrington, 1975; Colquhoun, 1993], so this aspect is considered here for individual observations. Only insignificant associations were found between nocturnal activity and nocturnal illumination and between nocturnal activity and the phase of the moon (illumination: $\tau = 0.256$, n = 26 activity periods, $P = 0.067$; phase: $\tau = -0.185$; n = 26; $P = 0.185$). However, the association between the transformed nocturnal illumination index, I_C, and nocturnal activity

Fig. 5. **a:** Mean hourly activity (±SEM) during the wet season based on data from two groups observed in December, March, and April (n = 6). Sunrise (SR) of 05:23 and sunset (SS) of 18:27 on 21 December 1994. **b:** Mean hourly activity (±SEM) during the dry season based on data from two groups observed from May to November (n = 20). SR of 06:22 and SS of 17:32 on 21 June 1995.

a

b

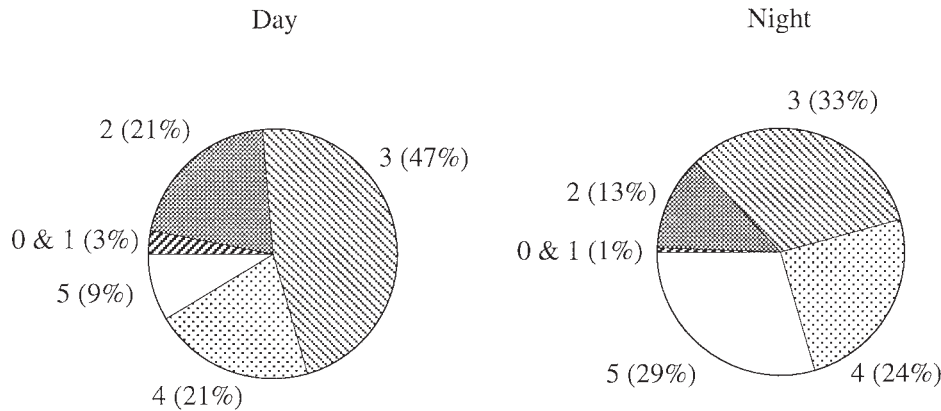Day   Night
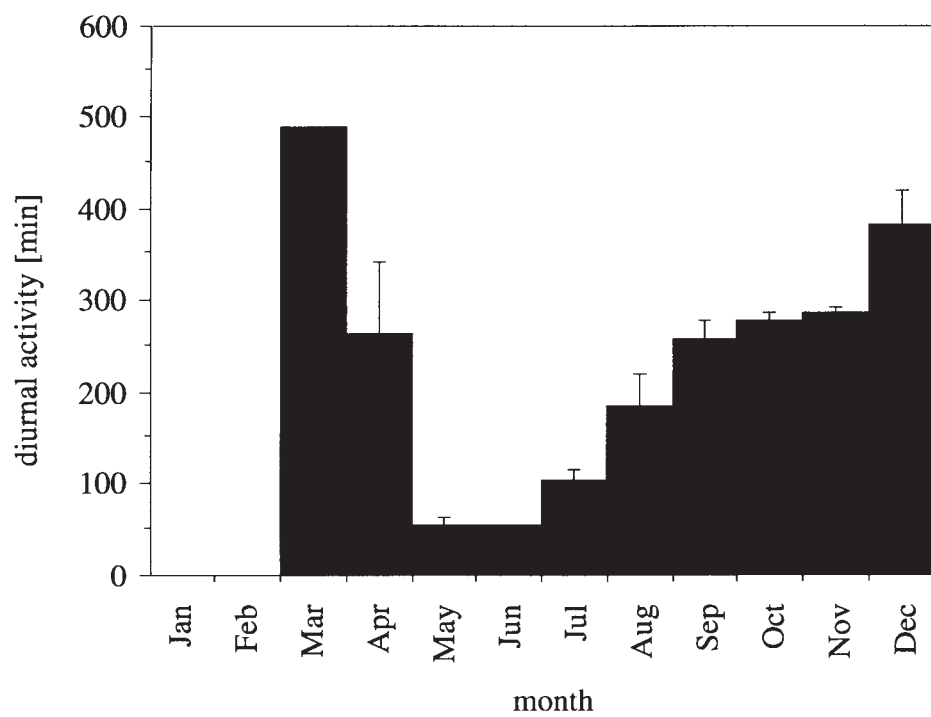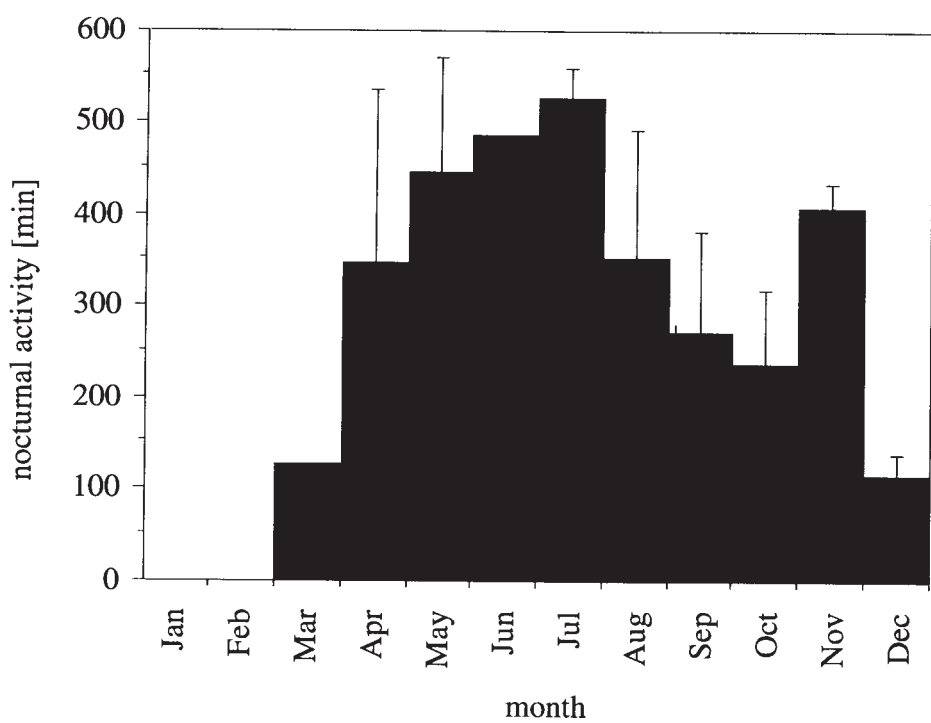
Fig. 7. Differences in the distribution of the use of different levels within the forest at night and during the day. Abbreviations for levels are as follows: 0, 0 m; 1, 0–2 m; 2, 2–5 m; 3, 5–10 m; 4, 10–15 m; 5, >15 m.

was significant (τ= 0.312; n = 26; P = 0.026) and implies that the mongoose lemurs were somewhat more active at night when light availability was higher.

Behavioral Variation During the Two Phases of the Light–Dark Cycle

Cathemerality and annual variation in the proportions of diurnal and nocturnal behavior in the mongoose lemur require the analysis of activity budgets over the full 24 h period. Testing for differences in the activity budget between nocturnal and diurnal behavior was carried out only for *feed,* as all categories in the budget were highly intercorrelated [Curtis, 1997]. No difference was found in the amounts of feeding behavior exhibited during nocturnal and diurnal activity (Wilcoxon-Signed Ranks: T^+= 173.5; T^-= 177.5 (Z = –0.051); n = 26 activity periods; P = 0.960).

Temporal variation was, however, evident in the use of different forest strata (Fig. 7). The emergents were used more frequently at night (5 in Fig. 7), and animals were never seen on the ground (0 in Fig. 7) after sunset. The lower strata of the forest (0–3 in Fig. 7) were generally frequented more often during the day. Levels 0 and 5 were chosen as representatives in order to test the significance of these differences, as intercorrelation between them was negligible (day: τ = –0.153, n = 26, P = 0.274; night: τ = 0.000, n = 26, P > 0.999). Significantly more time was spent in the emergents during the nocturnal activity phase than during the day (T^+= 23; T^-= 3; (Z = -3.899); n = 26; P < 0.001), and the inverse is true of time spent on the ground (T^+ = 0; T^- = 5; (Z = -2.023); n = 26; P = 0.043).

Food Availability, Diet and the Activity Cycle

Although associations were found between food availability and diurnal activity (Table II), these apparent correlations must be treated with caution, as both have a seasonal component. If the variable *abiotic factors* is held constant,

Fig. 6. **a:** Mean monthly diurnal activity (±SEM) throughout the study period based on data from two groups (n = 26). No data were collected for January and February. **b:** Mean monthly nocturnal activity (±SEM) throughout the study period based on data from two groups (n = 26). No data were collected for January and February.

the only weak association that remains is between the availability of flowers and diurnal activity (n=10 months: flowers: $\tau = 0.245$, $P > 0.1$; fruit: $\tau = 0.000$; $P > 0.999$; mature leaves: $\tau = -0.135$; $P > 0.25$). This implies that slightly more diurnal activity was exhibited when flower availability was high.

Annual variation was observed in the type of food resource exploited during this study [Curtis, 1997]. Immature fruit, leaves, and nectar were selected for analysis. These items were consumed with different frequencies during the wet and dry seasons [Curtis, 1997] and exhibited negligible intercorrelations between them (Table III). No significant associations were found between the time spent eating immature fruit, leaves, or nectar and the amount of diurnal activity exhibited by the study animals (Table III).

Crude fiber intake in percent of dry weight was higher during the wet season (mean 27%; SD 10%; n = 3 months) than during the dry season (mean 18%; SD 8%; n = 7 months). However, no significant association was found between crude fiber intake and the amount of diurnal activity exhibited by the mongoose lemurs ($\tau = 0.315$; n = 10 months; $P = 0.205$).

Interspecific Competition

The nocturnal niche was shared with two fruit bats (*Pteropus rufus, Rousettus madagascariensis*) and with the fat-tailed dwarf lemur (*Cheirogaleus medius*), all of which used resources exploited by *E. mongoz*. The only nocturnal confrontation recorded during the study occurred in April between a juvenile *E. mongoz* and *P. rufus*. Diurnal competitors seen feeding on resources exploited by *E. mongoz* were the crowned sifaka (*Propithecus verreauxi coronatus*), the greater vasa parrot (*Coracopsis vasa*), and the Madagascar green pigeon (*Treron australis*). Several different food items were consumed by both *E. mongoz* and *P. v. coronatus* (n = 8: fruit, leaves, flowers), but no agonistic interactions were ever observed [Curtis, 1997; Müller, 1997]. The only cathemeral competitor was the rufous brown lemur (*Eulemur fulvus rufus*). This species may have been the most important potential competitor, as it fed on several food items (n = 7: fruit, leaves) also consumed by *E. mongoz* and occupied a similar temporal niche. However, only seven interspecific confrontations involving feeding were observed during the entire study, all of which took place during daylight hours.

Predation

No instances of actual or attempted nonhuman predation were observed during the study, although a number of potential predators occur at Anjamena (Table IV). Two infants disappeared from groups other than the study groups during the first 4 months, and a third was found dead in November 1994. The cause of

TABLE II. Analysis of Associations Between Temporal Food Distribution and Diurnal Activity and Between Temporal Food Distribution and the Abiotic Factors

	Diurnal activity	Abiotic factors
Fruit	$\tau = 0.477$; n = 10; $P = 0.055$	$\tau = 0.614$; n = 10; $P = 0.014$[a]
Immature leaves	$\tau = -0.046$; n = 10; $P = 0.853$	$\tau = 0.000$; n = 10; $P > 0.999$
Mature leaves	$\tau = -0.474$; n = 10; $P = 0.056$	$\tau = -0.474$; n = 10; $P = 0.056$
Flowers	$\tau = 0.646$; n = 10; $P = 0.009$[a]	$\tau = 0.646$; n = 10; $P = 0.009$[a]

[a]Kendall-Rank Correlation: significantly correlated at the 0.05 level.

TABLE III. Intercorrelations Between the Frequencies With Which Food Items Were Consumed Over the 10 Month Study Period and Analysis of Associations Between Food Consumption and Diurnal Activity*

Intercorrelation	
Immature fruit/leaves	$\tau = 0.090$; n = 10; $P = 0.718$
Immature fruit/nectar	$\tau = 0.062$; n = 10; $P = 0.804$
Leaves/nectar	$\tau = -0.243$; n = 10; $P = 0.327$
Association with diurnal activity	
Immature fruit	$\tau = 0.180$; n = 10; $P = 0.469$
Leaves	$\tau = -0.333$; n = 10; $P = 0.180$
Nectar	$\tau = 0.183$; n = 10; $P = 0.462$

*Kendall-Rank Correlation: no significant correlations at the 0.05 level.

death in the latter case was a large flesh wound to the head and a puncture below the left eye, which might have been inflicted by *Cryptoprocta ferox* [Steve 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 [Steve Goodman, personal communication]. All responses to potential predators, usually raptors, were observed during twilight or daylight hours (n = 10), only one of which occurred during the wet season.

DISCUSSION

Results of this study of the mongoose lemurs at Anjamena revealed a cathemeral activity cycle throughout the wet and the dry seasons. However, significantly more diurnal activity was found during the warm, wet season and more nocturnal behavior during the cool, dry season. This activity pattern appears to be coordinated mainly with sunrise, sunset, and day length. The proximate role of these factors underlies the shift towards diurnality when days are long (during the wet season) and towards nocturnality when days are short (during the dry season). Through close negative association of onset and cessation of activity with sunrise and/or sunset, the main activity phase is shifted into one or other of the two temporal niches. With the exception of one out of the 26 activity periods, the main rest period of 6 h is maintained throughout the entire year but occurs during the day in the dry season and at night in the wet season. Ambient temperatures have also been cited as a possible factor affecting the activity pattern in the mongoose lemur [Schaaf & Stuart, 1983; Tattersall, 1976] and were

TABLE IV. Potential Nonhuman Predators at Anjamena

Class	Family	Species	Activity rhythm
Mammalia	Viverridae	*Cryptoprocta ferox*	Nocturnal
		Viverricula indica	Nocturnal
Reptilia	Boidae	*Sanzinia madagascariensis*	Nocturnal
		Acrantophis madagascariensis	Nocturnal
Aves	Falconidae	*Aviceda madagascariensis*	Diurnal
		Milvus migrans	Diurnal
		Polyboroides radiatus	Diurnal
		Accipiter henstii	Diurnal
		Accipiter francesii	Diurnal
		Buteo brachypterus	Diurnal

implicated in the diurnal activity observed in the mongoose lemur in the cool and humid highlands of Anjouan as well as during cold months in captivity. This is not consistent with observations at Anjamena, where nocturnality occurred predominantly during the cool months of the year. Low levels of luminance have been suggested as a further factor influencing activity. Luminance was described as relatively low in the Anjouan highlands (3,400 Lux) and is cited by Tattersall [1976] as a possible reason for diurnality in that particular habitat, whereas the mongoose lemurs in the lowlands were observed to be nocturnal. This is supported by evidence from Anjamena, as luminance was much lower during the wet season, when most diurnality was exhibited, than during the dry season, when most nocturnality was exhibited (wet: 716 Lux; dry: 5,155 Lux). Erkert [1989] carried out chronobiological experiments on *E. fulvus albifrons* and concluded that this species must be regarded as genuinely dark–active. This was based on the fact that, subsequent to the light–active behavior produced by very low illumination intensity in the dark phase, constant lighting at 10^{-1} Lux elicited an activity phase of the free-running circadian rhythm starting from the dark phase and not from the light phase. The light–active behavior "is not caused by a light-induced phase inversion of the endogenous circadian rhythm, but represents merely a total masking of the true circadian activity time caused by the strong inhibitory effect of low light intensities (Erkert, 1989)." If this conclusion is true for all cathemeral primates, then this activity pattern has its foundations in a nocturnal activity rhythm that is modulated by light intensity and results in diurnal activity under certain conditions.

The functional relevance, or survival value, of cathemerality is difficult to assess. Few advantages to food-related behavior emerged in relation to this activity pattern at Anjamena. No correlation was found between cathemerality and food availability, food consumption, or crude fiber intake. However, resource accessibility may be enhanced by nocturnal behavior during the dry season, leading to a reduction in interspecific competition. The hypothesis put forward by Engqvist and Richard [1991] is not supported by evidence from this study: *E. mongoz* at Anjamena actually consumed more crude fiber during the wet season, when activity was interspersed by only two rest periods as opposed to three during the dry season. Although there does not appear to be any link between cathemerality and digestion, it is possible that the overall pattern of two to three active periods interspersed with two to three rest periods is advantageous to digestion throughout the entire year.

Cathemerality could also represent a behavioral thermoregulatory mechanism. Morland [1993] suggests that lemurs rely primarily on behavioral rather than strictly physiological mechanisms for temperature regulation (e.g., reduction in activity levels, sunning behavior). Pereira [1995] proposes that *Lemur catta* shifts much of its activity into the night during the hottest months of the year in order to keep cool. This strategy would help *L. catta* to cope with the heavy winter coat that it grows during the hot season [Pereira, 1995]. The mongoose lemur at Anjamena exhibited no seasonal reduction in activity and no obvious sunning behavior. However, if we assume the energetics of *E. mongoz* are similar to those of the most closely related species studied to date (*E. fulvus*), the temporal shift in activity during the two seasons could be linked to thermoregulation. Nocturnal habits have been considered as a possible thermoregulatory adaptation in *Aotus,* which exhibits the same combination found in *E. fulvus* of a low basal metabolic rate (BMR) coupled to a high body temperature [Le Maho et al., 1981]. The thermoneutral zone (TNZ) in *E. fulvus* lies between 22°C and 30°C. Mean maximum monthly temperatures recorded at Anjamena were above TNZ during both

seasons, from March–December (31–36°C), and minimum monthly temperatures were below TNZ during the dry season, from May–October (18–21°C). This means that thermoregulatory measures would be needed during both seasons to counteract heat stress during the hottest part of the day as well as throughout the dry season to combat cold stress and maintain a high body temperature during the coldest nocturnal hours. The mongoose lemur was either resting or showed little activity during the hottest hours of the day, so heat production would have been low and heat stress minimized. Conversely, nocturnal activity during the dry season would have minimized cold stress and the energetic costs of maintaining a high body temperature during the coldest part of the 24 h period. During vigorous activity, heat dissipation would have been facilitated by the high temperature gradient between the body and the environment [Le Maho et al., 1981].

Finally, a shift in activity may aid *E. mongoz* in avoiding predators. A case in point is a second peak in nocturnal activity which occurred in November, just before the onset of the wet season and when least cover was afforded by vegetation. This coincides with part of the nesting period in most raptors at Anjamena [Langrand, 1990]. During November, many of the *E. mongoz* infants in the area were old enough to start actively investigating their environment and were probably at their most vulnerable to predation by raptors. Nocturnal activity would have provided valuable protection. A link between predation and cathemerality was postulated by Overdorff [1988]: nocturnal activity in *E. rubriventer* may have permitted feeding on nectar on exposed branches of emergent *Eucalyptus* trees while avoiding the threat of the diurnal raptors. There is also evidence from Paraguay that the usually nocturnal *Aotus* exhibits a diurnal activity pattern in areas where raptors are absent [Wright, 1983, 1989]. No behavioral differences were found between nocturnal and diurnal activity, apart from a preference exhibited by *E. mongoz* for higher levels of the forest at night. This could be interpreted as a mechanism in predator avoidance, as the main nocturnal threat to a lemur the size of *E. mongoz* is from the lower levels of the forest, from ground- and tree-dwelling viverrids (*Viverricula indica, Cryptoprocta ferrox*) [Goodman et al., 1993].

Two hypotheses have been proposed to explain the evolution of the cathemeral activity pattern, neither of which can be fully supported or refuted by evidence from the current study [Martin, 1972; Tattersall, 1982; van Schaik & Kappeler, 1996]. The first proposes that cathemerality represents a transitional stage between nocturnality and diurnality, while the second proposes that cathemerality should be regarded as a stable evolutionary strategy and as the ancestral activity pattern for the genus *Eulemur* [Tattersall, 1982]. The plasticity of cathemerality is evident in the differences found between the activity patterns exhibited by *E. mongoz* in the dry seasonal forest of Anjamena and those found in *E. f. rufus* and *E. rubriventer* in the less seasonal rain forest at Ranomafana [Overdorff & Rasmussen, 1995]: *E. mongoz* exhibited a shift towards more diurnal activity during the wet season and towards more nocturnal activity during the dry season. No such variation was observed in *E. f. rufus* and *E. rubriventer,* as nocturnal path length did not vary monthly for either species and both species travelled less at night than during the day. In addition, there are differences in the distribution of activity throughout the 24 h period within the same environment between the two cathemeral species at Anjamena and the two which were studied at Ranomafana [Overdorff & Rasmussen, 1995; Curtis, 1997]. At Anjamena in *E. mongoz* as well as at Ranomafana in *E. f. rufus* and *E. rubriventer* [Overdorff, 1988], any functional advantages of occupying one or other of the temporal niches appear to accrue to the nocturnal niche. However, a flexible strategy such as this

allows differential movement into either the diurnal or nocturnal niche, depending on selective seasonal pressures, and it appears to be highly adaptable to the many different climatic zones of Madagascar.

Based on this discussion, cathemerality could be either a recently evolved phenomenon (i.e., transitional) or ancestral to *Eulemur*. The variability in this activity pattern could be due to its recent evolution from an ancestral nocturnal pattern, where the variability is explained by the fact that cathemeral lemurs have not yet made the full transition to diurnality. On the other hand, this variability could be the result of new patterns evolving from an ancestral cathemeral pattern. Finally, if cathemerality is so successful in Malagasy lemurs—combined with the fact that nocturnal and diurnal activity has been reported in a small number of haplorhine primates [Wright, 1983; Dahl & Hemingway, 1988; Wright, 1989; P. Kessler, personal communication]—then why is this activity pattern not more widespread in primates?

CONCLUSIONS

1. Cathemerality in *E. mongoz* at Anjamena appears to be coordinated mainly with sunrise, sunset, and day length and is probably modulated by the inhibitory effect of low nocturnal light intensity in the forest during the wet season, which results in mainly diurnal activity.

2. The link between a high fiber diet and cathemerality predicted by Engqvist and Richard [1991] is not supported by this study, as more crude fiber was consumed during the wet season, when activity was interspersed by only two rest periods as opposed to three during the dry season.

3. Cathemerality may represent a behavioral thermoregulatory mechanism. Nocturnal activity during the cool dry season would have minimized cold stress and the energetic costs of maintaining a high body temperature during the coldest part of the 24 h period.

4. Nocturnal behavior during the dry season, when least cover is provided by vegetation, would allow *E. mongoz* to avoid predation by raptors.

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