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From darkness to daylight: cathemeral activity in primates

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Summary – *Within the primate order, Haplorrhini and Strepsirrhini are adapted to diurnal or nocturnal lifestyle. However, Malagasy lemurs exhibit a wide range of activity patterns, from almost completely nocturnal to almost completely diurnal, while others are active over the 24-hours. Cathemerality, the term minted by Tattersall (1987) to define the latter activity style, has been recorded in* Eulemur *and* Hapalemur*, as well as in some populations of the New World monkey* Aotus*. As most animals specialize in a particular phase of the 24-hour cycle, the cathemeral strategy is expected to be the consequence of powerful pressures. We will review hypotheses and findings on ultimate reasons of primate cathemeral activity, present proximate factors shaping the activity cycle and discuss the possible roles of feeding competition, food shortage and dietary quality, thermoregulation, and predation in making this activity advantageous. Overall, we will see how unstable environments and various community characteristics would tend to select for a flexible activity phase. Most attempts to explain cathemerality have relied on adaptive explanations, which assume that this activity is stable and deep-rooted. In contrast, some researchers have suggested that cathemerality represents a non-adaptive transitional state between nocturnality and diurnality. Chronobiology studies indicate that cathemeral species should be considered as dark active primates, thus favouring a recent origin. On the other hand, anatomical analyses demonstrate that the eye of cathemeral primates is a good compromise between the functional demands of vision under both nocturnal and diurnal conditions, thus suggesting an ancient origin. On the basis of recent phylogenetic trees we will discuss different scenarios for the evolution of cathemerality and diurnality in lemurs. Furthermore, we will evaluate the hypothesis that early primate ancestors may have needed to see well both in the daytime and at night, before becoming specialized in one direction. Finally, we will consider some interdisciplinary implications of the study of a day-night activity in primates.*

Keywords – *Activity phases, Lemurs, Aotus, Community ecology, Primate evolution.*

Introduction

"Ecologically speaking, the diurnal world and the nocturnal world are completely different". With this sentence Charles-Dominique (1975) introduced his historical paper describing the ecological interpretation of nocturnality and diurnality in primates. In fact, animals have to find different solutions to cope with these two opposing sensory environments which, consequently, have greatly influenced their evolution. Thus, from physiology to sociality several traits characterize the two choices of life, and they may tell us the activity phase of an animal. Generally speaking, the need to orientate, searching for food or escaping from predators, during the two phases of the 24-hour cycle improved a unique perception of the environment, while hampering others (Martin, 1990; Halle, 2006). So, a fine-grained sense of olfaction and/or a good hearing perception give a nocturnal animal the possibility to survive, while diurnal animals can solve the same problem with good vision during the hours of daylight. In evolutionary terms, the ancestral condition of

mammals is supposed to consist of a well developed olfactory region that gave them the opportunity to successfully occupy the nocturnal niche and avoid competition with reptiles (Jarison, 1973; Eisenberg, 1981; Kemp, 1982; Kermack & Kermack, 1984). Conversely, birds developed an extremely good sense of vision necessary for flight, thus enabling them to occupy the diurnal world (Charles-Dominique, 1975). While these two opposite temporal niches are recognized for mammals and birds, there are obviously a number of exceptions, especially in the former class. In fact, extant mammals appear in a widespread radiation and many forms occupy the diurnal niche avoiding competition with birds by a number of adaptations such as a large body size (Charles-Dominique, 1975; Martin, 1990).

This mammalian expansion into the diurnal life is well represented in the primate order which was traditionally split into two subdivisions: on the one side the prosimians which conserve ancestral characters, and on the other side the anthropoids which represent the suborder with more derived traits (Napier & Napier, 1985; Fleagle, 1988; Martin, 1990). While a number of exceptions are present, this phylogenetic duality largely reflects a duality in activity patterns. A solitary life, social communication mediated principally by olfactory and vocal signals, the presence of a *tapetum lucidum* (a reflecting retinal layer enhancing vision at night), and a low metabolic rate are among the traits wich are related to the nocturnal habits of prosimians. Conversely, a gregarious life, communication mediated mainly by visual signals and enhanced by color vision, and greater behavioural complexity correlate with the diurnality of anthropoids (Clutton-Brock & Harvey, 1977; Fleagle, 1988).

Traditionally, prosimians were considered as a group with a way of life nearer to that of the hypothetical ancestral primates, thought to be nocturnal, while the complexity of the anthropoid social life was assumed to be relatively recent during primate evolution (Napier & Napier, 1985; Martin, 1990). As noted above, this broad categorization is complicated by some relevant exceptions in the two directions. Several genera of prosimians, all included in the Malagasy lemur radiation, display a mainly diurnal activity, while the Neotropical anthropoid *Aotus* is nocturnal (Tattersall, 1982; Kappeler, 1998; Heesy & Ross, 2001).

However, the picture of primate activity is even more complicated. In his pioneering studies on lemur behavioural ecology, Petter (1962) noted that "some Malagasy diurnal lemuriformes have a certain disposition toward a crepuscular, or even occasionally, nocturnal, way of life". But only twelve years later Tattersall noticed and subsequently confirmed that *Eulemur fulvus* living on Mayotte island showed an activity evenly distributed throughout the 24-hour cycle (Tattersall, 1979; Tarnaud, 2006). Tattersall was able to conduct several complete nights of observation lumping into half-hour periods the activity/rest ratio of these previously hypothesized diurnal lemurs. This atypical activity, which did not match with the crepuscular term used to define animals active around sunrise and sunset, was defined as "cathemeral" (Tattersall, 1987), a term coined from the greek words "κατά" (through) and "ημήρα" (the day, read as the 24-hour daily cycle). Since then, by definition, cathemerality is meant as an activity, particularly feeding and travelling, which is distributed in "equal, or at least significant, amounts within both the light and the dark portions of the 24-hour daily cycle" (Tattersall, 1987). It is important, as noted by Halle (2006), to speak only about "cathemeral activity" or "cathemeral species" and not about a cathemeral biorhythm or pattern, since different patterns of activity may be included in a cathemeral type of activity. Thus, a cathemeral animal cannot be defined simply as diurnal, nocturnal or crepuscular.

In Madagascar during the last two decades, a routinely cathemeral activity, either year-round or on a seasonal basis, has been described in all species of the genus *Eulemur* (Appendix). A year-round cathemerality is exhibited by *Eulemur rufus* both in the eastern rain-forests (Overdorff & Rasmussen, 1995) and in the western deciduous forests (Donati *et al.*, 1999, 2001; Kappeler & Erkert, 2003), though in the latter habitat with a marked seasonal variation. A more or less even cathemeral activity over the year has been described for *E. coronatus* (Freed, 1996), *E. macaco* (Colquhoun, 1998; Andrews & Birkinshaw, 1998), *E. rubriventer* (Overdorff & Rasmussen, 1995), *E. sanfordi* (Freed,

1996). A seasonal fluctuation from a cathemeral activity during the dry season to a mostly diurnal activity in the wet season has been shown in *E. collaris* (Donati & Borgognini-Tarli, 2006), *E. fulvus* (Rasmussen, 1999; Tarnaud, 2006) and some populations of *E. mongoz* (Curtis *et al.*, 1999). An impressive shift from diurnality in the wet season to nocturnality during the drier months seems to be the case for other *E. mongoz* populations (Rasmussen, 1999). Cathemerality has been also recorded in *E. albifrons* (Vasey, 2000), while there are still no reports on the activity type of *E. albocollaris*, though it is suspected to be cathemeral.

Year-round cathemerality has been also reported in some species of the genus *Hapalemur*, namely *H. alaotrensis* (Mutschler, 1999, 2002) and *H. simus* (today *Prolemur simus*; Tan, 1999; Appendix), while the other species of the genus appear to be diurnal (Overdorff *et al.*, 1997; Tan, 1999; Grassi, 2001; Donati, pers. observ.). There are also some reports which indicate the presence of a cathemeral activity in the other two Lemuridae genera, *Lemur* (Traina, 2001) and *Varecia* (Britt, pers. comm.), but systematic nocturnal observations are lacking and, as far as we know, the two taxa are still considered mainly diurnal (Curtis & Rasmussen, 2002). Outside Madagascar, cathemerality has been clearly recorded in the platyrrhine *Aotus trivirgatus* (Wright, 1989, 1996) and, recently, in *Aotus azarai* (Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006) in contrast with the nocturnality observed in other species of this genus (Kinzey, 1997). Finally, there is a report which indicates the presence of cathemeral activity in the Belizian *Alouatta palliata* (Dahl & Hamingway, 1988), though this study was preliminary and further investigations are needed to confirm this activity in a genus otherwise considered strictly diurnal (Kinzey, 1997).

Given the opposite adaptations which a diurnal lifestyle requires compared to a nocturnal one as well as the benefits of specializing to either bright-light or darkness, peculiar constraints are expected to be at the origin of this activity in primates. In fact, Halle (2006) argued that cathemeral activity might have evolved in species for which the selective pressure for adequate time of activity is particularly demanding, and for which the disadvantage of not being adapted to day, night or twilight is compensated for by the advantage of not being constrained to a particular phase of the 24-hour cycle. This adaptive interpretation of cathemerality has been deeply investigated by long-term field research searching for testable ultimate reasons. A number of ecological factors has been suggested to determine the variation of diurnal and nocturnal acivities in cathemeral primates, even if the results do not indicate unitary explanations but rather the interaction among several variables (see also Curtis & Rasmussen, 2006). Summarizing, cathemeral activity may possibly be advantageous as a thermoregulatory strategy in the presence of adverse climatic conditions (Tattersall, 1977; Curtis *et al.*, 1999; Mutschler, 1999, 2002; Fernandez-Duque, 2003), minimizing predation risk (Overdorff, 1988; Curtis *et al.*, 1999; Donati *et al.*, 1999; Rasmussen, 1999; Colquhoun, 2006), allowing survival during lean periods and/or in the presence of a low-quality diet (Engqvist & Richard, 1991; Wright, 1999; Tarnaud, 2006), and reducing food competition (Rasmussen, 1999; Curtis & Rasmussen, 2006). The presence of ecological constraints able to shape the activity of cathemeral primates would favour an adaptive vision of cathemerality, possibly as a stable strategy which might be ancestral at least for the genera involved (Tattersall, 1982; Curtis & Rasmussen, 2002, 2006). However, questioning the possible adaptive basis of this activity, van Schaik and Kappeler (1996) suggested that cathemerality might represent a non-adaptive shift from nocturnality to diurnality due to an evolutionary disequilibrium caused by the Holocene extinction of competitive lemurs and, particularly, large predators (see also Kappeler & Erkert, 2003).

The purpose of this paper is to review supporting and contradicting evidence for the main ecological hypotheses suggested to explain cathemerality in primates. This will help us to evaluate whether this activity has an adaptive value in the two regions where has been discovered in primates, i.e. Madagascar and Neotropics. We will try to frame the argument in a broader perspective, taking into consideration chronobiology, visual anatomy, forest ecology, community structure and recent phylogenetic findings.

Potential ultimate factors of cathemerality

Thermoregulation strategy

The island of Madagascar is located at the southern periphery of the tropics. The morphology of the island as well as its location create very different climatic situations ranging from the desertic weather of the southern spiny forests to the perhumid conditions of the eastern rainforests (Fig. 1). Thus, a variable and sometimes severe climate is expected to have had a major impact on the evolution of lemur traits (Ganzhorn *et al.*, 1999; Wright, 1999; van Schaik *et al.*, 2005). On the basis of his observations on *E. mongoz* of the Comoro islands, Tattersall (1976) first hypothesized that cathemerality could be an adaptation to avoid harsh climatic conditions.



Fig. 1 - Habitat types and distribution in Madagascar. North is up.

In particular, Tattersall recorded a mainly nocturnal activity in *E. mongoz* populations living in the warm lowland forests of Mohéli and Anjouan, while the same species was diurnal in the cold central highlands of the latter island (Tattersall, 1976, 1978). More recently, the avoidance of high temperatures during daytime by increasing nocturnal activity has been shown in *Hapalemur alaotrensis* living in the reed beds of the lake Alaotra (Mutschler, 1999, 2002) and in *Aotus azarai* in the Argentinean seasonal Chaco (Fernandez-Duque, 2003), though for the latter species the relationship was significant only during full moon nights. In contrast to the avoidance of heat and/or cold stress by inactivity as seen above, some *Eulemur* populations seem to behave in the opposite direction being more active when temperatures are very low. Negative correlations between low temperatures at night and levels of nocturnality were reported in the deciduous forests on *E. mongoz* from Anjamena (Curtis *et al.*, 1999) and *E. rufus* from Kirindy (Donati *et al.*, 1999; Kappeler & Erkert, 2003), as well as in *E. rubriventer* living in the montane rainforests (Overdorff & Rasmussen, 1995). Based on these findings, Curtis and colleagues (1999) suggested that cathemerality may represent a behavioural mechanism fit to reduce thermoregulatory costs during cold periods. In this context, it is interesting to consider that *E. fulvus* has been shown to have a very low basal metabolic rate, among the lowest in prosimians, ranging 28-56% of the expected value based on the Kleiber equation (Le Maho *et al*, 1981; Daniels, 1984; Müller, 1985; McNab, 1986; Kurland & Pearson, 1986; Schmid & Ganzhorn, 1996; Genoud, 2002; Genoud *et al.*, 1997). This hypometabolism is coupled with high body temperatures and a thermoneutral zone between 20°C and 28°C (Daniels, 1984). Thus, for these lemurs being active during the colder part of the 24-hour cycle might be a strategy to maintain high body temperatures when ambient temperatures are well below the thermoneutral zone (Curtis *et al.*, 1999; Curtis & Rasmussen, 2002). This intriguing hypothesis is supported by the evidence that lemurs

use other behavioural mechanisms to thermoregulate such as sunning behaviour (Jolly, 1966; Sussman, 1974) or postures which increase or reduce exposed surface (Morland, 1993; Ostner, 2002). However, other cathemeral primates living in less seasonal habitats show an increase of nocturnal activity not associated with low temperatures (Andrews & Birkinshaw, 1998; Donati & Borgognini-Tarli, 2006; Tarnaud, 2006).

Food availability and quality

As we will see in detail later, seasonal fluctuations in food availability may represent a challenging task for primates both in Malagasy forests (Ganzhorn, 2002; Ganzhorn *et al*., 1999, 2003; Wright, 1999; Wright *et al*., 2005; Bollen & Donati, 2005) and in Neotropical habitats (van Schaik *et al*., 1993, 2005; Janson & Chapman, 1999; Stevenson, 2005). The first field studies on *Eulemur* species indicated a shift in activity patterns that coincides with consistent changes in dietary composition, e.g. from frugivory to nectarivory and/or folivory (Tattersall, 1979; Overdorff, 1988). In particular, a reduction of diurnal activity during the dry season associated with an increased proportion of leaves in the diet was observed in *E. fulvus* (Tattersall, 1979) and in *E. macaco* (Colquhoun, 1993). This observation led Engqvist and Richard (1991) to hypothesize that small-bodied primates without digestive specializations might cope with a seasonal increase of fibrous food items during lean periods by extending their activity bouts throughout the 24-hour period to minimize the time in which no food is being processed. In support of this hypothesis, comparisons of gut passage rate in frugivorous/folivorous lemurs (*Lemur* and *Eulemur*) compared to that of specialized folivores (*Hapalemur*) demonstrated that the former do not have the possibility to retain food in the gut for extended periods of time (Overdorff & Rasmussen, 1995). First appearance of markers indicated a passage rate 25 times faster in *E. fulvus* as compared to *H. griseus* (Overdorff & Rasmussen, 1995).

However, as seen above, some *Hapalemur* species are also cathemeral (Mutschler, 1999, 2002; Tan, 1999). Moreover, recent field studies on the dietary composition of *E. macaco* (Colquhoun, 1998), *E. rubriventer* and *E. rufus* (Overdorff & Rasmussen, 1995; Donati *et al*., 1999), *E. mongoz* (Curtis *et al*., 1999; Rasmussen, 1999) and *E. fulvus* (Rasmussen, 1999) revealed a non significant relationship between broad food category consumption and activity patterns. Also, so far, variation in forest food availability, measured by tree phenology, did not reveal any particular association with changes of activity in cathemeral primates (Curtis *et al*., 1999; Rasmussen, 1999; Fernandez-Duque, 2003). In fact, Overdorff and Rasmussen (1995), revisiting data on gut morphology and dentition in cathemeral species (Kay & Hylander, 1978; Sheine, 1979), questioned the hypothesis by Engqvist and Richard (1991) considering that these animals are probably able to process and effectively break down leafy food items. The hypothesis was tested in detail only recently, however, via the quantification of food intake and subsequent analysis of nutrient contents. The results were contradictory: *E. fulvus* in the Mayotte dry forest (Tarnaud, 2006) and *E. collaris* in the littoral rainforest (Donati *et al*., in prep.) showed an activity spread over the 24-hours (as opposed to a mainly diurnal activity) during the dry season, when they consumed more fibres, while no relation between activity and fibre consumption was found in the case of *E. mongoz* living in the deciduous forest of Anjamena (Curtis *et al*., 1999).

Antipredator strategy

Access to given food items is also influenced by factors other than mere availability or quality. Several *Eulemur* species exploit the upper layer of the forest during nocturnal feeding, while they feed in the middle and lower layers during the day (Overdorff, 1988; Andrews & Birkinshaw, 1998; Curtis *et al*., 1999; Donati *et al.,* 1999; Rasmussen, 1999). Response to predation pressure by diurnal raptors has been proposed as a possible factor for the evolution of cathemerality and selective use of forest layers (van Schaik & Kappeler 1996; for a review see Curtis & Rasmussen, 2002). In fact, at least three species of diurnal birds of prey, namely *Polyboroides radiatus*, *Accipiter henstii*, and *Buteo brachypterus* seem to represent a threat even for large lemur species (Goodman, 2003; Goodman *et al*., 1993). Karpanty (2006) found that lemurs represent 30.7% and 37.3% of the prey biomass in *A. henstii* and *P. radiatus*, respectively. In particular,

it has been calculated that diurnal raptor predation removes an average 5.8% per year of the total *E. rufus* population, with more than 20% of the adult mortality due to predation by *A. henstii* and *P. radiatus* (Karpanty, 2006). Moreover, the cathemeral *E. rufus* strongly reacts when raptors are flying overhead and possesses specific alarm-calls for different birds of prey (Fichtel & Kappeler, 2002). Because of the relevance of raptor predation for lemurs, seasonal variations of the leaf cover and subsequent changes in lemur diurnal exposure to raptors have been assumed to shape cathemerality in different habitats. In particular, lemurs living in deciduous forests should have a seasonal activity pattern, being more diurnal during the wet season when leaf cover is present and more nocturnal during the dry season when leaf cover is reduced (Curtis & Rasmussen, 2002). This idea is partly supported by the records of a seasonal cathemerality in the deciduous forests (Curtis *et al.*, 1999; Donati *et al.*, 1999; Rasmussen, 1999) as well as by the report of a non-seasonal, year-round cathemerality in several evergreen rainforests (Overdorff & Rasmussen, 1995; Andrews & Birkinsaw, 1998; Colquhoun, 1998). However, recent long-term studies in less seasonal forests which provide leaf-cover throughout the year revealed a seasonal cathemerality as well (Donati & Borgognini-Tarli, 2006).

Very recently, lemur cathemerality has also been related to the most powerful predator of Madagascar, the viverrid fossa, *Cryptoprocta ferox*. Lemurs may represent between 50 and 80 % of the diet of this carnivore (Hawkins, 2003). In his review on the interface between cathemerality and predation, Colquhoun (2006) proposed a co-evolutionary relationship between cathemeral lemurs and fossas. As observed in other mammals (Halle & Stenseth, 2000), being active irregularly over the 24-hour cycle might represent a sort of temporal cripticy for lemurs because of the lack of a fixed temporal window when predators may focus their efforts to capture preys (Colquhoun, 2006). Given that fossas are also cathemeral and belong to a later mammal radiation than lemurs, Colquhoun (2006) went a step further in his reasoning and suggested that fossa's cathemerality might be an adaptation to lemur cathemerality. This idea of cathemerality as a temporal cripticity against fossas has still to be evaluated with fine-grained, *ad hoc* data. However, while seasonal shifts in the ratio between diurnal and nocturnal activity are common, two main activity peaks centered around the hours of sunrise and sunset seem to be the norm for cathemeral lemurs (Curtis *et al.*, 1999; Curtis & Rasmussen, 2002; Kappeler & Erkert, 2003; Donati & Borgognini-Tarli, 2006) and *Aotus* (Fernandez-Duque & Erkert, 2006). These two activity peaks are very common among mammals (Aschoff *et al.*, 1982; Halle & Stenseth, 2000) and provide predators, especially the cathemeral ones, consistent temporal windows when concentrating predatory efforts.

Being cathemerality a strategy to avoid predation in the Neotropics, this idea has been also suggested to explain the observation of diurnal activity in some populations of the otherwise nocturnal *Aotus*. In particular, *Aotus* of the Paraguayan Chaco seems to show diurnal activity only where the nocturnal great horned owl, *Bubo virginianus*, occurs and the presence of diurnal raptors, e.g. harpy eagle, has not been recorded (Wright, 1989, 1996). However, in other cathemeral populations of *Aotus*, the influence of birds of prey on activity variations does not seem to be clear-cut (Fernandez-Duque, 2003). Also, in a study from Bolivia, diurnal activity has been reported in the local owl monkeys in spite of the occurrence of harpy eagles at the site (Mann, 1956, quoted in Fernandez-Duque, 2003).

Interspecific competition

As observed in other mammals, a variable activity might be advantageous also in minimizing competition for food resources. According to the concept of temporal eco-niche, diurnality and nocturnality may allow co-existence of sympatric species (Charles-Dominque, 1975; Halle & Stensteth, 2000). Curtis and Rasmussen (2006), reviewing the occurrence of cathemerality in primates and other mammals, argued that an activity spread over the 24-hour cycle may have contributed to increase the impressive diversity of Malagasy lemurs via a third temporal niche, i.e. the cathemeral one. This hypothesis was previously suggested by Tattersall and Sussman (1998), who noted the tendency for cathemeral *Eulemur* species to co-occur in sympatry in Northern Madagascar.

The hypothesis was first supported by a preliminary study of the feeding pattern of *Hapalemur simus* (today *Prolemur simus*) and *H. griseus* in captivity (Santini-Palka, 1994) where two different profiles of cathemerality were observed. In the field, the idea was supported by the finding of non-overlapping activity periods in sympatric *Hapalemur* species in Ranomafana (Tan, 1999). Also, a long-term field work at Ampijoroa showed two different cathemeral patterns in sympatric *E. fulvus* and *E. mongoz* (Rasmussen, 1999). In particular, *E. fulvus* seems to remain active over the 24-hour cycle year-round, while *E. mongoz* shifts from diurnality during the wet season to nocturnality during the dry season (Rasmussen, 1999). Rasmussen (1999) proposed that these two activities may mitigate the co-existence of these two similar-sized species with overlapping home-ranges and diets. Nocturnality and/or cathemerality has also been suggested as the main evolutionary strategy for *Aotus* to avoid feeding competition with several diurnal platyrrhines (Wright, 1989). As we discussed for other ultimate explanations, the avoidance of food competition fails to explain the whole variation observed so far in cathemeral species, though it can provide additional advantages in various habitats. In fact, several cathemeral species such as *E. collaris* (Donati & Borgognini-Tarli, 2006), *E. fulvus* (Tarnaud, 2006), and *H. alaotrensis* (Mutschler, 1999, 2002) neither occur with congeneric species nor seem to live in habitats with strong feeding competition.

The chronobiological basis of cathemeral activity

After reviewing the ultimate reasons which were advocated to answer the question *why* cathemeral primates developed their activity, we can describe *how* these primates may schedule their time. This basic question is investigated by chronobiology, the science which studies the circadian rhythms of animals (Aschoff, 1966; Bunning, 1977). Like every animal on earth, primates are capable of keeping their rhythm by an intrinsic, genetically determined biological clock even in the absence of environmental signals (Erkert, 2003). Thus, in constant light or darkness the activity phase continues to follow its natural schedule, called free-running rhythm, for an extended period (Aschoff *et al.*, 1982). In natural conditions, the biological clock is reset by the periodicity of some highly predictible factors, such as the day-night cycle, though some factors may bypass the clock and directly influence the activity via a so-called "masking" effect (Aschoff *et al.*, 1982). Erkert and Cramer (2006) argued that the analysis of the characteristics of the biological clock in cathemeral primates and comparisons with those of strictly diurnal and nocturnal species may provide insight to understand the transition from an originally nocturnal to a diurnal life-style in ancestral mammals. Chronobiological experiments indicated that the activity rhythm of *Eulemur* and *Aotus* is regulated by a circadian timing system which is entrained by the light-dark cycle (Erkert & Thiemann, 1983; Erkert, 1989; Erkert & Cramer, 2006). Also in the field, photoperiodic changes appear to be the most influential factor on the distribution of cathemeral lemur activity (Curtis *et al.*, 1999; Donati & Borgognini-Tarli, 2006). Monthly activity over the 24-hour period shows that cathemeral lemurs are largely biphasic throughout the year, and the two peaks of activity move towards the diurnal phase with increasing daylength and towards the nocturnal phase with decreasing daylength. Donati and Borgognini-Tarli (2006) demonstrated that the seasonal shift of activity peaks seems to be due to a specific response to sunrise and sunset time, as indicated by the negative year-round correlations between sunset time and onset of afternoon activity in collared lemurs. With increasing daylength and the increasing delay of sunset, afternoon activity begins earlier, thus increasing the proportion of activity that occurs during daylight hours. Conversely, with decreasing daylength and the advance of sunset, daily activity begins later, thus increasing the proportion of nocturnal activity. Since total activity of collared lemurs is constant during the year, the increase or decrease of diurnal activity corresponded to a parallel decrease or increase of nocturnal activity (see also Curtis *et al.*, 1999 for a similar pattern in *E. mongoz*). Erkert's chronobiological studies (1989) showed that both *Eulemur* and *Aotus* have their activity phase set to the dark part of the light-dark cycle to which they were exposed in laboratory conditions. Specifically,

constant lighting at 10^{-1} lux elicited an active phase of the free-running circadian rhythm starting from the dark phase and not from the light phase (Erkert, 1989). This would imply that cathemeral *Eulemur* and *Aotus* should be regarded as essentially dark-active species from a chronobiological point of view, since under natural environmental conditions the dark phase would correspond to the night-time (Erkert, 1989; Erkert & Cramer, 2006). In his laboratory experiments, Erkert (1989) also varied the illumination intensity during the dark-phase showing that *E. albifrons* is totally light-active when exposed to a dark phase of 10^{-6} lux, cathemeral at 10^{-3} lux, and dark-active at 10^{-1} lux. Thus, the luminosity prevailing during the dark phase strongly influences the lemur activity and low light intensities have activity-inhibiting effects via a masking phenomenon (Erkert & Grober, 1986; Erkert & Cramer, 2006). In natural conditions, the masking effect of low luminosity at night has been clearly demonstrated in *E. rufus* (Donati *et al.*, 1999, 2001; Kappeler & Erkert, 2003), *E. macaco* (Colquhoun, 1998), *E. collaris* (Donati & Borgognini-Tarli, 2006) and *A. azarai* (Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006). In the lattermost species, a lunar periodic variation of activity characterized by stronger nocturnality around full moon and more diurnal behaviour around new moon has been recorded. Interestingly, the activity seems to be strictly related to the presence of the moon, and it can be suddenly interrupted by unpredictable events such as a lunar eclipse (Donati *et al.*, 2001). However, in other cathemeral primates, i.e. *E. mongoz* (Curtis *et al.*, 1999), *E. rubriventer* (Overdorff & Rasmussen, 1995), several *E. fulvus* populations (Overdorff & Rasmussen, 1995; Rasmussen, 1999; Tarnaud, 2006), and *H. alaotrensis* (Mutschler, 1999), a relationship between nocturnal activity and luminosity has not yet been recorded.

Summarizing, from a chonobiological point of view cathemeral primates seem to possess a nocturnal-like biorythm, though they need some luminosity to be active at night.

Visual adaptations of cathemeral primates

Given the need of cathemeral primates to be fully active in light intensities ranging from full sunlight to new moon night, the study of their visual anatomy represents an important step for understanding physical adaptations to this lifestyle (Fig. 2). Before describing the characteristics of the cathemeral eye, it is worth noting that, with some relevant exceptions, great visual sensitivity and dichromacy characterize the visual performances of nocturnal primates, while diurnal primates generally exhibit great visual acuity and trichromacy (Jacobs, 2002). Starting from macroscopic retinal adaptations, *Eulemur* seems to show a rudimentary, weakly developed, *tapetum*



Fig. 2 - Picture showing the external visual adaptations of nocturnal, cathemeral, and diurnal lemurs. From the left to the right side: **Lepilemur leucopus, Eulemur collaris, *and* Propithecus verreauxi.**

lucidum (a typical nocturnal adaptation) and a lack of a *fovea*-like *area centralis* (a diurnal adaptation consisting in an area with high receptor density which increases acuity), whereas *Hapalemur*, together with *Lemur*, shows both structures (Castenholz, 1965; Pariente, 1970; 1976). However, there is much debate as to whether or not *Eulemur* possess a real *tapetum* (Rohen & Castenholz, 1967; Kirk, 2006). Cathemeral species show an intermediate degree of retinal summation (which increases acuity) between those observed in nocturnal and diurnal primates (Kay & Kirk, 2000; Kirk & Kay, 2004). Also, *E. fulvus* exhibits peaks of rod and cone densities which are intermediate between nocturnal and diurnal prosimians (Peichel *et al.*, 2001), though the cones/rods ratio in diurnal prosimians is much lower than in Anthropoids (Pariente, 1979; Heesy & Ross, 2001). Cathemeral lemurs also show orbit size and general eye morphology intermediate between those of diurnal and nocturnal prosimians (Kay & Kirk, 2000; but see also van Schaik & Kappeler, 1996) and more similar to the structures observed in other cathemeral mammalian taxa (Kirk, 2006). As for color vision, *Eulemur* and *Hapalemur* appear to be dichromatic, having the autosomal short-wavelength opsin gene and a single class of medium-long wavelength x-linked opsin gene (Jacobs & Degaan, 1993; Jacobs, 2002). A polymorphic character of the medium-long wavelength opsin gene, localized on the X-chromosome, revealed the capacity of trichromacy in females of *Varecia*, *Propithecus*, and, interestingly, *Cheirogaleus* (Tan & Li, 1999).

While the majority of platirrhines shows trichromacy polymorphisms, *Aotus* appears to be monochromatic (Jacobs, 2002). In particular, the owl monkey shows only an active medium-long wavelength opsin gene, while the short-wavelength, though present, does not express a pigment anymore (Jacobs *et al.*, 1996). Except for the very large, nocturnal-adapted, orbit size, *Aotus* possesses many traits which characterize a diurnal visual system, such as a retinal *fovea* and the lack of a *tapetum lucidum* (Noback, 1975).

Thus, even if visual carachteristics of cathemeral primates are rather mixed, there are some trends which indicate intermediate traits between nocturnal and diurnal adaptations.

The ecological context: Madagascar and Neotropics

Distribution of cathemeral primates

Before discussing in detail the ecological context where cathemeral primates are currently found it is worth to look first at their distribution in Madagascar and South-America. *Eulemur* species are relatively ubiquitous in Madagascar, ranging from the western deciduous forests to the eastern rainforests, while they do not occur in the very dry spiny forest which characterizes the southwest of the island (Tattersall, 1982; Fig. 1). *Eulemur* species are cathemeral in every habitat they have been studied in so far.

Even if not as widespread as *Eulemur*, *Hapalemur* species are distributed all over the eastern rainforest as well as in part of the north-west of the island (Tattersall, 1982). Moreover, some *Hapalemur* species are adapted to unique habitats such as lakeside reed bed (Mutschler, 2002) and swamp areas (Donati, pers. observ.). In the former habitat, *H. alaotrensis* is cathemeral (Mutschler, 1999; 2002), while in the others the genus seems to be mostly diurnal (Overdorff *et al.*, 1997; Grassi, 1997; Tan, 1999).

Moving from Madagascar to South America, *Aotus*, together with *Alouatta* and *Cebus*, is one of the most ubiquitous platyrrhine genera, occuring from Mesoamerica to Northern Argentina (Peres & Janson, 1999). As far as we know, the owl monkey is nocturnal over the majority of its range, while cathemerality has been recorded in the seasonal forests of Gran Chaco, at the southern eadge of the genus distribution (Wright, 1997; Fernandez-Duque, 2003).

Resource seasonality

As evident from an overview of the main hypotheses suggested to explain the adaptive significance of cathemerality, it is important to briefly review and compare the ecological contexts in which this activity has been recorded in primates, i.e. Madagascar and Neotropics. Climatic and environmental factors are obviously one of the most powerful external cause underlying adaptive developments. Sunlight, soil type, rainfall, and seasonality determine the tree phenology cycle, thus influencing the communities of primates which use

plant parts as food resources. In particular, resource productivity and seasonality have been demonstrated to directly affect the primate assemblages (Fleagle *et al.*, 1999). In spite of the common opinion that tropical forests represent stable and rich habitats, long-term studies have demonstrated that they face rainy and dry periods able to constrain plant productivity (for a review see Fleagle *et al.*, 1999). Overall, in all continents flower, leaf, and fruit production exhibit seasonal changes and high between-years variation (Janson & Chapman, 1999). In this section we will focus our attention only on fruit availability, since fruits form the bulk of the diet for most cathemeral species. Moreover, as described above, variations in fruit availability are at the basis of one of the main hypotheses postulated to explain the adaptive significance of cathemerality (Engqvist & Richard, 1991).

Compared to Neotropics, Malagasy habitats experience a strong seasonality characterized by occasional drops of temperature, droughts, and even cyclone damages (Wright, 1999). Also, a combination of poor soil fertility and low plant productivity relative to other continental forests characterizes the island (Ganzhorn *et al*, 1999). Long-term phenological studies have indicated that Malagasy rainforests, unlike other tropical habitats, present extended periods of fruit scarcity, up to six months a year, as well as irregular, asynchronous year cycles (Overdorff, 1993; Hemingway, 1996; Wright, 1999; Bollen & Donati, 2005; Wright *et al.*, 2005). As a consequence, the peak of fruit abundance in Malagasy rainforests is, on average, three months shorter compared to those recorded in South-America and mainland Africa (Strushaker, 1997; Chapman *et al.*, 2005; Stevenson, 2005). Moreover, some key-stone resources which allow primates to survive during scarcity periods, such as figs, are much rarer in Madagascar compared to other tropical sites (Goodman & Ganzhorn, 1997). Looking in more detail on the two main cathemeral lemur habitats, dry deciduous forests and rainforests, one can see important patterns. While fruits are more or less available year-round in dry deciduous forests (Sorg & Rohner, 1996; Curtis *et al.*, 1999), those available during the dry season present very low nutritional-quality values (Bollen *et al.*, 2005). On the other side of the island in the eastern rainforests, Ganzhorn and colleagues (1999) recorded a density of trees with fruits eaten by lemurs 3.4 times higher than in the western dry forests. However, the small crown diameters, possibly due to poor soil and cyclone impact, and the low probability of fruiting which characterize the Malagasy wet forests create dramatic bottle-necks for frugivorous lemurs during the scarcity periods (Ganzhorn *et al.*, 1999, 2003; Wright, 1999; Wright *et al.*, 2005; Bollen & Donati, 2005).

A pattern of marked fruiting seasonality seems to be common in the Neotropical forests (Terborgh, 1983; van Schaik *et al.*, 1993). Periods of high fruit productivity, however, are relatively long compared to lean periods making possible the existence of a mostly frugivorous community of primates (van Schaik *et al.*, 1993; Terborgh & van Schaik, 1987; Reed & Bidner, 2004). Also, in Neotropical forests keystone species, such as figs and palms, produce fruits during lean periods and are supposed to provide food for the frugivore community (Terborgh, 1986; Wright, 1989; but see Stevenson, 2005). In Colombia a unimodal pattern of fruit availability characterizes the forest with peaks starting from the middle of the dry season to the end of the rainy season (Stevenson, 2005). In Brazil, most fruits are produced from January to July, i.e. the end of the dry season to the end of the wet season, while very few plants produce fruits during the early dry season (Boubli, 2005). Even in the Argentinean Chaco, at the southern edge of Neotropical area, though Fernandez-Duque (2003) recorded a 4-month period of fruit scarcity during the dry season, the monthly average percentage of fruiting species was relatively high, being close to 50%.

Summarizing, compared to Neotropical habitats both the Malagasy dry and humid forests seem to represent a challenging place to survive for frugivorous primates.

Community characteristics and species interactions

Looking into similarities between the communities where cathemeral species occur, in both Madagascar and Neotropics, the primate assemblages are the result of an initial colonization event and a successive isolation from other primate radiations (Reed & Binder, 2004). About 45% of the primate species within South-American and Malagasy communities are in the 1-5 kg body size

range (Reed, 1999). In fact, today all platyrrhines and Malagasy lemurs (with the partial exception of *Lemur catta*) are arboreal, thus showing an upper limit in body size. As a consequence, though trophic adaptations seem to be quite different (Terborgh & van Schaik, 1987), the two communities share greater similarities when compared to Asian and African assemblages. Moreover, Neotropical primates are similar to the lemur assemblage in having few sympatric congeneric species (Peres & Janson, 1999), though it is important to note that the extant Malagasy community is more taxonomically and ecologically limited as compared to those of the very recent past (van Schaik & Kappeler, 1996). In fact, while at least 16 species of large, slow moving lemurs have gone extinct within the last millenium in Madagascar (Tattersall, 1982), extinct platyrrhines show an overall similarity to the modern lineages (Fleagle, 1988).

As compared to other primate communities, lemurs radiated tremendously, possibily due to the poor representation of other mammalian taxa (Wright, 1999; Reed & Binder, 2004). Besides the 15 lemur genera, only 25 genera of non-flying mammals have been described in Madagascar to date (Goodman *et al.*, 2003). Ungulates, monkeys, and many carnivores simply never reached this island (Tattersall, 1982). As noted by Reed and Binder (2004) bearing in mind the much larger eco-space occupied by the past Malagasy lemur community, this implies that primates filled an impressive quantity of niches on the island. Interestingly, there are no specialized frugivore primates in Madagascar with the only exception of *Varecia* (Ganzhorn *et al.*, 1999). Also, in contrast to the Neotropical situation, the guilds of frugivorous birds and bats are depauperate in Madagascar (Goodman & Ganzhorn, 1997; Wright, 1997). Moreover, almost all bat species living on the island are insectivores (Peterson, 1995) and only 8% of birds are frugivores (Fleming *et al.*, 1987).

Compared to those of Madagascar, the American primate community is ecologically uniform being biased toward small-bodied frugivore-insectivores, lacking specialized folivores and more than one nocturnal genus (Terborgh & van Schaik, 1987; Fleagle & Reed, 1996, 1999). This homogenity has been thought to be a consequence of the occupation of folivorous niches by other taxa such as sloths (Wright, 1997; Reed & Binder, 2004) and/or of seasonal coincidence of leaf and fruit production in Neotropical forests which should not make folivory advantageous (Terborgh & van Schaik, 1987). However, the ovelap among leaf and fruit production in the Neotropics has been questioned and is no longer considered to be a general phenomenon (Dew & Boubli, 2005)

As for interactions with predators, being the two communities mostly arboreal a relevant threat is represented by large diurnal raptors (Reed & Binder, 2004; Colquhoun, 2006). Hart reported (quoted in Reed & Binder, 2004) that raptor attacks make up 78% of the predatory events on primates in the Neotropics. We already showed that raptor predation is severe also for Malagasy lemurs (Karpanty, 2006). Besides predation from birds of prey, the fossa in Madagascar and a number of felids in the Neotropics are other threats for local primates, though the former appears to be much more specialized on primates than the latters (Colquhoun, 2006).

Cathemeral activity in primates: an assessment of evolutionary issues

Adaptive significance

This review shows that cathemerality in primates is not the result of an unitary ultimate reason but rather the capacity to be behaviourally flexible to different biotic and abiotic factors. A common denominator seems to be strong seasonality either on a climatic point of view or in resource availability (see also Bearded *et al.*, 2006). In fact, both Malagasy and Neotropical deciduous forests appear to be harsh habitats for arboreal, frugivorous animals (Peres & Janson, 1999; Fernandez-Duque, 2003; Bollen *et al.*, 2005). Even the Malagasy rainforests are far from being stable environments and they show dramatic resource seasonality compared to other continental wet forests (Ganzhorn *et al.*, 1999; Wright, 1999; Wright *et al.*, 2005).

On the basis of the available data, we propose to distinguish between two forms of day-night activity in primates: a primary and a secondary cathemerality. The primary cathemerality seems to be a key-adaptation of *Eulemur* species, while a

secondary cathemerality characterizes some populations of the genera *Hapalemur* (included the species *simus* recently moved into the separated genus *Prolemur*) and *Aotus*. The primary cathemeral *Eulemur* shows this kind of activity in all species and in every habitat they have been studied in so far. An activity spread over the 24-hour cycle seems to be well-rooted in this group of lemurs and used systematically as a strategy to cope with diverse ecological situations. Among the constraints which appear to influence *Eulemur*'s activity the availability of resources and, as a consequence, the quality of the diet (Engqvist & Richard, 1991) as well as the predation both by diurnal raptors and/or by cathemeral viverrids (Curtis & Rasmussen, 2002; Rasmussen, 2005; Colquhoun, 2006) seem to play a major role. These two biotic factors act in every habitats of Madagascar due to the general resource seasonality of Malagasy forests (Ganzhorn *et al.*, 1999) and the ubiquitous presence of fossas and large diurnal raptors (Langrand, 1990; Hawkins, 2003; Goodman, 2003). Moreover, high resource seasonality (Wright, 1999; Wright *et al.*, 2005) and heavy cathemeral predation (Colquhoun, 2006) seem to make Madagascar unique as compared to other primate habitats, thus suggesting the adaptive role of cathemerality on the island.

Even if food competition and temporal niche separation may certainly have an importance in some situations (for a review see Curtis & Rasmussen, 2006), this variable seems to be weakly present in several habitats where *Eulemur* species have been shown to be cathemeral. Furthermore, in a comparative context, Madagascar presents a few situations with congeneric species and a depauperate community of competitors among other mammals and birds (Goodman & Ganzhorn, 1997; Wright, 1997). The thermoregulation hypothesis, though important for other cathemeral primates, does not show a clear-cut pattern in the case of *Eulemur* species. In fact, seasonal change of the diurnal/nocturnal activity ratio are observed both in habitats where climatic changes are significant (Curtis *et al.*, 1999; Donati *et al.*, 1999; Kappeler & Erkert, 2003), i.e. the deciduous forests, and in regions where only a slight variation in temperature is recorded (Andrews & Birkinshaw, 1998; Donati & Borgognini-Tarli, 2006; Tarnaud, 2006). Interestingly, the only occasion where cathemeral activity is not observed in *Eulemur* species is captivity, where they appear to be mostly diurnal (Traber & Müller, 2006; Rasmussen, pers.comm.; but see Conley, 1975). So, in the absence of one or more of the above ecological constraints, the species of *Eulemur* appear to be very flexible to different situations, as opposed to being limited to a unique type of activity distribution. It is possible that diurnality in captivity is driven by some masking effects such as food supplying bouts, which are normally scheduled during the day.

Thus far, a secondary cathemerality is observed only in some populations of *Hapalemur*, otherwise mainly diurnal, and *Aotus*, otherwise nocturnal. In these populations, cathemerality seems to be the result of unusual (for these genera) ecological constraints due to the very peculiar situation in which they occur. In particular, thermoregulatory constraints to avoid heat stress are likely to be the reasons for the cathemerality observed in *Hapalemur alaotrensis* in the lake-side reed bed (Mutschler, 1999; 2002) and *Aotus azarai* in the very seasonal Argentinean Chaco (Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006). The unusually high interspecific competition recorded in the Ranomafana rainforest, with three sympatric bamboo lemur species, seems to be the main reason for the observed cathemerality in *H. simus* (today *Prolemur simus*; Tan, 1999). However, in other areas of the *Hapalemur* distribution, other species of bamboo lemurs (*H. aureus, H. griseus, H. meridionalis*) are diurnal (Overdorff *et al.*, 1997; Grassi, 1997; Tan, 1999; Donati, pers.observ.). We suggest that, in absence of the peculiar conditions described above, the gastric specialization typical of bamboo lemurs (Overdorff & Rasmussen, 1995; Tan, 1999) makes the cathemeral niche not especially advantageous for these species. As for *Aotus*, predation by large diurnal birds (Wright, 1997; Colquhoun, 2006) and availability of key-stone species during food scarcity periods (Dew & Boubli, 2005) which characterize Neotropical forests might limit these primates to a nocturnal lifestyle throughout most of the wide distribution of this genus.

Evolutionary scenarios

There is still an open controversy whether cathemeral activity represents an ancestral, adaptive strategy (Tattersall, 1982; reviewed by Curtis & Rasmussen, 2002) or if it is the result of a disequilibrium from nocturnality to diurnality due to the Holocene extinction of large diurnal raptors and competitive lemurs in Madagascar (van Schaik & Kappeler 1996; Kappeler & Erkert 2003). According to the latter hypothesis, all extant lemurs were nocturnal until the human arrival on the island around 2000 years ago. Thus, the extant diurnal and cathemeral lemurs should be in a "non-adaptive" phase which would be shown by a mismatch between their activity pattern and their anatomical adaptations (van Schaik & Kappeler, 1996). As for an adaptive emergence of cathemerality, this review on the last decade's research on cathemeral primates points to the adaptive significance of this activity in the peculiar context of Madagascar (see also Curtis *et al.*, 2006). Concerning the non-adaptive hypothesis, van Schaik and Kappeler (1996) based their reasoning on two main arguments. First, the transition from nocturnality to diurnality, presumably due to the demise of large diurnal raptors, would have been possible only if extant diurnal birds of prey do not represent an effective threat for the cathemeral/diurnal lemurs. This argument would be supported by comparative data from other continents showing the absence of cathemeral arboreal mammals in habitats where large diurnal raptors occur (van Schaik & Kappeler, 1996). However, an increasing number of reports (Goodman *et al.*, 1993; Powzyk, 1997; Karpanty & Goodman, 1999; Goodman, 2003; Karpanty, 2006) as well as behavioural and reproductive lemur traits (Sauther, 1989; Csermely, 1996) indicate that extant raptors can effectively prey upon large, diurnal and cathemeral lemurs. The second argument proposed by van Schaik and Kappeler (1996) would lie on the observation that cathemeral and diurnal lemurs do not possess clear-cut adaptations to their lifestyle but rather a puzzle of nocturnal/diurnal traits. In fact, reviewing anatomical and physiological lemur adaptations van Schaik and Kappeler (1996) showed that some traits (reduced *tapetum*, increased density of cones, pelage color) indicate a trend toward diurnality while others (dicromatism, brain size, metabolism, chronobiology) were typical of nocturnal species. However, recent findings on the anatomy of the visual system demonstrate that cathemeral primates possess intermediate, well distinguished traits between the nocturnal and the diurnal eye morphology, thus calling into question the basic assumption of the disequilibrium hypothesis (Kay & Kirk, 2000; Kirk, 2006). Moreover, the low levels of glutathione (a lens antioxidant which prevents ultraviolet damages) found in diurnal lemurs, cited as an indication of a recent nocturnality (van Schaik & Kappeler, 1996), though lower than those of anthropoids, have been shown to be comparable with those of other cathemeral and diurnal mammals (Heesy & Ross, 2001). In fact, Kirk (2006) observes that anthropoids appear to be unique and higly derived in their eyes and a comparison with them, as carried out by van Schaik and Kappeler (1996), does not clarify how recently cathemerality evolved in Madagascar (see also Heesy & Ross, 2001). Furthermore, Kay and Kirk (2000) showed that diurnal lemurs exhibit degrees of retinal summation comparable to those of some Eocene primates which, the authors observed, were presumably not in a state of evolutionary disequilibrium.

The fact that from a chronobiological point of view *Eulemur* behaves as a dark-active animal was also considered by van Schaik and Kappeler (1996) a piece of evidence supporting the recent nocturnality of the genus and thus the non adaptive hypothesis (see also Kappeler & Erkert, 2003). However, as far as we know, it is not clear how long the biological clock takes to change phase and the nocturnal/cathemeral *Aotus* shows a nocturnal circadian ryhthm as well (Erkert & Cramer, 2006), while this monkey originated from a diurnal ancestor (Martin, 1990). Thus, on the basis of all the above arguments, it seems parsimonious at present to hypothesize an old, adaptive origin of cathemerality in lemurs.

Looking at the Neotropics, in evolutionary terms *Aotus* cathemerality might be considered a conserved flexibility shown as the result of intense ecological pressures in peripheral populations of this genus (see also Kirk, 2006). Given the diurnal

ancestor of this anthropoid (Kinzey, 1997), it seems reasonable that the potential of a flexible activity was retained in this otherwise nocturnal species.

So, if we are right in considering cathemerality old in lemurs, it is of interest to briefly discuss when and why this unusual activity appeared in Madagascar. Recent phylogenetic reconstructions based on large-scale molecular analyses and multiple fossil calibrations suggest different scenarios (Yoder & Yang, 2004; Roos *et al.*, 2004). At this point, it is worth noting that, besides the cathemeral/diurnal family of Lemuridae (the diurnal *Varecia* and *Lemur*, the cathemeral *Eulemur*, and the diurnal/cathemeral *Hapalemur*), the Indridae are diurnal except for the nocturnal genus *Avahi* (Erkert & Kappeler, 2004), while the other lemur families are all nocturnal (Kappeler, 1998; Appendix). Also, in all the following analyses we did not distinguish between the genera *Hapalemur* and *Prolemur*, since the latter genus was coined only recently to define *H. simus* (Mittermeier *et al.*, 2006). Yoder and Yang (2004) analysis suggests an estimated age of 62-65 mya for the lemuriform clade, an initial separation of *Daubentonia* (42mya), and a divergence between Indridae, Lemuridae, Cheirogaleide, and Lepilemuridae within a period of 10 myr (42-32 mya) (Fig. 3A). Partly resolving the separation among families, Roos and colleagues (2004) by their analysis of short interspersed elements in the mitochondrial DNA indicate an ancient common ancestor for Indridae and Lemuridae dating approximately 42 mya (Fig. 3B).

Both the above analyses would seem to suggest a possible origin of cathemerality or diurnality in Madagascar nearly 40 mya and a later reversal to nocturnality by the genus *Avahi*. It is interesting to note, as observed by Yoder and Yang (2004), that this period coincides with major changes in global climate, rapid turnover of terrestrial biota, and a major extinction event occuring around 41-40 mya. In particular, paleoclimatic evidence clearly indicates global cooling and increased aridity during the late middle Eocene until the Eocene/Oligocene boundary (Berggren & Prothero, 1992). Thus, if cathemerality is a strategy to deal with seasonal harsh conditions, as suggested in our review, we may speculate that an ancestor of the Lemuridae, or even of the entire clade Lemuridae/Indridae, would have adopted a 24-hour foraging activity to survive lean periods. If this hypothesis is correct, cathemerality would have been one of the key adaptations of the early lemur radiation, being a possible alternative strategy to hibernation/torpor (the impressive trait which characterizes the Cheirogaleidae family). However, this scenario is not the most parsimonious one.

To visualize possible alternative scenarios for the

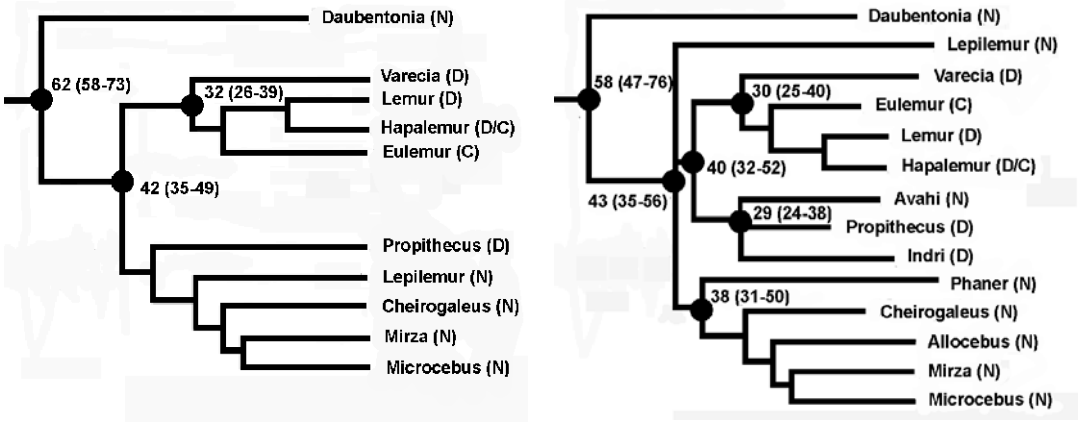


Fig. 3 – Two examples of phylogenetic trees for lemur genera. (a): reconstruction based on Yoder & Yang (2004) analysis; (b): reconstruction based on the analysis of Roos* et al. *(2004). Numbers (millions of years ago) represent estimated dates of divergence. N: nocturnal; C: cathemeral; D: diurnal. See text for details on the analyses used to build the two trees.

evolution of cathemerality, we referred to the phylogenetic tree built by Roos and colleagues (2004) since all the Malagasy genera are included in the picture (with the only exception of *Prolemur*; Fig. 4A,B,C). If cathemerality characterized the ancestor of the clade Lemuridae/Indridae (Fig. 4A), this vision requires at least (considering, parsimoniously, *Hapalemur* group diurnal) three independent gains of diurnality (in *Varecia*, the clade *Hapalemur*/*Lemur*, and the clade *Propithecus*/*Indri*) and one reverse to nocturnality (in *Avahi*). Alternatively, if the ancestral activity was diurnality (Fig. 4B) the panel requires one switch to cathemerality (in *Eulemur*) and one reverse to nocturnality (in *Avahi*). The second scenario remains the most parsimonious one even if we consider the *Hapalemur* group cathemeral.

Thus, parsimony would suggest that cathemeral activity is likely to be a key adaptation of the *Eulemur* group, therefore presuming an appearence in Madagascar at the initial radiation of this genus, around 8-12 mya (Yoder & Yang, 2004), from a diurnal form. Unfortunately, as we saw in our review, the mixed visual anatomy of the extant lemurs sheds little light on this issue, though it is certainly not indicative of a very recent origin of cathemerality (Curtis & Rasmussen, 2002; Kirk, 2006).

Recently, on the grounds of the presence of medium-long wavelength opsin genes in the nocturnal *Cheirogaleus* and a functional small wavelength opsin gene in most extant lemurs, Tan

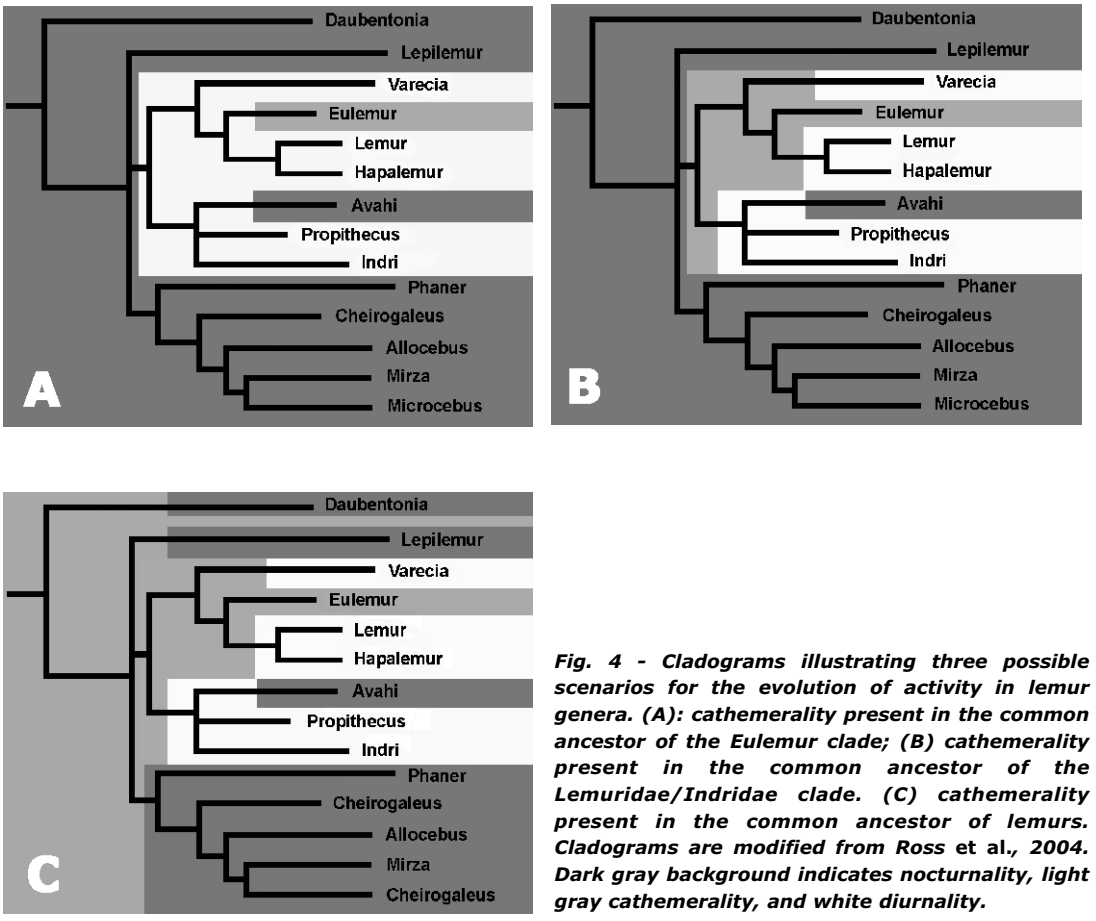


Fig. 4 - Cladograms illustrating three possible scenarios for the evolution of activity in lemur genera. (A): cathemerality present in the common ancestor of the Eulemur clade; (B) cathemerality present in the common ancestor of the Lemuridae/Indridae clade. (C) cathemerality present in the common ancestor of lemurs. Cladograms are modified from Ross et al., 2004. Dark gray background indicates nocturnality, light gray cathemerality, and white diurnality.

and colleagues (2005) suggested that the ancestral primate may have been cathemeral before specializing toward the nocturnal and the diurnal niche (see also Pariente, 1979). These authors discuss the importance for the ancestral primate to possess both a *tapetum* (for the nocturnal phase) and trichromacy (for the diurnal phase), and argue that this might interpret (but not resolve) the puzzling distribution of these two traits in extant lemurs (Tan *et al.*, 2005). Interestingly, the possibility of the body mass of an early primate being very tiny, perhaps shrew-sized (less than 30g), as recent evidence suggests it might have been (Gebo, 2004), would imply a very high metabolism and the need to forage over the 24-hour cycle as most extant shrews do (Merritt & Vessey, 2000; Halle, 2006), thus making a cathemeral eye advantageous. In Fig. 4c we present the scenario proposed by Tan and colleagues (2005) for the specific case of the lemur radiation. It is immediately apparent, however, that the hypothesis is weakened by the principle of parsimony, requiring three independent gains of diurnality and four gains of nocturnality (Fig. 4C). Moreover, the reconstruction of a nocturnal activity pattern for the majority of nodes in the most parsimonious tree of primates (based on Eocene fossils), the nocturnal activity of most archontans (the sister groups of primates) as well as the nocturnal morphology of most strepsirrhine eyes (for a review see Heesy & Ross, 2001) indicate that this revolutionary scenario must be considered as speculative until additional evidence is available.

Prospects for future studies and multidisciplinary implications

The emergence of cathemerality/diurnality represents a subject of basic importance to understand the adaptations behind primate radiations. The passage to a daylight activity has deeply influenced the subsequent evolution of anthropoids and, obviously, of Hominidae. However, while in almost every primatological text much space is devoted to describe the many anatomical, physiological, and behavioural adaptations related to this choice of life, there is still much debate "when, how, and why" this fundamental step has been completed during primate evolution. As appropriately noted by Martin (1990) the reconstruction of an ancestral primate as well as of an ancestral lemur should not just be a list of characters but rather a biological understanding of its lifestyle in an ecological context. Today, lemurs offer an excellent opportunity to study the transition from nocturnality to diurnality, since Madagascar is the only place where we can find a monophyletic, Eocene-like radiation which shows nocturnal, diurnal and cathemeral traits.

Being, however, the activity patterns a final output of many other adaptations, a huge number of complementary competences are needed for this kind of research. In this review we briefly gave an idea of the extensive data set from very diverse domains that are needed to compare and contrast in search for proximate and ultimate factors at the basis of cathemerality. Competences from comparative anatomy and physiology are certainly necessary to overcome the present fragmentary picture.The very first gap to be filled is to deepen our knowledge of the adaptations of primate visual systems, given their strict link with activity patterns. As noted by Kirk (2006), many features of *Eulemur* visual anatomy were described via old analyses conducted before the evolution of modern techniques such as the opsin-labelling methods. Recent advances in genetics are also likely to change our understanding of the visual complexity of cathemeral primates. Thus, the possibility to identify genes coding for opsin at different wavelengths (Tan *et al.*, 2005) as well as their expression deficits are today sheding light on diffusion and evolution of chromatic vision. Another promising avenue seems to be the reconstruction of fossil lifestyle via anatomical estimates associated to activity, such as orbit size and dimensions of optic nerve foramen (Kay & Kirk, 2000; Heesy & Ross, 2001). Apart from the obvious importance of the visual system, metabolic rate and body temperature regulation are other poorly-known aspects of lemur physiology that are deeply related to activity phase (Genoud, 2002). Preliminary data on basal metabolic rate show a surprising result in *Eulemur fulvus* (the lowest metabolism among primates), while the modern remote-sensing techniques may permit to draw profiles of energy consumption during the entire

activity period even in the field (Drack *et al.*, 1999). Finally, coupled with our knowledge on energy requirements, there is a growing need to ascertain the real nutritional values of the food items consumed by cathemeral primates. In fact, until a decade ago in most studies on the relation between dietary habits and activity, nutritional analyses were not included, and general food categories (fruits, leaves, insects, etc..) were used as a rough measure for food quality. However, recent data from the field point to the relevance of nutritional analyses in assessing dietary value. For example, while fruits are traditionally considered as highly-energetic, easy-to-digest food, recent studies in Madagascar show that there is tremendous variation in their nutritional quality among plant species and over the forest yearly cycles (Bollen *et al.*, 2005).

Traditionally primatology occupies a world apart from zoology, due to the differences between primates and the other taxa and, most importantly, for their proximity to humans. Nevertheless, if we want to evaluate initial, fundamental adaptations of the ancestral primates, such as activity patterns, it is clear that we need to integrate our primate database with those of other mammals (Halle, 2006). As shown in our review, chronobiology, is one of these examples. Another example is the precise definition of the ecological niche occupied by predators and competitors within the communities where primates live. Even in this field, new technological advances in remote tracking should now allow to follow animals otherwise impossible to observe, possibly revaluating the importance of environmental factors previously undetected or considered unimportant. This is immediately apparent if we consider, for example, how difficult it is for a researcher to observe and quantify predatory events.

Finally, it is of extreme importance to reconstruct the biotic and abiotic matrix where primates evolved. This include not only the climatic and ecological profiles of the extant tropical forests, but it requires a reasonably accurate reconstruction of the habitats where ancestral primates lived. This fundamental step requires competences from Earth science domains such as paleoclimatology. Only if we know the habitat conditions during the entire evolution of primates we may really judge whether present selective pressures may have been at the origin of a particular adaptation.

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Info on the web

http://www.duke.edu/web/primate/
Web site of the Duke University Primate Center. DUPC (one of the best place to study lemurs in the US) works for preservation and study of endangered prosimians through research, education, and conservation. You can find there educational opportunities available for undergraduate and graduate. Field work opportunities are often available.

http://icte.bio.sunysb.edu/
Web site of the Institue for Conservation of Tropical Ecology (at SUNY Stony Brook, New York). ICTE is dedicated to research, conservation, and training in tropical environment with a special focus on Madagascar.

http://www.dpz.gwdg.de/
Web site of the Deutsches Primaten Zentrum. The DPZ is one of the best center of research on lemurs in Europe. The Department of Behavioral Ecology and Sociobiology focus on the diversity and evolution of social systems in lemurs and platyrrhines, as well as the structure and function of their communities. Here you can read the contents of the Lemur News (http://www.dpz.gwdg.de/lnews/lemur.htm), the IUCN newsletter dedicated to Madagascar.

http://www.savethelemur.org/index.html/
Web site of the Madagascar Fauna Group. MFG is a consortium of North American and European zoos working in Madagascar to preserve its wildlife and also involved in field research. Captive propagation and release in the native habitats are some of the main goals of this group.

http://www.conservation.org/xp/CIWEB/regions/africa/madagascar.xml
Conservation International web site which provides detailed information on Madagascar conservation projects.

References

Andrews J., Birkinshaw C. 1998. A comparison between the daytime and night-time diet, activity and feeding height of the black lemur, *Eulemur macaco* (Primates: Lemuridae), in Lokobe Forest, Madagascar. *Folia Primatol.*, 69: 175-182.

Aschoff J. 1966. Circadian activity pattern with two peaks. *Ecology*, 47: 657-662.

Aschoff J., Daan S. & Groos G.A. 1982. *Vertebrate circadian systems*. Springer-Verlag, Berlin

Bearder S.K., K.A.I. Nekaris & D.J. Curtis 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatol.*, 77: 50-71.

Berggren W.A. & Prothero D.R. 1992. Eocene-Oligocene climatic and biotic evolution: an overview. In D.R. Prothero & W.A. Berggren (eds): *Eocene-Oligocene Climatic and Biotic Evolution*, pp. 1-28. Princeton University Press, Princeton.

Bollen A. & Donati G. 2005. Phenology of the Malagasy littoral forest of Sainte Luce, south-east Madagascar. *Biotropica*, 37(1): 32-43.

Bollen A., Donati G., Fietz J., Schwab D., Ramanamanjato J.-B., Randrihasipara L., Van Elsacker L. & Ganzhorn J.U. 2005. Fruit characteristics in a dry deciduous and a humid littoral forest of Madagascar: evidence for selection pressure through abiotic constraints rather than through coevolution by seed dispersers. In L. Dew & J.P. Boubli (eds): *Tropical Fruits and Frugivores: The Search for Strong Interactors*, pp. 92-118. Springer Publishers, Netherlands.

Boubli J.P. 2005. Floristics, primary productivity, and primate diversity in Amazonia: Constrasting an euthrophic Varzea forest and an oligotrophic Caatinga forest in Brazil. In J.L. Dew & J.P. Boubli (eds): *Tropical Fruits and Frugivores: The Search for Strong Interactors*, pp. 59-74. Springer Publishers, Netherlands.

Bunning E. 1977. *Die physiologische Uhr. Circadiane rhythmik und biochronometrie.* Springer, Berlin Heideleberg New York.

Castenholz E. 1965. Über die struktur der nezhautmitte der primaten. *Zeitsch. Zellforsch.*, 65: 646-661.

Chapman C.A., Chapman L.J., Zanne A.E., Poulsen J.R. & Clark C.J. 2005. A 12-year phenological record of fruiting: Implications for frugivore populations and indicators of climate changes. In J.L. Dew & J.P. Boubli (eds): *Tropical Fruits and Frugivores: The Search for Strong Interactors*, pp. 75-92. Springer Publishers, Netherlands.

Charles-Dominique P. 1975. Nocturnality and diurnality: an ecological interpretation of these two modes of life by an analysis of the higher vertebrate fauna in tropical forest ecosystems. In W.P. Luckett & F.S. Szalay (eds): *Phylogeny of the Primates*, pp 69-88. Plenum, New York.

Clutton-Brock T.H & Harvey P.H. 1977. Primate ecology and social evolution. *J. Zool. Lond.*, 183: 1-39.

Colquhoun I.C. 1993. The socioecology of *Eulemur macaco*: A preliminary report. In P.M. Kappeler & J.U. Ganzhorn (eds): *Lemur Social Systems and Their Ecological Basis*, pp. 13-26. Plenum Press, New York.

Colquhoun I.C. 1998. Cathemeral behaviour of

Eulemur macaco macaco at Ambato Massif, Madagascar. *Folia Primatol.*, 69: 22-34.

Colquhoun I.C. 2006. Predation and cathemerality: comparing the impact of predators on the activity patterns of lemurids and ceboids. *Folia Primatol.*, 77(1-2): 143-166.

Conley J.M. 1975. Notes on the activity pattern of *Lemur fulvus*. *J. Mammal.*, 56: 712-715.

Csermely D. 1996. Antipredator behavior in lemurs: evidence of an extinct eagle on Madagascar or something else? *Int. J. Primatol.*, 17: 349-354.

Curtis D.J., Donati G. & Rasmussen M.A. 2006. *Cathemerality*. *Folia Primatol.* 77: 1-194.

Curtis D.J. & Rasmussen M.A. 2002. Cathemerality in lemurs. *Evol. Anthropol.*, 11 [(Suppl]): 83-86.

Curtis D.J. & Rasmussen M.A. 2006. The evolution of cathemerality in primates and other mammals: a comparative and chronoecological approach. *Folia Primatol.*, 77(1-2): 178-193.

Curtis D.J., Zaramody A. & Martin R.D. 1999. Cathemeral activity in the mongoose lemur, *Eulemur mongoz*. *Am. J. Primatol.*, 47: 279-298.

Dahl J.F.& Hamingway C.A. 1988. An anusual activity pattern for the mantled howler monkey in Belize. *Am. J. Phys. Anthropol.*, 75: 201.

Daniels H.L. 1984. Oxygen consumption in *Lemur fulvus*: Deviation from the ideal model. *J. Mammal.*, 65: 584-592.

Dew J.L. & Boubli J.P. 2005. *Tropical fruits and frugivores: The search for strong interactors*. Springer Publishers, Netherlands.

Donati G. & Borgognini-Tarli S.M. 2006. Influence of abiotic factors on cathemeral activity: The case of *Eulemur fulvus collaris* in the littoral forest of Madagascar. *Folia Primatol.*, 77: 104-122.

Donati G., Lunardini A. & Kappeler P.M. 1999. Cathemeral activity of red-fronted brown lemurs (*Eulemur fulvus rufus*) in the Kirindy Forest/CFPF. In B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn & S.M. Goodman (eds): *New Directions in Lemur Studies*, pp. 119-137. Plenum Press, New York.

Donati G., Lunardini A., Kappeler P.M. & Borgognini-Tarli S.M. 2001. Nocturnal activity in the cathemeral red-fronted lemur (*Eulemur fulvus rufus*), with observations during a lunar eclipse. *Am. J. Primatol.*, 53: 69-78.

Drack S., Ortmann S., Bührmann N., Schmid J., Warren R.D., Heldmaier G. & Ganzhorn J.U. 1999. Field metabolic rate and the cost of ranging of the red-tailed sportive lemur (*Lepilemur ruficaudatus*). In B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn & S.M. Goodman (eds): *New Directions in Lemur Studies*, pp. 83-91. Plenum Press, New York.

Eisenberg J.F. 1981. *The mammalian radiations: An analysis of trends in evolution, adaptations and behaviour*. Athlone press, London.

Engqvist A. & Richard A. 1991. Diet as a possible determinant of cathemeral activity patterns in primates. *Folia Primatol.*, 57: 169-172.

Erkert H.G. 1989. Lighting requirements of nocturnal primates in captivity: a chronobiological approach. *Zoo Biol.*, 8: 179-191.

Erkert H.G. 2003. Chronobiological aspects of primate research. In J.M. Setchell & D.J. Curtis (eds): *Field and Laboratory Methods in Primatology*, pp. 252-270. Cambridge University Press, Cambridge.

Erkert H.G. & Cramer B. 2006. Chronobiological background to cathemerality: Circadian rhythm in *Eulemur fulvus albifrons* (Prosimii) and *Aotus azarai boliviensis* (Anthropoidea). *Folia Primatol.*, 77: 87-103.

Erkert H.G. & Grober J. 1986. Direct modulation of activity and body temperature of owl monkeys (*Aotus lemurinus griseimembra*) by low light instensities. *Folia Primatol.*, 47: 171-188.

Erkert H.G. & Kappeler P.M. 2004. Arrived in the light: Diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi*; Primates: Indridae). *Behav. Ecol. Sociobiol.*, 57: 174-186.

Erkert H.G. & Thiemann A. 1983. Dark switch in the entrainment of circadian activity rhythms in night monkeys, *Aotus trivirgatus* Humboldt. *Comp. Bioch. Physiol.*, 74A: 307-310.

Ficthel C. & Kappeler P.M. 2002. Anti-predator behaviour of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behav. Ecol. Sociobiol.*, 51: 262-275.

Fernandez-Duque E. 2003. Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys *(Aotus azarai)*. *Behav. Ecol. Sociobiol.*, 54: 359-369.

Fernandez-Duque E., Erkert H.G. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinean Chaco. *Folia Primatol.* 77(1-2): 123-138

Freed B.Z. 1996. Co-occurence among crowned lemurs (*Lemur coronatus*) and Sanford's lemurs (*Lemur fulvus sanfordi*) of Madagascar. PhD thesis, Washington University.

Fleagle J.G. 1988. *Primate adaptations and evolution*. Academic Press, London.

Fleagle J.G., Janson C. & Reed K.E. 1999. *Primate communities*. Cambridge University Press, Cambridge.

Fleagle J.G. & Reed K.E. 1996. Comparing primate communities: a multivariate approach. *J. Hum. Evol.*, 30: 489-510.

Fleagle J.G. & Reed K.E. 1999. Phylogenetic and temporal perspectives on primate ecology. In J.G. Fleagle, C. Janson & K.E. Reed (eds): *Primate Communities*, pp. 92-115. Cambridge University Press, Cambridge.

Fleming T.H., Breitwisch R. & Whitesides G.H. 1987. Patterns of tropical frugivore diversity. *Ann. Rev. Ecol. Syst.*, 18: 91-109.

Ganzhorn J.U. 2002. Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. *Oecologia*, 131: 427-435.

Ganzhorn J.U., Klaus S., Ortmann S. & Schmid J. 2003. Adaptation to seasonality: some primate and non-primates examples. In P.M. Kappeler & M.E. Pereira (eds): *Primate Life Histories and Socioecology*, pp. 132-148. University of Chicago Press, Chicago.

Ganzhorn J.U., Wright P.C. & Ratsimbazafy J. 1999. Primate communities: Madagascar. In J.G. Fleagle, C. Janson & K.E. Reed (eds): *Primate Communities*, pp. 75-89. Cambridge University Press, Cambridge.

Gebo D.L. 2004. A shrew-sized origin for primates. *Yrbk. Phys. Anthropol.*, 47: 40-62.

Genoud M. 2002. Comparative studies of basal rate of metabolism in primates. *Evol. Anthropol.*, 11 [Suppl]: 108-111.

Genoud M., Martin R.D. & Glaser D. 1997. Rate of metabolism in the smallest Simian primate, the Pigmy Marmoset (*Cebuella pygmaea*). *Am. J. Primatol.*, 41: 229-245.

Goodman S.M. 2003. Predation on lemurs. In S.M. Goodman & J.P. Benstead (eds): *The Natural History of Madagascar*, pp. 1221-1207. University of Chicago Press, Chicago.

Goodman S.M. & Ganzhorn J.U. 1997. Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. *Revue d'Ecologie- La Terre et la Vie*, 52: 321-329.

Goodman S.M., O'Connor S. & Langrand O. 1993. A review of predation in lemurs: implications for the evolution of social behavior in small, nocturnal primates. In P.M. Kappeler & J.U. Ganzhorn (eds): *Lemur Social Systems and Their Ecological Basis*, pp. 51-66. Plenum Press, New York.

Goodman S.M., Ganzhorn J.U. & Rakotondravony D. 2003. Mammals. In S.M. Goodman & J.P. Benstead (eds): *The Natural History of Madagascar*, pp. 1159-1186. University of Chicago Press, Chicago.

Grassi C. 2001. *The behavioural ecology of Hapalemur griseus griseus: The influence of microhabitat and population density on this small-bodied prosimian folivore*. PhD Thesis, University of Austiny, USA

Halle S. 2006. Polyphasic activity patterns in small mammals. *Folia Primatol.*, 77: 15-26.

Halle S. & Stenseth N.C. 2000. *Activity patterns in small mammals. An ecological approach*. Springer, Berlin Heidelberg New York.

Hamingway C.A. 1996. Morphology and phenology of seeds and whole fruits eaten by Milne Edward's sifaka, *Propithecus diadema edwardsi*, in Ranomafana National Park, Madagascar. *Int. J. Primatol.*, 17: 637-660.

Hawkins C.E. 2003. *Cryptoprocta ferox*, Fossa, *Fosa*. In S.M. Goodman & J.P. Benstead (eds): *The Natural History of Madagascar*, pp. 1360-1363. University of Chicago Press, Chicago.

Heesy C.P. & Ross C.F. 2001. Evolution of activity

patterns and chromatic vision in primates: morphometrics, genetics and cladistics. *J. Hum. Evol.*, 40: 111-149.

Jacobs G.H. 2002. Progress towards understanding the evolution of primate color vision. *Evol. Anthropol.,* 11[Supp1]: 132-135.

Jacobs G.H. & Deegan II J.F. 1993. Photopigments underlying color vision in ringtail lemurs (*Lemur catta*) and brown lemurs (*Eulemur fulvus*). *Am. J. Primatol.*, 30: 243-256.

Jacobs G.H., Neitz M. & Neitz J. 1996. Mutations in S-cone pigment genes and the absence of colour vision in two species of nocturnal primate. *Proc. R. Soc. Lond.* [Biol], 263: 705-710.

Janson C.H. & Chapman C.P. 1999. Resource and primate community structures. In J.G. Fleagle, C.H. Janson & K.E. Reed (eds): *Primate Communities*, pp. 237-267. Cambridge University Press, Cambridge.

Jarison H.J. 1973. *Evolution of the brain and intelligence*. Academic Press, New York.

Jolly A. 1966. *Lemur behaviour*. University of Chicago Press, Chicago.

Kappeler P.M. 1998. Nest, tree holes, and the evolution of primate life histories. *Am. J. Primatol.*, 46:7-33.

Kappeler P.M. & Erkert H.G. 2003. On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (*Eulemur fulvus rufus*). *Behav. Ecol. Sociobiol.*, 54: 359-369.

Kappeler P.M. & Ganzhorn J.U. 1993. The evolution of primate communities and societies in Madagascar. *Evol. Anthropol.*, 2: 159-171.

Karpanty S.M. 2006. Direct and indirect impacts of raptors predation on lemurs of Southeastern Madagascar. *Int. J. Primatol.*, 27: 239-261.

Karpanty S.M. & Goodman S.M. 1999. Diet of the Madagascar Harrier-Hawk, *Polyboroides radiatus*, in Southeastern Madagascar. *J. Raptor Res.*, 33: 313-316.

Kay R.F. & Hylander W.L. 1978. The dental structure of mammalian folivores with special references to primates and Phalangeroidea (Marsupialia). In G.G. Montgomery (ed): *Arboreal Folivores*, pp. 173-187. Smitshonian Institution Press, Washington DC.

Kay R. & Kirk E.C. 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. *Am. J. Phys. Anthropol.*, 113: 235-262.

Kemp T.S. 1982. *Mammal-like reptiles and the origin of mammals.* Academic Press, London.

Kermack D.M. & Kermack K.A. 1984. *The evolution of mammalian characters*. Croom Helm, London.

Kinzey W.G. 1997. *New world primates: Ecology, evolution, and behavior.* Aldine de Gruyter, New York.

Kirk E.C. 2004. Comparative morphology of the eye in primates. *The Anatomical Record*, 281A: 1095-1103.

Kirk E.C. 2006. Eye morphology in cathemeral lemurids and other mammals. *Folia Primatol.*, 77:27-24.

Kirk E.C. & Kay R. 2004. The evolution of high visual acuity in the Anthropoidea. In C.F. Ross & R.F. Kay (eds.): *Anthropoids Origin: New Visions*, pp.539-602. Kluwer Academic/Plenum Publishers, New York.

Kurland J.A. & Pearson J.D. 1986. Ecological significance of hypometabolism in nonhuman primates: allometry, adaptation and deviant diets. *Am. J. Phys. Anthropol.*, 71: 445-457.

Langrand O. 1990. *Guide to the birds of Madagascar*. Yale University Press, New Haven.

Le Maho Y., Goffart M., Rochas A., Felabel H. & Chatonnet J. 1981. Thermoregulation in the only nocturnal simian: the night monkey *Aotus trivirgatus*. *Am. J. Physiol.*, 240: 156-165.

Martin R.D. 1990. *Primate origins and evolution*. Chapman and Hall, London.

McNab B.K.1986. The influence of food habits on the energetic of eutherian mammals. *Ecol. Monogr.*, 56: 1-19.

Merritt J.F. & Vessey S.H. 2000. Shrews - small insectivores with polyphasic patterns. In S. Halle & N.C. Stenseth (eds): *Activity Patterns in Small Mammals: An Ecological Approach*, pp. 235-251. Springer, Berlin Heideleberg New York.

Mittermeier R.A., Konstant W.R., Hawkins F., Louis E.E., Langrand O., Ratsimbazafy J.H., Rasoloarison R., Ganzhorn J.U., Rajaobelina

S., Tattersall I. & Meyers D.M. 2006. *Lemurs of Madagascar* (2nd edition). Conservation International, Washington D.C.

Morland H.S. 1993. Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*). In P.M. Kappeler & J.U. Ganzhorn (eds): *Lemur Social Systems and Their Ecological Basis*, pp. 193-203. Plenum Press, New York.

Müller E.F. 1985. Basal metabolic rates in primates: the possible role of phylogenetic and ecological factors. *Comp. Bioch. Physiol.*, 81: 707-711.

Mutschler T. 1999. Folivory in a small-bodied lemur: the nutrition of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). In B. Rakotosamimanana, H. Rasamimanana, J.U. Ganzhorn & S.M. Goodman (eds): *New Directions in Lemur Studies*, pp. 221-239. Kluwer Academic/Plenum Publishers, New York.

Mutschler T. 2002. Alaotran gentle lemur: some aspects of its behavioral ecology. *Evol. Anthropol.*, 11 [(Suppl]): 101-104.

Napier J.R. & Napier P.H. 1985. *The natural history of the primates*. Cambridge University Press, Cambridge.

Noback C.R. 1975. The visual system of primates in phylogenetic studies. In P. Luckett & F.S. Szalay (eds): *Phylogeny of the Primates*, pp. 199-218. Plenum Press, New York.

Ostner J. 2002. Social thermoregulation in redfronted lemurs (*Eulemur fulvus rufus*). *Folia Primatol.*, 73: 175-180.

Overdorff D.J. 1988. Preliminary report on the activity cycle and diet on the red-bellied lemurs (*Eulemur rubriventer*) in Madagascar. *Am. J. Primatol.*, 16: 143-153.

Overdorff D.J. 1993. Similarites, differences and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. *Int. J. Primatol.*, 14: 721-753.

Overdorff D.J. & Rasmussen M.A. 1995. Determinants of nighttime activity in "diurnal" lemurid primates. In L.G. Alterman, G.A. Doyle & K. Izard (eds): *Creatures of the Dark: The Nocturnal Prosimians*, pp. 61-74. Plenum Press, New York.

Overdorff D.J., Strait S.G. & Telo A. 1997. Seasonal variations in activity and diet in small bodied folivorous primates, *Hapalemur griseus*, southeastern Madagascar. *Am. J. Primatol.,* 43: 211-223.

Pariente G.F. 1970. Rétinographie comparée des lémuriens malgasche. *C. R. Acad. Science Paris*, 270: 1404-1407.

Pariente G.F. 1976. Les différents aspects de la limite du *tapetum lucidum* chez les prosimiens. *Vision Res.*, 16: 387-391.

Pariente G.F. 1979. The role of vision in prosimian behavior. In G.A. Doyle & R.D. Martin (eds): *The Study of Prosimian Behavior*, pp. 411-459. Academic Press, New York.

Peichel L., Rakotondraparany F. & Kappeler P.M. 2001. Photoreceptor types and distributions in nocturnal and diurnal Malagasy primates. *Invest. Ophtal. Vis. Sci.*, 42: S48.

Peres C.A. & Janson C.H. 1999. Species coexistence, distribution, and environmental determinants of Neotropical primate richness: a community-level zoogeographic analysis. In J.G. Fleagle, C.H. Janson & K.E. Reed (eds): *Primate Communities*, pp. 55-74. Cambridge University Press, Cambridge.

Peterson R.L. 1995. Chiroptères. *Faune de Madagascar*, 84: 1-204.

Petter, J.J. 1962. Recherche sur l'écologie et l'éthologie de lémuriens malgasche. *Mem. Mus. Hist. Nat.*, 27: 1-146.

Powzyk J.A. 1997. *The socio-ecology of two sympatric Indriids:* Propithecus diadema diadema *and* Indri indri, *a comparison of feeding strategies and their possible repercussions on species-specific behaviors.* Ph.D Thesis, Duke University.

Rasmussen M.A. 1999. *Ecological influences on activity cycle in two cathemeral primates,* Eulemur mongoz *(mongoose lemur) and* Eulemur fulvus fulvus *(common brown lemur).* Ph.D. Thesis, Duke University.

Rasmussen M.A. 2005. Seasonality and predation risk: varying activity periods in lemurs and other primates. In D.K. Brockman & C.P. van Schaik (eds): *Seasonality in Primates: Implications for Human Evolution*, pp. 105-128. Cambridge University Press, Cambridge.

Reed K.E. 1999. Population density of primates in communities: difference in community

structure. In J.G. Fleagle, C.H. Janson & K.E. Reed (eds): *Primate Communities*, pp. 116-140. Cambridge University Press, Cambridge.

Reed K.E. & Bidner L.R. 2004. Primate communities: past, present, and possible future. *Yrbk. Phys. Anthropol.*, 47: 2-39.

Rohen J.W & Castenholz A. 1967. Über die zentralisation der retina bei primaten. *Folia Primatol.*, 5: 92-147.

Roos C., Schmitz J. & Zischler H. 2004. Primate jumping genes elucidate strepsirrhine phylogeny. *Proc. Natl. Acad. Sci.* USA, 101: 10650-10654.

Santini-Palka M.E. 1994. Feeding behaviour and activity patterns of two malagasy bamboo lemurs, *Hapalemur simus* and *Hapalemur griseus*, in captivity. *Folia Primatol.*, 63: 44-49.

Sauther M.L. 1989. Antipredator behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *Int. J. Primatol.*,10: 595-606.

Schaik C.P. van & Kappeler P.M. 1996. The social systems of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? *Ethology*, 102: 915-941.

Schaik C.P. van, Madden R. & Ganzhorn J.U. 2005. Seasonality and primate communities. In D.K. Brockman & C.P. van Schaik (eds): *Seasonality in Primates: Implications for Human Evolution*, pp. 445-463. Cambridge University Press, Cambridge.

Schaik van C.P., Terborgh J. & Wright S.J. 1993. The phenology of tropical forests: adaptive significance and the consequences for primary consumers. *Ann. Rev. Ecol. Syst.*, 24: 353-377.

Sheine W.S. 1979. The effect of variations in molar morphology on masticatory effectiveness and digestion of cellulose in prosimian primates. Ph. D. Thesis, Duke University.

Schmid J. & Ganzhorn J.U. 1996. Resting metabolic rate of *Lepilemur ruficaudatus*. *Am. J. Primatol.*, 38: 169-174.

Sorg J.P. & Rohner U. 1996. Climate and tree phenology of the dry deciduous forest, the Kirindy forest. *Prim. Rep.*, 46(1): 57-80.

Stevenson P. 2005. Potential keystone plant species for the frugivore community at Tinigua Park, Colombia. In L. Dew & J.P. Boubli (eds): *Tropical Fruits and Frugivores: The Search for Strong Interactors*, pp. 37-57. Springer Publishers, Netherlands.

Struhsaker T.T. 1997. *Ecology of an African rain forest logging in Kibale and the conflict between conservation and exploitation.* University Press of South Florida, Gainesville.

Sussman R.W. 1974. Ecological distinctions in sympatric species of lemurs. In R.D. Martin, G.A. Doyle & A.C. Walker (eds): *Prosimian Biology*, pp. 75-108. Duckworth, London.

Tan C.L. 1999. Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus *Hapalemur*) in Ranomafana National Park, Madagascar. *Int. J. Primatol.*, 20: 547-566.

Tan I. & Li W.H. 1999. Vision-Trichromatic vision in prosimians. *Nature*, 402: 36.

Tan I., Yoder A.D., Yamashita N. & Wen-hsiung L. 2005. Evidence from opsin genes rejects nocturnality in ancestral primates. *Proc. Natl. Acad. Sci.* USA, 102: 14712-14716.

Tarnaud L. 2006. Cathemerality in the Mayotte brown lemur (*Eulemur fulvus*): Seasonality and food quality. *Folia Primatol.*, 77(1-2): 166-177.

Tattersall I. 1976. Group structure and activity rhythm in *Lemur mongoz* (Primates, Lemuriformes) on Anjouan and Moheli islands, Comoro archipelago. *Anthropol. Papers Am. Mus. Nat. Hist.*, 53: 368-380.

Tattersall I. 1977. Ecology and behavior of *Lemur fulvus mayottensis*. *Anthropol. Papers Am. Mus. Nat. Hist.*, 54: 421-482.

Tattersall I. 1978. Behavioral variations in *Lemur mongoz*. In D.J. Chivers & K.A. Joysey (eds): *Recent Advances in Primatology*, *Vol.3: Evolution*, pp. 127-132. Academic Press, London.

Tattersall I. 1979. Patterns of activity in the Mayotte lemur, *Lemur fulvus mayottensis*. *J. Mammol.*, 60: 314-323.

Tattersall I. 1982. *The primates of Madagascar*. Columbia University Press, New York.

Tattersall I. 1987. Cathemeral activity in primates: A definition. *Folia Primatol.*, 49: 200-202.

Tattersall I. & Sussman R.W. 1998. 'Little brown lemurs' of Northern Madagascar. *Folia Primatol.*, 69: 379-388.

Terborgh J. 1983. *Five new world primates*. Princeton University Press, New Jersey.

Terborgh J. 1986. Keystone plant resources in a tropical forest. In M.E. Soule (ed): *Conservation Biology: The Science of Scarsity and Diversity*, pp. 330-344. Sunderland Sinauer Press, New York.

Terborgh J. & Schaik van C.P. 1987. Convergence vs. nonconvergence in primate communities. In J.H. Gee & P.S. Giller (eds): *Organization of Communities, Past and Present*, pp. 205-226. Bleckwell Scientific Publications, Oxford.

Traber S.Y. & Müller A.E. 2006. A note on the activity cycle of captive white-fronted lemurs (*Eulemur fulvus albifrons*). *Folia Primatol.*, 77(1-2): 139-142.

Traina A. 2001. Activity pattern and feeding behaviour of ringtailed lemurs *(Lemur catta)* at Berenty Reserve in Madagascar during the day and night. *Folia Primatol.,* 72: 188.

Vasey N. 2000. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: I. Interspecific patterns. *Am. J. Phys. Anthropol.*, 112: 411-431.

Wright P.C. 1989. The nocturnal primate niche in the New World. *J. Hum. Evol.*, 18: 635-658.

Wright P.C. 1996. The Neotropical primate adaptation to nocturnality: Feeding in the night (*Aotus nigriceps* and *A. azarae*). In M. Norkonk, A. Rosenberger & P. Garber (eds): *Adaptive Radiations of Neotropical Primates*, pp. 369-382. Plenum Press, New York.

Wright P.C. 1997. Behavioral and ecological comparisons of Neotropical and Malagasy primates. In W.G. Kinzey (ed.): *New World Primates: Ecology, Evolution, and Behavior*, pp. 127-143. Aldine de Gruyter, New York.

Wright P.C. 1999. Lemur traits and Madagascar ecology: coping with an island environment. *Yrbk. Phys. Anthropol.,* 42: 31-72.

Wright P.C., Razafindratsita V.R., Pochron S.T. & Jernvall J. 2005. The key to Madagascar frugivores. In L. Dew & J.P. Boubli (eds): *Tropical Fruits and Frugivores: The Search for Strong Interactors*, pp. 121-138. Springer Publishers, Netherlands.

Yoder A.D. & Yang Z. 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Mol. Ecol.,* 13: 757-773.

Appendix - Activity phase reported or suspected for Lemuriform species. Data from Tattersall, 1982; Kappeler & Ganzhorn, 1993; Kappeler, 1998; Curtis et al., 2006; Mittermeier et al., 2006.

Lemur taxon	Common name	Activity
CHEIROGALEIDAE		
Allocebus trichotis	hairy-eared dwarf lemur	nocturnal
Cheirogaleus major	greater dwarf lemur	nocturnal
Cheirogaleus crossleyi	furry-eared dwarf lemur	nocturnal
Cheirogaleus medius	fat-tailed dwarf lemur	nocturnal
Cheirogaleus adipicaudatus	southern fat-tailed dwarf lemur	nocturnal
Cheirogaleus minusculus	lesser iron-gray dwarf lemur	nocturnal
Cheirogaleus ravus	greater iron-gray dwarf lemur	nocturnal
Cheirogaleus sibreei	sibree's dwarf lemur	nocturnal
Microcebus berthae	madame berthe's mouse lemur	nocturnal
Microcebus griseorufus	reddish-gray mouse lemur	nocturnal
Microcebus lehilahytsara	goodman's mouse lemur	nocturnal
Microcebus myoxinus	pygmy mouse lemur	nocturnal
Microcebus murinus	gray mouse lemur	nocturnal
Microcebus ra\velobensis	golden-brown mouse lemur	nocturnal
Microcebus rufus	brown mouse lemur	nocturnal
Microcebus sambiranensis	sambirano mouse lemur	nocturnal
Microcebus tavaratra	northern mouse lemur	nocturnal
Mirza coquereli	coquerel's giant mouse lemur	nocturnal
Mirza zazai	northern giant mouse lemur	nocturnal
Phaner electromontis	amber mountain fork-marked lemur	nocturnal
Phaner furcifer	eastern fork-marked lemur	nocturnal
Phaner pallescens	pale fork-marked lemur	nocturnal
Phaner parienti	pariente's fork-marked lemur	nocturnal
DAUBENTONIIDAE		
Daubentonia madagascariensis	aye-aye	nocturnal
INDRIDAE		
Avahi cleesei	behemara wolly lemur	nocturnal
Avahi laniger	eastern wolly lemur	nocturnal
Avahi occidentalis	western wolly lemur	nocturnal
Avahi unicolor	sambirano wolly lemur	nocturnal
Indri indri	indri	diurnal
Propithecus candidus	silky sifaka	diurnal
Propithecus coquereli	crowned sifaka	diurnal
Propithecus coronatus	coquerel's sifaka	diurnal
Propithecus deckenii	decken's sifaka	diurnal
Propithecus diadema	diademed sifaka	diurnal
Propithecus edwardsi	milne-edward's sifaka	diurnal

Appendix - (continued)

Lemur taxon	Common name	Activity
Propithecus perrieri	perrier's sifaka	diurnal
Propithecus tattersalli	tattersall's sifaka	diurnal
Propithecus verreauxi	verreaux's sifaka	diurnal
LEMURIDAE		
Eulemur albocollaris	white-collared brown lemur	cathemeral
Eulemur albifrons	white-fronted brwon lemur	cathemeral
Eulemur collaris	collared brown lemur	cathemeral
Eulemur coronatus	crowned lemur	cathemeral
Eulemur fulvus	common brown lemur	cathemeral
Eulemur macaco ssp.	black lemur	cathemeral
Eulemur mongoz	mongoose lemur	cathemeral
Eulemur rubriventer	red-bellied lemur	cathemeral
Eulemur rufus	red-fronted brown lemur	cathemeral
Hapalemur alaotrensis	lac Alaotra bamboo lemur	cathemeral
Hapalemur aureus	golden bamboo lemur	diurnal
Hapalemur griseus	eastern lesser bamboo lemur	diurnal
Hapalemur meridionalis	southern lesser bamboo lemur	diurnal
Hapalemur occidentalis	western lesser bamboo lemur	diurnal
Lemur catta	ring-tailed lemur	diurnal
Prolemur simus	greater bamboo lemur	cathemeral
Varecia rubra	red ruffed lemur	diurnal
Varecia variegata ssp.	black-and-white ruffed lemur	diurnal
LEPILEMURIDAE		
Lepilemur ankaranensis	ankarana sportive lemur	nocturnal
Lepilemur dorsalis	gray-backed sportive lemur	nocturnal
Lepilemur edwardsi	milne-edward's sportive lemur	nocturnal
Lepilemur leucopus	white-footed sportive lemur	nocturnal
Lepilemur mustelinus	weasel sportive lemur	nocturnal
Lepilemur microdon	small-toothed sportive lemur	nocturnal
Lepilemur ruficaudatus	red-tailed sportive lemur	nocturnal
Lepilemur septentrionalis	northern sportive lemur	nocturnal