

Proximate and ultimate determinants of cathemeral activity in brown lemurs

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Among primates, only two lemur genera, *Eulemur* and *Hapalemur*, and a population of the platyrrhine *Aotus azarai* are known to be cathemeral (i.e. show a mixture of daytime and night-time activity). Given the rarity of this phenomenon in primates except for Malagasy lemurs, its proximate and ultimate factors are still debated. The adaptive reasons for this apparently odd lifestyle are mainly based on four not mutually exclusive hypotheses: thermoregulatory benefits, antipredator strategy, competition avoidance and metabolic dietary-related needs. However, little effort has been made to tease apart proximate cues from potential ultimate factors in the multivariate context of activity correlates. To investigate these hypotheses, we compared the year-round cathemeral activity of two groups of *Eulemur collaris* and one group of hybrids *E. collaris* × *Eulemur fulvus rufus* in a humid littoral and in a dry gallery forest of southern Madagascar. Data were collected using a 5 min instantaneous method, with sampling equally distributed between day and night. We weighted the different effects of proximate and ultimate factors via the ANCOVA analysis using as the dependent variable the ratio between diurnal and nocturnal activity. Photoperiodic changes and nocturnal luminosity were the two proximate factors that accounted for most of the variability at the two sites. Diet quality was the only ultimate factor that had a significant effect on the diurnality index of the two lemur populations, suggesting a role of metabolic dietary-related needs in determining cathemeral activity in these lemurs.

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The consequences of being active during the day or at night have been pervasive at the beginning of each animal radiation, given the opposite sensorial worlds represented by the two segments of the 24 h cycle (Charles-Dominique 1975; Aschoff et al. 1982; Halle 2006). However, some mammals routinely show the ability to shift activity over the 24 h cycle despite the challenge of compromising between opposite adaptations (Halle & Stenseth 2000; Curtis & Rasmussen 2006). So far, the adaptive reasons for diel activity patterns in mammals are mainly based on four nonmutually exclusive explanations: thermoregulatory benefits (Beltran & Delibes 1994; Chiarello 1998; Zielinsky 2000; Rezende et al. 2003), predator–prey strategies (Zielinsky 1988; Lode 1995), avoidance of competition (Ziv et al. 1993; Fenn & Macdonald 1995; Kronfeld-Schor & Dayan 1999; Jones et al. 2001) and metabolic dietary-related needs (Halle 2000; Merritt & Vessey 2000).

Two decades ago, a diel activity pattern (termed ‘cathemerality’) was described in primates, which were traditionally viewed as strictly nocturnal or strictly diurnal (Tattersall 1987). This lifestyle seems to be rather rare in this order compared to other mammalian groups (Curtis & Rasmussen 2006). So far, only two lemur genera, *Eulemur* and *Hapalemur*, and a platyrrhine population, *Aotus azarai*, are known to show a mixture of daytime and night-time activity (Curtis et al. 2006). Given the rarity of cathemeral activity in primates, there is an intense debate as to which proximate cues and ultimate factors are related to this flexible biorhythm. Two proximate determinants, photoperiodic changes and nocturnal luminosity, have been shown to influence the activity profile of cathemeral primates. As in many other taxa, photoperiodic changes seem mainly to entrain the activity rhythm, that is, they act as a Zeitgeber (Curtis et al. 1999; Donati & Borgognini-Tarli 2006; Fernandez-Duque & Erkert 2006), while low nocturnal luminosity seems to inhibit activity via a negative masking effect (Aschoff 1988; Erkert 1989; Kappeler & Erkert 2003; Donati & Borgognini-Tarli 2006; Fernandez-Duque & Erkert 2006). As for the ultimate determinants, the hypotheses proposed so far are in accordance with the selection pressures demonstrated for other mammals. Thermoregulatory advantages to avoid heat stress or cold stress (*Aotus azarai*: Fernandez-Duque 2003; *Hapalemur griseus alao-trensis*: Mutschler 1999; *Eulemur mongoz*: Curtis et al. 1999) and

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avoidance of exposure to diurnal birds of prey (*Eulemur fulvus rufus*: Donati et al. 1999; *Eulemur mongoz*: Curtis et al. 1999; Rasmussen 1999, 2005; *Eulemur rubriventer*: Overdorff 1988) have been postulated as possible determinants of activity shifts in cathemeral primates living in very seasonal habitats. Benefits of having a flexible temporal niche that avoids the activity peaks of competitors have been proposed for sympatric lemur species (*Haplemur* spp.: Santini-Palka 1994; *E. f. fulvus* and *E. mongoz*: Rasmussen 1999, 2005; Curtis & Rasmussen 2006). Finally, prolonged foraging activity, associated with a seasonal increase of fibrous low-quality food, to extract enough energy to meet metabolic demand, seems also to be relevant in some areas (Engqvist & Richard 1991; *E. f. fulvus*: Tarnaud 2006; *Eulemur collaris*: Donati et al. 2007). Some authors have also hypothesized that cathemerality in lemurs is the product of a nonadaptive disequilibrium from nocturnality to diurnality caused by the recent extinction of large diurnal raptors and of competitive lemur species (van Schaik & Kappeler 1996; Kappeler & Erkert 2003).

Since cathemerality is a flexible response, we can expect its proximate factors to fluctuate according to environmental variation. Therefore, it is difficult to establish a definite and stable hierarchy among its environmental correlates (Curtis & Rasmussen 2006; Ossi & Kamilar 2006). Nevertheless, the fact that cathemeral primates are almost exclusively found in Madagascar points to the presence of a possible common factor. However, the methodological heterogeneity used to measure both the activity profile and the various abiotic and biotic variables hampers comparisons between study sites (Donati & Borgognini-Tarli 2006). Also, proximate and ultimate factors have often been analysed independently, and little effort has been made to tease apart the latter after having accounted for the former.

The southeastern region of Madagascar allows us to investigate the above hypotheses in a comparative context where the same cathemeral primate lives in two different ecological situations. There, two brown lemur populations, *E. collaris* and *E. collaris* × *E. f. rufus* hybrids, live in geographical proximity but in very different habitats, the aseasonal humid littoral forest and the seasonal dry gallery forest, respectively (Pinkus et al. 2006; Donati et al. 2007; Tanaka 2007). We tested the four hypotheses formulated to account for the adaptive underpinnings of cathemerality by comparing year-round activity data collected on the above two lemur populations. At the same time, we weighed and separated the influence of the two proximate cues known to influence lemur activity, photoperiodic changes and nocturnal luminosity. In particular, we addressed the following questions: (1) do proximate factors have similar effects on brown lemur activity in different habitats and (2) once the effect of proximate factors has been removed, which, if any, of the four ultimate factors proposed so far explains variation in activity at the two sites?

METHODS

Study Sites and Study Species

Data were collected at two study sites: the Sainte Luce Conservation Area (STL) and the Berenty Private Reserve (BER). At STL, observations were conducted on two groups of *E. collaris* between December 1999 and January 2001 by G.D., N.B., and V.M. in 'S9', a 377 ha fragment of the littoral forest (24°45'S, 47°11'E) close to the village of Manafiafy, 50 km north of Fort Dauphin, Tolagnaro, southeastern Madagascar. This area is characterized by a tropical wet climate, with average monthly temperatures of 23 °C, annual rainfall of 2480 mm and no clear-cut dry season (Bollen & Donati 2005; Fig. 1). Littoral forest grows on sandy soils and occurs within 2–3 km of the coast, at an altitude of 0–20 m (Dumetz 1999). In addition to *E. collaris*, four lemur species (*Microcebus rufus*,

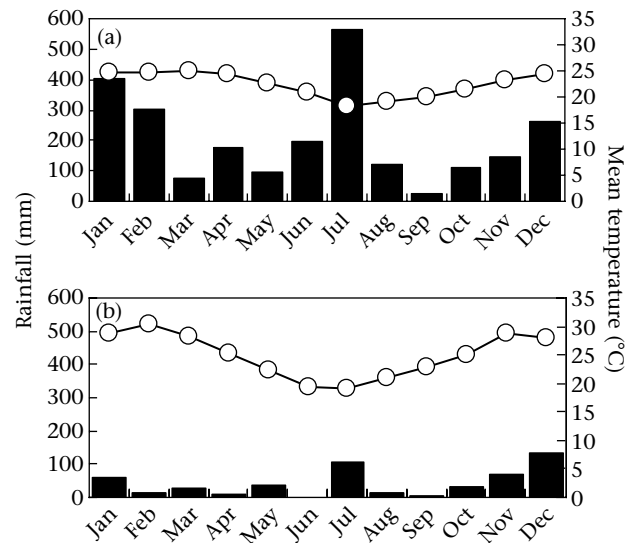


Figure 1. Comparison of climatic factors at (a) Sainte Luce and (b) Berenty during the study period. Bars represent total monthly rainfall and circles mean monthly temperature.

Cheirogaleus medius, *Cheirogaleus major*, *Avahi laniger*), all nocturnal, are found in this area. At BER, data collection was carried out by G.D., N.B., and V.M. on one group of *E. collaris* × *E. fulvus rufus* hybrids from April 2000 to February 2001. It is difficult to assess the effect of hybridization on activity pattern in our comparative study, but a role of a phylogenetic component in determining activity differences between the two brown lemur populations cannot be ruled out. Berenty Reserve is a 240 ha private reserve located in a section of gallery forest bordering the Mandrare river in southern Madagascar (25°03'S, 46°18'E). The climate at Berenty is characterized by a short wet season, generally lasting from November to March, while the remaining months correspond to the dry season (Jolly et al. 2006). During the study period the average temperature was 25 °C, and the annual rainfall 561 mm (Fig. 1). In addition to brown lemur hybrids, two diurnal (*Lemur catta* and *Propithecus verreauxi*) and three nocturnal lemur species (*Microcebus murinus*, *C. medius*, *Lepilemur leucopus*) are found in this area.

Measuring Cathemeral Activity

Three lemur groups (STL: group A: 8–13 individuals; group B: 4–6 individuals; BER: 16 individuals) were followed for 3 days and 3 nights each month from 0600 to 1800 hours during diurnal sessions and from 1800 to 0600 hours during nocturnal sessions. We carried out observations for 1716 h at STL and 720 h at BER, equally distributed between the two phases of the day–night cycle. At STL, where observation conditions are difficult and groups have much larger ranging areas, 12 individuals from the two groups (A, B) were captured and marked with nylon collars and coloured pendants (15 × 2 cm; R. C. Steele, Pasadena, CA, U.S.A.) prior to the observations. One individual per group was also radiocollared (TW3 transmitter from Biotrack, Wareham, U.K. collar weight: 40 g, 1.9% of the lightest individual). Captures were carried out by an experienced Malagasy technician via a blow-pipe darting which induced a brief anaesthesia (0.6 ml of ketamine hydrochloride; Ketanest, Parke-Davis, Freiburg, Germany; Ancrenaz et al. 2003). Only adults without dependent infants were captured and animals recovered from anaesthesia within 1.5 h ($\bar{X} \pm SD = 71.43 \pm 15.74$ min). There were no injuries as a consequence of the captures. Collars were not removed from the animals after the study, since adverse effects on behaviour resulting from the collars

were not noticed. Given the much easier observation conditions, animals were not captured or marked at BER. At STL, the lemurs were fully habituated in about 3 months, when it was possible to approach them to within a few metres. At BER, the lemurs observed were already habituated because of the frequent presence of tourists in this reserve. During the observations the lemurs were followed at a distance of about 4–50 m. This study was conducted with the authorization of the Commission Tripartite of the Direction des Eaux et Forêts de Madagascar.

During the day, animal activity was recorded using the instantaneous focal method (Altmann 1974) at 5 min intervals. Focal animals were chosen evenly from all adult individuals in both study groups. Activity (active behaviours: feeding, foraging, moving and social behaviours; nonactive behaviours: resting, sleeping), food type consumed (mature and unripe fruits; mature and young leaves; nectar; flowers; animal matter; other) and canopy level above ground (measured at 2 m intervals) were recorded during observations. As individual identification and classification of behavioural items were difficult at night, we used an auditory group sampling method (Andrews & Birkinshaw 1998) during nocturnal observations, recording the general activity of the entire group based on visual and auditory cues every 5 min. The usual synchrony of brown lemur groups suggests that this approximation is acceptable (Donati et al. 2007). Specific noises were associated with particular feeding activities. At night, when it was not possible to see the animals, food items were identified from fragments falling to the ground and/or from knowledge of the category exploited at a particular plant species based on diurnal observations.

Measuring Abiotic Variables

To account for the whole range of variation in nocturnal luminosity, observation nights were evenly distributed across lunar phases. As direct recording of nocturnal luminosity in the forest has proved to be impossible, indirect evaluations were obtained by using an ad hoc program (Curtis et al. 1999). The program allowed us to calculate a nocturnal luminosity index (I) derived from the lunar phase (P), using sunrise, sunset, moonrise and moonset times as shown in the following formula:

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

where $a < b$ ($dt = 0.24$ h). When sunset precedes moonset, 'a' corresponds to sunset time; when sunset precedes moonrise, 'a' corresponds to moonrise time; when moonset precedes sunrise, 'b' corresponds to moonset time; when sunrise precedes moonset, 'b' corresponds to sunrise time. During nocturnal observations, the above index ranged from 0 to 0.6.

Sunset and sunrise, moonset and moonrise times were also calculated with the above-mentioned program.

Temperature was registered at 2 h intervals by a data logger, Hobo H8 pro, operated by custom software (BoxCar 3.51 for Windows, Onset Computer Corporation, Bourne, MA, U.S.A.).

Measuring Biotic Variables

To estimate the degree of competition, we recorded all interactions with conspecific groups or with other large lemur species by the ad libitum method (Altmann 1974) throughout the 24 h cycle. Interactions were divided into three categories: neutral (when the group did not react to the presence of other groups/animals), aggressive threat (when the reaction was limited to vocalizations and threats but no physical contact was observed)

and aggressive contact (when the reaction involved physical contact). Only the second and third categories were taken as a proxy measure of intra- and interspecific interference competition.

Feeding trees used by the focal animals for more than 5 s as well as resting trees used for more than 10 min were marked during observation sessions and identified with the help of a local expert on a subsequent day. In addition, diameter at breast height, crown volume and height were measured or estimated. From these data we calculated the average height of the forest used by the lemurs in their home range. To evaluate seasonal changes in exposure to diurnal birds of prey an index of canopy exposure was then evaluated at each site. The index of canopy exposure consists of the ratio between the monthly average height at which animals were seen and the monthly average height of the trees used by the lemurs in their home range. For this analysis we considered only the diurnal observations, as the evaluation of animal height at night was often inaccurate. Canopy exposure during the day was considered a reasonable proxy of exposure to predators at the two sites, because, besides diurnal raptors, there are virtually no other predators for these lemurs, that is, large viverrids were absent in both STL and BER. Although large snakes were found in the two forests and they may sporadically kill brown lemurs (Goodman et al. 1993), they are not thought to remove a significant portion of the population. Two species of hawk are present at the two study sites, *Polyboroides radiatus* and *Accipiter henstii* (G. Donati, personal observation), which both represent a threat for adult brown lemurs (Karpanty & Wright 2006). Given the various hunting strategies of these two raptors (Brockman 2003) and the habitat differences, our method may not provide an accurate measure of predation risk. However, we were interested in comparative measures and we consider this an acceptable proxy. Also, the typical lemur reaction to the attack of these birds, that is, moving down to the lower forest layers (Brockman 2003), is a clear indication that height in the trees is an important factor.

To evaluate variation in diet quality, we estimated the quantity of ingested fibres. For this, biochemical analyses of food items were conducted at the Department of Animal Ecology and Conservation at Hamburg University. A total of 112 food samples (representing different plant parts of the total number of species eaten during the study period) at STL and 23 at BER, eaten by brown lemurs, most of which were fruits, were analysed (see also Bollen et al. 2005). Samples were weighed with an electronic balance, dried in an oven at 40 °C for a standard period, weighed again (dry weight), ground to pass a 2 mm sieve and dried again at 50–60 °C before the analyses. Samples were analysed for neutral detergent fibres (NDF; Goering & van Soest 1970; van Soest 1994; modified according to the instructions for use in an 'Ankom Fibre Analyser'). NDF represents all the insoluble fibres (cellulose, hemicellulose and lignin), partly digestible in species with hindgut fermentation. The fibre intake was obtained as the weighted percentage of dry matter per month, with the proportion of feeding records for each food item as the weighting coefficient (Kurland & Gaulin 1987):

$$\text{Intake} : \sum (F_i \times X_i)$$

where F_i is the monthly proportion of feeding records and X_i is the percentage of dry matter for the i th item. We estimated animal intake by using the proportion of feeding records, since it was impossible to quantify the absolute amount of items consumed at night.

Data Analyses

The records of activity were weighted by the total number of instantaneous records. Hourly and daily average activity

frequencies were calculated for each individual lemur during the day, and for the whole group at night. Then, data were pooled by month, and daily grand means per month were obtained. Because the two STL groups did not show significant differences in monthly averages of activity, data were pooled (Mann–Whitney U test: $Z = 1.2$, $N_1 = 13$ months for group A, $N_2 = 8$ months for group B, $P = 0.238$). We considered activity to be nocturnal if it occurred between the end of the astronomical evening twilight (from when the sun is 18° below the horizon) and the beginning of astronomical morning twilight (until the sun is 18° below the horizon). Diurnal activity included morning and evening twilights.

We used the nonparametric Mann–Whitney test to evaluate the differences between monthly averages of abiotic and biotic variables recorded at the two sites (STL: $N = 14$; BER: $N = 10$). Then, all the dependent variables used for the analysis of the factors affecting activity were log transformed to allow the use of multivariate parametric tests. As a first step, we evaluated the influence of proximate factors on diurnal and nocturnal activity. For this, a two-way ANOVA (with Scheffe's post hoc tests) was used to analyse the hourly and monthly differences in the activity patterns between brown lemurs in STL and BER, as well as the effect of nocturnal luminosity in the two lemur populations. For the two-way ANOVA we used as the dependent variable log daily data on diurnal and nocturnal activity. Independent factors were sites, months, time blocks (morning: 0400–1000 hours; day: 1000–1600 hours; evening: 1600–2200 hours; night: 2200–0400 hours), and nocturnal luminosity blocks (low luminosity: $I < 0.1$; intermediate luminosity: $0.1 < I < 0.3$; high luminosity: $I > 0.3$). Second, we evaluated the effect of the four potential ultimate factors proposed to determine lemur cathemerality after having accounted for the effect of site and proximate factors via a two-way ANCOVA. Removing the proximate factors is necessary because by acting on the endogenous clock they are likely to hide local environmental effects. Controlling for the effect of site is also necessary to account for other environmental variables that were not considered in this study and the potential phylogenetic differences between the two brown lemur populations. For the ANCOVA we used as the dependent variable the log monthly ratio between diurnal and nocturnal activity (diurnality index). Independent factors were sites, temperature (as a proxy of thermoregulatory stress), canopy exposure (as a proxy of exposure to birds of prey), aggressive interactions (as a proxy of feeding competition) and fibre intake (as a proxy of diet quality). Except for site, independent variables were grouped from numerical data into three ordinal categories, each one including 33.3% of the sample. For the covariates, daylength and nocturnal luminosity, we used monthly averages, which also entered the analysis after log transformation to improve their linearity.

All tests were two tailed.

RESULTS

Abiotic and Biotic Variables

Table 1 shows the monthly variation in the abiotic and biotic factors measured at the two sites during the observation period. As expected by the geographical proximity of the two study sites, daylength and nocturnal luminosity changes did not reveal significant variation between the two sites, showing that observations were balanced among different months and moon phases. Although monthly average temperature was higher in BER than in STL, this difference was not significant during the year. The index to evaluate the canopy exposure of the brown lemurs appeared similar between the two forests and, accordingly, there were no significant differences in animal exposure. In STL brown lemurs had a diet significantly richer in fibre than BER lemurs. Also, monthly aggressive interactions were almost three times higher in BER than in STL.

The Role of Proximate Factors

Annual and daily activity

Although a marked seasonality was recorded, in both populations of brown lemurs cathemeral activity occurred throughout the year, and was not limited to a specific season (Fig. 2). The diurnal daily activity varied significantly over the year at the two study sites (ANOVA: $F_{19,61} = 6.80$, $P < 0.001$). A significant effect of time of year (months: $F_{9,61} = 6.39$, $P < 0.001$) and site ($F_{1,61} = 26.97$, $P < 0.001$), as well as an interaction effect ($F_{9,61} = 2.20$, $P = 0.034$), were found. At both study sites diurnal activity was prolonged during the months of the austral summer and decreased during the austral winter (Scheffe's post hoc test: significant differences between January–February and July–September blocks). Also, in BER diurnal activity ($\bar{X} \pm SE = 52.09 \pm 6.32\%$) was higher than in STL ($43.30 \pm 11.10\%$).

Daily nocturnal activity varied even more than diurnal activity during the year ($F_{19,59} = 14.83$, $P < 0.001$). There were also significant effects of time of year (months: $F_{9,59} = 20.56$, $P < 0.001$) sites ($F_{1,59} = 55.25$, $P < 0.001$) and the interaction month*site ($F_{9,59} = 10.76$, $P < 0.001$) for nocturnal activity (Fig. 2). Seasonal variation in nocturnal activity showed, at both sites, an opposite pattern to that of diurnal activity, increasing during the austral winter, and decreasing during the summer (Scheffe's post hoc test: significant differences between November–January and April–September blocks). Also, in STL brown lemurs were more nocturnal ($\bar{X} \pm SE = 35.65 \pm 17.21\%$) than in BER ($20.35 \pm 17.24\%$). The diurnality index, that is, the ratio between diurnal and nocturnal activity, was consistently higher in BER ($\bar{X} \pm SE = 3.51 \pm 17.21$) than in STL (2.35 ± 17.21) but in February. In both populations

Table 1

Comparison between the monthly averages of the abiotic and biotic variables considered as proximate and ultimate factors at the two study sites

	Daylength (h)	Nocturnal luminosity	Temperature ($^\circ\text{C}$)	Fibre intake	Agonistic interactions	Canopy exposure
S. Luce						
Median	12.46	0.18	23.85	37.51	3.25	0.70
Range	10.61–13.66	0.01–0.38	18.2–25.76	29.50–44.76	0.50–9.00	0.55–0.75
N	14	14	14	14	14	14
Berenty						
Median	11.83	0.06	25.14	24.88	9.00	0.69
Range	10.59–13.69	0.01–0.37	19.20–30.30	13.15–35.13	5.00–16.00	0.55–0.91
N	10	10	10	10	10	10
Mann–Whitney test						
Z	0.44	1.29	1.05	3.57***	2.99**	0.23

** $P < 0.01$; *** $P < 0.001$.

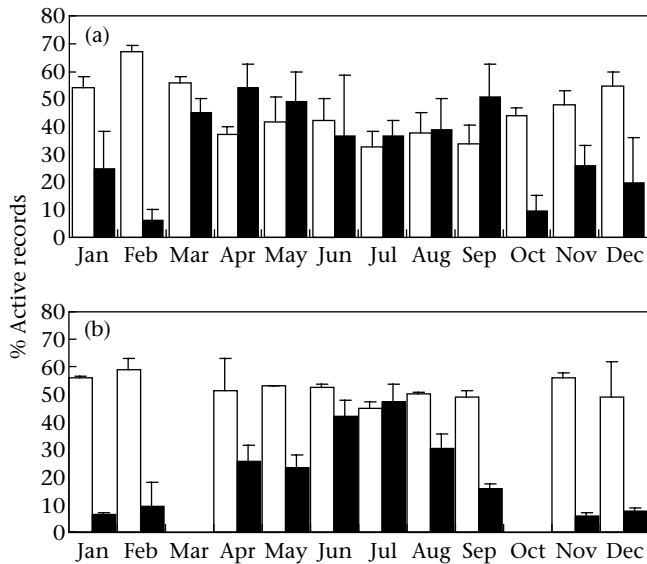


Figure 2. Monthly mean + SE of diurnal (white bars) and nocturnal (black bars) activity of (a) *Eulemur collaris* at Sainte Luce and of (b) hybrids *E. collaris* × *E. fulvus rufus* at Berenty. At Berenty no data were recorded in March and October.

brown lemurs were mostly diurnal from October to February (maximum in BER: 9.38 in November; maximum in STL: 10.42 in February), whereas during the austral winter they were equally active during the day and at night (minimum in BER: 0.95 in July; minimum in STL: 0.67 in September).

The distribution of brown lemur activity over the 24 h cycle showed a typical bimodal pattern at both study sites (Fig. 3). Hourly activity varied significantly during the 24 h ($F_{7,88} = 6.89, P < 0.001$), but only the time of day ($F_{3,88} = 12.79, P < 0.001$) and the interaction hours*site ($F_{3,88} = 3.54, P = 0.018$) showed a significant effect on activity, while the site effect was not significant ($F_{1,88} = 1.45, P = 0.232$). Activity peaked during the morning hours (BER: $\bar{X} \pm SE = 63.01 \pm 8.8\%$; STL: $57.89 \pm 13.3\%$) as well as during the evening segment (BER: $39.24 \pm 6.2\%$; STL: $50.45 \pm 5.28\%$), while it dropped during the central hours of the day (BER: $31.16 \pm 4.7\%$; STL: $24.83 \pm 11.70\%$; Scheffe's post hoc test: significant differences between morning hours and day hours; morning hours and night hours; evening hours and night hours).

Daily activity at different nocturnal luminosity levels

Nocturnal activity was significantly influenced by the available luminosity in both lemur populations ($F_{5,73} = 4.86, P < 0.001$;

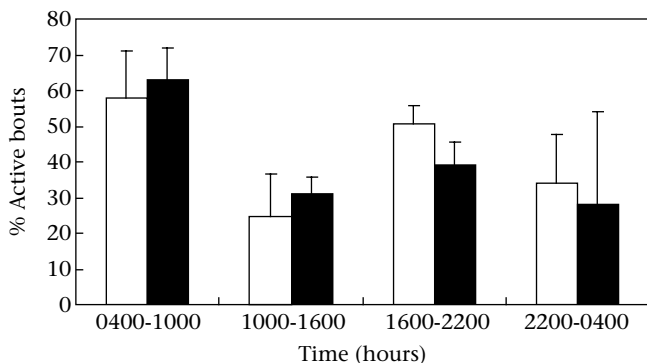


Figure 3. Annual mean + SE of activity during four time intervals (morning: 0400–1000 hours; day: 1000–1600 hours; evening: 1600–2200 hours; night: 2200–0400 hours) of *Eulemur collaris* at Sainte Luce (white bars) and of hybrids *E. collaris* × *E. fulvus rufus* at Berenty (black bars).

Fig. 4). The effect of nocturnal luminosity on activity remained significant ($F_{2,73} = 3.47, P = 0.036$) after we accounted for the difference between sites ($F_{1,73} = 10.19, P = 0.002$). Although STL brown lemurs were always more active at night than BER animals, in both populations a similar trend was evident. Activity peaked during nights with a high luminosity index (BER: $\bar{X} \pm SE = 36.09 \pm 21.11\%$; STL: $46.94 \pm 11.38\%$), and dropped when luminosity was low (BER: $14.51 \pm 12.6\%$; STL: $24.87 \pm 18.91\%$), showing a significant difference between the two conditions (Scheffe's post hoc test: $P = 0.003$). Activity inhibition at low luminosity levels was much more marked for BER brown lemurs.

The Role of Ultimate Factors

Table 2 shows the effect of the four ultimate factors proposed to shape the diurnality index of cathemeral lemurs after we accounted the site effect, as well as the effect of the proximate factors, day-length and nocturnal luminosity. As expected, in all four models the effects of the covariates, represented by the proximate factors, on the diurnality index were always highly significant. The model that explained most of the variability in the diurnality index ($R_{adj}^2 = 88.3\%$) was the one that accounted for the quality of the diet, expressed as fibre intake. This model is also the only one in which the effect of a potential ultimate factor was significant (ANCOVA: $F_{2,18} = 5.02, P = 0.019$). Although the models with the other three ultimate factors considered here were also highly significant, the covariates and the site effect explained most of that variability. This means that the quality of the diet explained most of the remaining year-round variation in the brown lemur diurnality, once the strong effect of proximate factors and site differences were accounted for.

DISCUSSION

Proximate Factors

Although living in different habitats, the two brown lemur populations were influenced by photoperiodic cues in a similar way. *Eulemur* activity was largely biphasic with peaks at dawn and dusk. This is an indication that the activity phase is entrained by the main Zeitgeber, sunrise and sunset, which seems to control their biorhythm year-round (Aschoff et al. 1982; Heldmaier et al. 1989; Curtis et al. 1999; Donati & Borgognini-Tarli 2006). In fact, day-length variation was the single most important variable explaining the activity fluctuations recorded at the two sites during the year. Although the BER group appeared to be generally more diurnal, both populations tended to be mostly diurnal during the long days of the austral summer, whereas their diurnal and nocturnal activity was similar during the austral winter. In *E. mongoz* and *E. collaris*

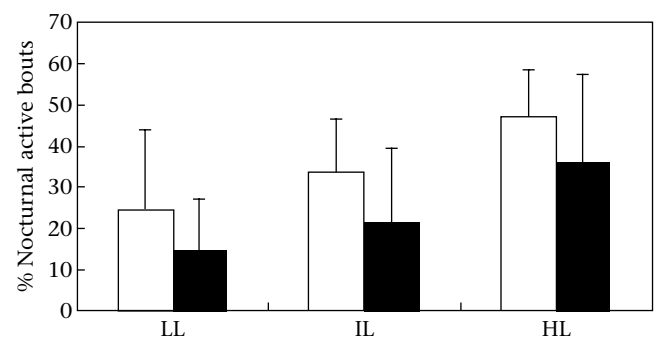


Figure 4. Annual mean + SE of nocturnal activity of *Eulemur collaris* at Sainte Luce (white bars) and of hybrids *E. collaris* × *E. fulvus rufus* at Berenty (black bars) during three nocturnal luminosity blocks. LL: low luminosity ($I < 0.1$); IL: intermediate luminosity ($0.1 < I < 0.3$); HL: high luminosity ($I > 0.3$).

Table 2

The results of the two-way analysis of covariance using as dependent variable the monthly average of the diurnality index (ratio between diurnal and nocturnal activity) and as independent variables the monthly averages of the four ultimate factors considered (fibre intake, aggressive interactions, canopy exposure and temperature)

Source of variation	df	F	P	R ² _{adj} (%)
Fibre intake	2	5.02	0.019	
Site	1	0.69	0.417	
Fibre intake*site	1	4.72	0.044	
Daylength	1	72.22	<0.001	
Nocturnal luminosity	1	27.15	<0.001	
Model	6	30.00	<0.001	88.3
Aggressive interactions	2	0.26	0.777	
Site	1	3.39	0.083	
Aggressive interactions*site	1	0.29	0.595	
Daylength	1	29.18	<0.001	
Nocturnal luminosity	1	18.25	0.001	
Model	6	18.40	<0.001	81.9
Canopy exposure	2	0.56	0.580	
Site	1	5.35	0.034	
Canopy exposure*site	1	0.54	0.591	
Daylength	1	28.23	<0.001	
Nocturnal luminosity	1	19.89	<0.001	
Model	6	15.57	<0.001	81.6
Temperature	2	0.53	0.597	
Site	1	6.63	0.020	
Temperature*site	1	0.31	0.740	
Daylength	1	22.37	<0.001	
Nocturnal luminosity	1	11.97	0.003	
Model	6	15.53	<0.001	81.6

The covariates are the monthly averages of the two proximate factors daylength and nocturnal luminosity ($N = 24$).

the seasonal activity shift is mediated by a specific response, that is, an increase in daylight activity with increasing daylength, and a decrease in diurnal activity when daylength is decreasing (Curtis et al. 1999; Donati & Borgognini-Tarli 2006). The activity profiles recorded in STL and BER match the pattern described for most cathemeral lemurs in Madagascar (Curtis & Rasmussen 2002; Curtis et al. 2006; but see Andrews & Birkinshaw 1998), pointing to the presence of seasonal fluctuations of this activity pattern. A tight entrainment with the seasonal changes of the day–night cycle is also common in nocturnal (Charles-Dominique 1977; Petter-Rousseaux 1980; Aujard et al. 1998; Genin & Perret 2000; Schmid 2001) and diurnal lemur species (Pereira et al. 1999; Erkert & Kappeler 2004). This pattern seems to be the consequence of the island seasonality characterizing Malagasy habitats (Wright 1999; Ganzhorn et al. 2003; Dewar & Richard 2007) and, in this sense, lemur cathemerality is no exception.

Brown lemurs were also influenced in a similar way by moon luminosity. Although the overall nocturnal activity was lower in BER than in STL, the lemurs showed a clear pattern of increased nocturnality ranging from low to high luminosity levels at night. These findings match the results that low luminosity levels have a negative masking effect on the circadian activity of cathemeral primates (Erkert 1989; Donati et al. 2001; Fernandez-Duque 2003; Kappeler & Erkert 2003; Donati & Borgognini-Tarli 2006; Schwitzer et al. 2007). Given that the endogenous rhythm of brown lemurs is basically nocturnal (Erkert & Cramer 2006), the masking effect of low luminosity levels at night seems to move these primates into an obligatory diurnality during new moon days. While the proxy effect of moon luminosity on the activity balance of cathemeral primates has been repeatedly demonstrated, the possible benefits of lunarphilia are still vague (Bearder et al. 2006). In this respect, cathemeral and nocturnal primates behave in an opposite way to the majority of the other nocturnal mammals, which appear rather lunarphobic (Bearder et al. 2006; Nash 2007). Since the eyes of

cathemeral primates have intermediate adaptations between diurnal and nocturnal lifestyles (Kirk 2006) and, with the exception of *Hapalemur* spp., do not possess a true tapetum lucidum (Pariente 1976; but see Kirk 2006), it has been proposed that lunarphilia might be related to visual advantages (Donati et al. 2001; Bearder et al. 2006), such as an improved ability to spot predators and/or detect food items in the forest.

Ultimate Factors

Four nonmutually exclusive ultimate reasons have been suggested to explain the adaptive value of cathemeral activity in primates: thermoregulatory benefits, antipredator strategy, avoidance of competition and metabolic dietary-related needs.

Shifting the activity phase to avoid temperature extremes seems to be one of the most common reasons for a diel activity pattern in many taxa (Valdimarsson et al. 1997; Halle & Stenseth 2000). This is particularly relevant for animals living at high latitudes (Chappell 1980; Zielinsky 2000) or in arid regions (Grenot 1992; Daly et al. 2000) to avoid cold and/or heat stress. While cold stress is unlikely to be relevant in our two study sites, average diurnal temperature was higher in the arid environment of BER than in STL. Thus, the heat stress avoidance hypothesis would predict more nocturnal activity in BER during the warm season, that is, November–March, than in STL. Our results, however, do not support this idea and the BER brown lemurs were actually more diurnal than their congeners in STL. Also, the model that accounts for temperature variation at the two sites does not explain more variance than that explained by proximate factors. These results are in accordance with other studies reporting a seasonal shift in activity in habitats without strong temperature seasonality (Andrews & Birkinshaw 1998; Donati & Borgognini-Tarli 2006; Tarnaud 2006).

The importance of predation pressure by diurnal raptors in determining the activity shift is supported by observations in deciduous forests, where cathemeral lemurs increase their nocturnal activity when the leaves fall, that is, with increased canopy exposure (Curtis et al. 1999; Donati et al. 1999; Rasmussen 1999, 2005). This hypothesis would predict no need for an activity shift where canopy exposure is constant year-round. The index of canopy exposure, our proxy of predation pressure by diurnal raptors, did not differ between the two forests year-round. Since the two lemur populations are exposed to a similar range of diurnal raptors and large carnivores are absent in these forest fragments (Jolly et al. 2006; Ganzhorn et al. 2007), predation pressure may not differ significantly between the two sites. Accordingly, in the multivariate analysis, the annual variation in canopy exposure turned out to be unable to explain any activity variation once the influence of proximate factors was removed. Also, a seasonal shift of lemur activity has been observed at sites where large raptors are absent (Tarnaud 2006).

Temporal partitioning as a mechanism of coexistence among species has rarely been explored and is generally considered to be uncommon (Schoener 1974; Ganzhorn 1989; Kronfeld-Schor & Dayan 1999). However, cathemeral activity may be advantageous in the presence of sympatric congeneric species (Tattersall & Sussman 1998; Rasmussen 1999; Curtis & Rasmussen 2006). Intra- and interspecific interference competition was a potential ultimate factor that differed significantly between the two sites. The presence of diurnal lemur competitors at BER (see also Simmen et al. 2003) would predict a greater avoidance of the diurnal niche at this site, and a consequent expansion of the nocturnal component. However, our results are again in contrast with the prediction. Brown lemurs in BER consistently showed more diurnality than in STL. Most importantly, aggressive interactions as a proxy of interference competition did not emerge as a significant factor in the ANCOVA model.

According to the food quality hypothesis, activity over the whole 24 h cycle would be necessary in cathemeral lemurs to spread out the ingestion of low-quality food, that is, food with high fibre content, during periods of resource scarcity (Engqvist & Richard 1991). This strategy would be necessary because of a lack of digestive specializations in truly cathemeral species, such as *Eulemur* spp. (Hill 1953; Overdorff & Rasmussen 1995). In fact, the quality of the diet differed significantly in our two lemur populations, being much richer in fibre in STL than in BER. Following the diet hypothesis, this difference would predict a greater activity expansion over the 24 h cycle in STL than in BER. Our results supported this prediction, and the fibre content in the diet was able to explain a significant part of the activity variation even after we controlled for proximate factors and the site effect. While the link between food content and the activity changes in previous studies on cathemeral primates is rather controversial (Andrews & Birkinshaw 1998; Colquhoun 1998; Curtis et al. 1999; Rasmussen 1999; Fernandez-Duque 2003; Kappeler & Erkert 2003), food quality has rarely been tested in detail via nutritional analyses. The importance of nutritional analyses is demonstrated by our findings given that, in STL, brown lemurs had a more frugivorous diet (79.4%; monthly range: 47.2–93%) than in BER (70.2%; monthly range: 19.8–100%) but they actually had a diet that contained much more fibre (37.5% at STL and 24.9% at BER). A similar relation between fibre content in food items and activity changes was recently found for *E. f. fulvus* (Tarnaud 2006), whereas the nutritional intake of *E. mongoz* does not show any association with its activity pattern (Curtis et al. 1999). Our results stand in apparent contrast with studies on brown lemur dental morphology (Kay & Hylander 1978) and NDF digestibility (58.9%; Klein 1991) which show that these species are comparable to folivorous primates. However, recent research showed a much lower ability of brown lemurs to digest NDF (41.5%) than previously thought and an even lower ability to digest total insoluble fibre (27.7%), which seems to be a more reliable index of fibre digestibility (Campbell et al. 2004a). These figures are substantially lower than those recorded for folivorous lemurs and comparable with the strictly frugivorous *Varecia* (Campbell et al. 2004a) which might also be cathemeral (A. Britt, personal communication). This observation, coupled with the fact that brown lemurs have a food transit time scaled on body size similar to that of specialized fruit eaters (Lambert 2002; Campbell et al. 2004b; Donati et al. 2007), supports the idea that they need alternative solutions to meet their energy requirements during periods of low-quality food availability.

The strategy observed in these lemurs resembles that reported for several groups of small mammals. In fact, the relationship between cathemeral or ultradian activities and foraging frequency, caused by digestive constraints, has been well documented in mammals of small, energy-demanding taxa such as weasels (Zielinsky 2000), shrews (Merritt & Vessey 2000) and voles (Halle 2006). Although comparative long-term data from different Malagasy habitats are still scarce, the seasonal and unpredictable fluctuation in the availability of high-quality food (Ganzhorn et al. 1999; Wright 1999; Bollen & Donati 2005; Wright et al. 2005) and the general low food quality (Voigt et al. 2004; Bollen et al. 2005) that characterizes the island, are among the possible reasons for this adaptation. This is in accordance with other strategies used by lemurs to cope with extended periods of scarcity (Wright 1999; Ganzhorn 2002; Wright et al. 2005). Torpor, hypometabolism, and gut adaptations to survive on a leafy diet are some of these strategies, adopted, respectively, by Cheirogaleidae (Ganzhorn et al. 2003; Fietz & Dausmann 2006) Megaladapidae and Indridae (Irwin 2006; Thalmann 2006). Cathemerality, that is, the flexible activity without limiting specializations adopted by Lemuridae, seems to be an alternative solution to the same problem. It must be stressed, however, that no unitary factors are expected to explain activity

variation in cathemeral primates. Rather, a mixture of nonmutually exclusive pressures are likely to be relevant in different areas and/or for different species (Curtis & Rasmussen 2006). For example, the fact that some populations of the specialized folivore *Hapalemur* are also cathemeral (Mutschler 1999) points to the existence of additional factors to determine cathemerality in Malagasy lemurs.

Conclusions

In summary, we found that the cathemeral activity of two brown lemur populations living in two different habitats is mainly and similarly influenced by two proximate factors, photoperiod and moon luminosity, and one ultimate factor, diet quality. If brown lemurs were originally nocturnal, as indicated by chronobiological experiments (Erkert 1989; Erkert & Cramer 2006), we need to explain which masking factors keep them strictly (BER) or mainly (STL) diurnal during certain periods of the year. As it seems unlikely that these animals shift their endogenous activity rhythm, because of the evolutionary rigidity that characterizes the internal endogenous rhythmicity (Fenn & Macdonald 1995; Kronfeld-Schor et al. 2001), masking agents seem to be the best candidates to adjust and fine tune temporal programmes to local environmental factors (Marques & Waterhouse 1994). Following this reasoning, we suggest that the activity of our two brown lemur populations is the result of a photoperiodic entrainment, a monthly lunar masking and a seasonal-habitat masking, caused by variation in food quality, of the circannual rhythm of a nocturnal primate.

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