# A Re-Evaluation of the Role of Vision in the Activity and Communication of Nocturnal Primates

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**Abstract**

This paper examines the importance of vision in the lives of nocturnal primates in comparison to diurnal and cathemeral species. Vision is the major sense in all primates and there is evidence that the eyesight of nocturnal species is more acute and variable than has previously been recognized. Case studies of the behaviour of a galago and a loris in open woodland habitats in relation to ambient light show that *Galago moholi* males are more likely to travel between clumps of vegetation along the ground when the moon is up, and during periods of twilight, whereas they retreat to more continuous vegetation and travel less when the moon sets. This is interpreted as a strategy for avoiding predators that hunt on the ground when it is dark. The travel distances of *Loris lydekkerianus* are not affected by moonlight but this species reduces its choice of food items from more mobile prey to mainly ants when the moon sets, indicating the importance of light when searching for high-energy supplements to its staple diet. Evidence is presented for the first time to indicate key aspects of nocturnal vision that would benefit from further research. It is suggested that the light and dark facial markings of many species convey information about species and individual identity when animals approach each other at night. Differences in the colour of the reflective eye-shine, and behavioural responses displayed when exposed to white torchlight, point to different kinds of nocturnal vision that are suited to each niche, including the possibility of some degree of colour discrimination. The ability of even specialist nocturnal species to see well in broad daylight demonstrates an inherent flexibility that would enable movement into diurnal niches. The major differences in the sensitivity and perceptual anatomy of diurnal lemurs compared to diurnal anthropoids, and the emergence of cathemerality in lemurs, is interpreted as a reflection of evolution from different ancestral stocks in very different ecosystems, and not a recent shift towards diurnality due to human disturbance.

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## Introduction

The major division within the Order Primates is between the Suborder Haplorhini and the Suborder Strepsirhini, showing deep-rooted adaptations to diurnal and nocturnal lifestyles, respectively. Within each suborder there are exceptions that prove the rule. Tarsiers and owl monkeys, although haplorhines, have become secondarily specialized for nocturnal niches, whereas some lemurs (strepsirhines) are fully diurnal, despite an anatomy that reflects a nocturnal ancestry [Martin, 1990]. Indeed there is evidence for shifts from nocturnality to diurnality and back again in the history of certain species (e.g., *Tarsius*, *Avahi*) [Martin, 1990; Müller and Thalmann, 2000]. Although some night vision has been retained, most haplorhines remain inactive at night. Their activity begins at sunrise and ends at sunset [Moore-Ede et al., 1982]. Similarly, the majority of strepsirhines (i.e., species in the Lorisidae, Cheirogaleidae, Daubentoniidae, Megaladapidae [Groves, 2001; Grubb et al., 2003]) are relatively hard-wired for a nocturnal life, with the onset and cessation of activity triggered by precise levels of luminosity at dusk and dawn [Pariente, 1974; Kavanau and Peters, 1976; Pages and Petter-Rousseaux, 1980]. However, members of two strepsirhine families in Madagascar, Lemuridae and Indriidae, exhibit a wide range of activity cycles, from almost completely nocturnal to almost completely diurnal, and several lemurids (e.g., *Eulemur* spp., *Hapalemur* spp., *Lemur catta*) are capable of being active by day and/or by night (cathemeral) depending on a variety of abiotic and ecological circumstances [Overdorff and Rasmussen, 1995; Mutschler, 1998; Tattersall and Sussman, 1998; Wright, 1999; Traina, 2001; Curtis and Rasmussen, 2002]. The ability to survive in the very different sensory worlds of day and night has, in the case of most primates, led to the fine-tuning of the senses and perceptual abilities towards a more diurnal or a more nocturnal type [Charles-Dominique, 1975]. However, many mammal species are cathemeral for a variety of physiological, ecological and behavioural reasons and their visual systems appear to be adapted accordingly [Zielinski, 2000; Curtis and Rasmussen, 2006; Kirk, 2006].

Variation between species points to the existence of different grades of diurnal, nocturnal and cathemeral vision, suited to the particular conditions of each ecological niche [Deegan and Jacobs, 1996; Kirk, 2006]. Among these categories, cathemeral mammals, including a small number of cathemeral primates, have eyes that are adapted to provide the greatest flexibility across different light conditions [Kay and Kirk, 2000; Kirk and Kay, 2004; Kirk, 2006]. This general classification into three adaptive types should not be taken to suggest lack of variation within each category. Individuals of even specialist diurnal species can be active at night, for example howler monkeys (*Alouatta* sp.) [Dahl and Hemingway, 1988], toque macaques *(Macaca sinica)* [Nekaris, pers. obs.], and white-throated capuchins *(Cebus capucinus)* [Curtis, pers. obs.], and those that are usually strictly nocturnal can become active during the day [Pariente, 1979]. In this paper we examine variability in the behaviour of nocturnal strepsirhine primates in relation to varying light conditions throughout the 24-hour cycle. We present a broad comparative view of what is known about visual anatomy and the role of vision in nocturnal primates, based largely on two case studies where details of the behaviour of individuals are known. We start by describing the study sites and methods used to investigate a lesser galago and a grey slender loris living in open woodland habitats. We then discuss results from these two species in relation to the available literature under the headings: The Influence

of Ambient Light on Activity Cycles at Night; Diurnal Activity in Nocturnal Strepsirhines; An Assessment of the Visual Capabilities of Nocturnal Specialists, and A Review of Nocturnal Vision and the Evolution of Cathemerality. We conclude by suggesting possible avenues for further research.

## Case Studies

### Subjects and Study Sites

Data collected for two nocturnal strepsirhines provide long-term records of travel distance in relation to ambient light throughout the night in structurally similar open woodland habitats. Southern African lesser galagos *(Galago moholi)* were studied using radio tracking over a 2-year period in acacia thornveld on the cattle ranch 'Mosdene' in the Northern Province of South Africa (28° 47′ E; 24° 35′ S) [Bearder and Martin, 1980a, b]. Mysore slender lorises *(Loris lydekkerianus lydekkerianus)* were followed at close range for 1 year in umbrella thorn woodland at Ayyalur Interface Forestry Division in Dindigul District, Tamil Nadu, South India (77° 55′ E; 10° 04′ S) [Nekaris, 2000, 2001, 2003a]. Each site consisted of seasonally-arid vegetation, dominated by acacia species with clumps of trees and bushes below 15 m separated from one another by scrubby undergrowth or open grassland that enabled the animals to be followed without difficulty [Charles-Dominique and Bearder, 1979; Nekaris, 2003a].

### Methods

Focal individuals of known age and sex were tracked throughout the night and their position recorded using instantaneous point sampling [Altmann, 1974] with a 10-min sampling interval for galagos (n = 3,456) and a 5-min interval for lorises (n = 13,717). The tree in use at the end of each interval was marked with a plastic tag and its position mapped on the following day. This protocol allowed for accurate measurement of path length (the combined distance between all marked trees) and night range length (the furthest distance between two points of travel on one night). In an earlier investigation of the effect of moonlight on these two species, light phases of the night were considered to be whenever the moon was above the horizon and dark phases were whenever the moon had set, irrespective of cloud cover [Bearder et al., 2001]. Phases of the moon were obtained from moon tables and periods of twilight were calculated as 1.5 h after sunset and before sunrise.

We have re-analysed the galago data, and analysed the loris data for the first time, using NewMoon v.1.0. This permits a more detailed analysis of the effects of light levels on activity through the use of a nocturnal illumination index *(I)* calculated on an hourly, as well as a daily basis [Curtis et al., 1999; Thomas and Curtis, 2001; Thomas, 2003]. The magnitude of $I$ varies according to illumination provided by the moon alone ($0 \geq I \leq 0.5$), with $I = 0$ during total lunar darkness and arbitrarily set here at $I = 1$ during solar illumination. Hourly $I$ was used to demonstrate the effect of light levels on nocturnal galago activity during different phases of the moon. Four individual observation nights were selected for each of the four main moon phases (new moon, first quarter, full moon, last quarter), on the basis of sex (males), reproductive status (nonmating season) and weather (nights without freezing temperatures). Daily $I$ was employed to investigate the overall effects of different levels of nocturnal illumination on loris and galago activity. We assessed only the influence of moonlight on activity during the astronomical night, to exclude any twilight effects. Cessation and onset of astronomical twilight, defined as when the sun (centre of the disc) is 18° below the horizon, was used to set the limits for the beginning and end of the night. Twilight effects on activity, resulting in an activity pattern with peaks at dawn and dusk, are a common phenomenon and have been documented in nocturnal, diurnal and cathemeral animals [Aschoff, 1966; Bearder et al., 2001; Curtis and Rasmussen, 2002; Erkert and Cramer, 2006].
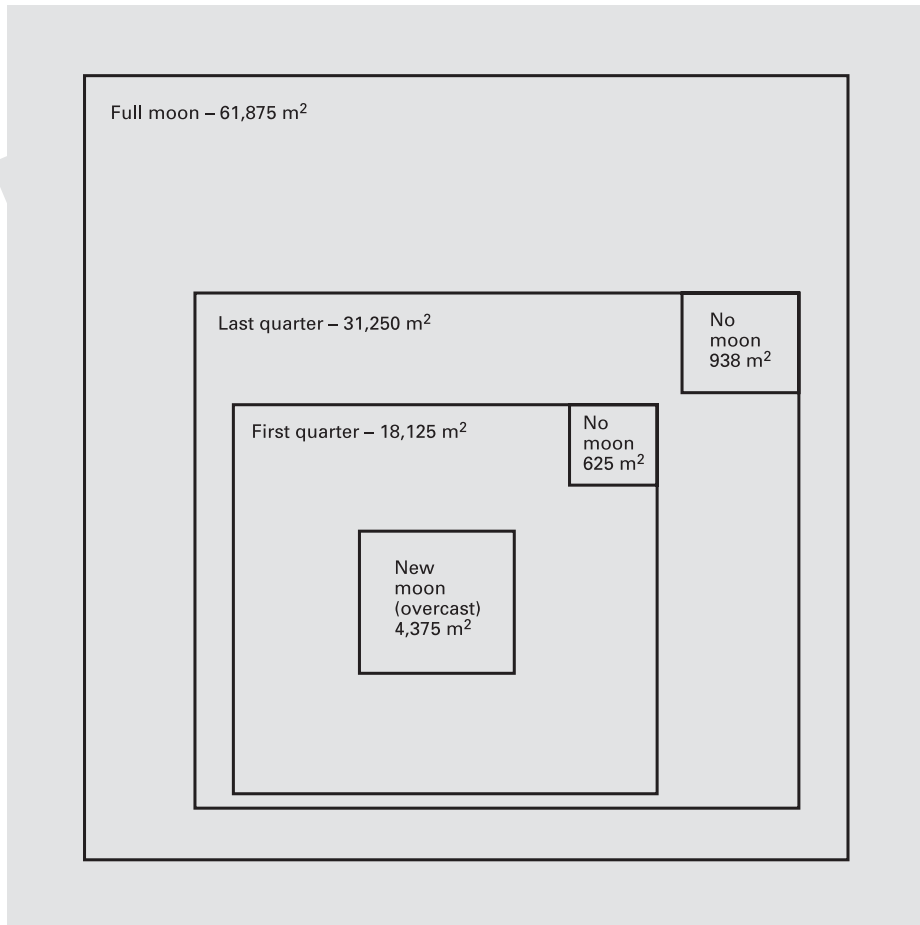
**Fig. 1.** Schematic diagram showing differences in the area traversed per night by a single adult male *G. moholi* at four phases of the moon (larger squares: excluding dawn and dusk). The ranging area when there was no moon is depicted by the smaller squares.
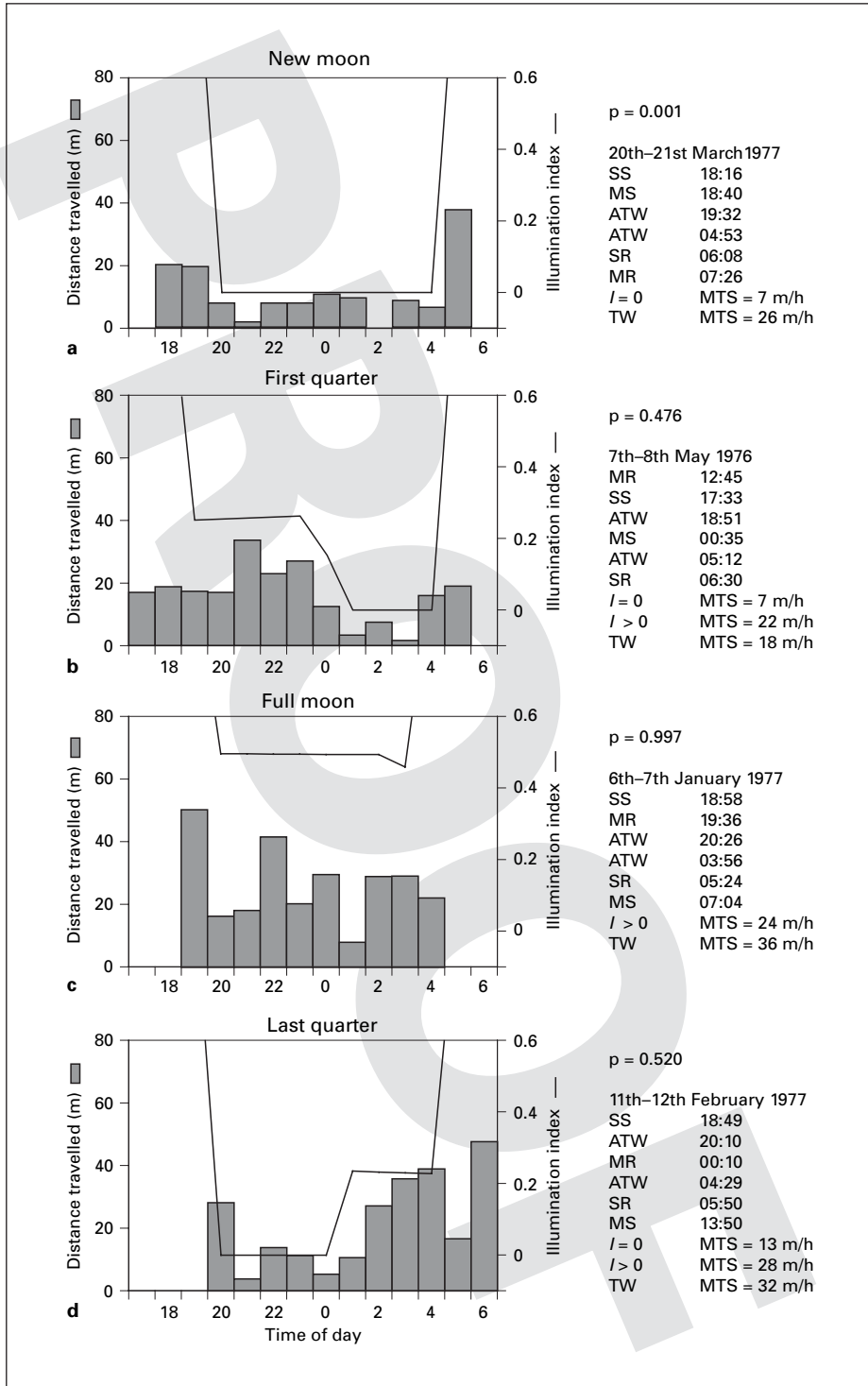
### The Influence of Ambient Light on Activity Cycles at Night

Bearder et al. [2001] demonstrated that, in the case of male galagos, there is a significant positive correlation between travel distance and intensity of moonlight, with the greatest length and range of travel when the moon was full and the least at the time of new moon (fig. 1). The tendency for males to be most active at higher levels of ambient light was also reflected by significantly greater distances travelled during twilight periods at dusk and dawn. Females did not show the same pattern and did not change the extent of travel in moonlight. For adult males the general pattern is to travel during periods of moonlight and retreat to a safe feeding area when the moon is absent [Bearder et al., 2001]. This was interpreted as a predator

avoidance strategy, since predation by genets *(Genetta tigrina)* coincided with moonless and cloudy periods of the night, particularly when there was a strong wind. But, although males preferred to travel when the moon was up, it was clear that they were perfectly able to travel just as far even when there was no moon. In one instance, when a brief mating season happened to coincide with a period of new moon, a male ignored the risk of predation and covered nearly 3 km in one night when there was no moon (compared to an overall average of 2 km per night). This unusual activity brought him into contact with oestrous females far outside his normal home range [Bearder et al., 2001]. The more in-depth analysis conducted here confirms much of the above. However, the greater resolution provided by the use of the nocturnal illumination index, as opposed to the use of a simple classification of night-time light and dark phases, and the more precise definition of 'night' reveals some details not apparent in the earlier analysis [Bearder et al., 2001].

Figure 2 shows the increase in travel distance by male galagos during the astronomical night, mirroring nocturnal illumination levels when the moon is waxing (first quarter) and waning (last quarter). In both cases, activity is increased when the moon is up and decreased when it has set or before it has risen (fig. 2b, 2d). Peaks of activity during twilight are evident at dawn and dusk during the last quarter, but not during the first quarter. During full moon, there is a clear peak in activity at dusk, with subsequent activity more or less evenly distributed throughout the night and mean travel speed during moonlit hours similar to that observed when the moon was up during the first and last quarters (fig. 2c). At new moon, galagos exhibited low levels of activity comparable to those observed during the first and last quarter in the absence of lunar illumination. A clear peak occurred in activity at dawn and mean travel speed during twilight was much higher than during the rest of the active period (fig. 2a).

The analysis of year round activity (mean travel speed) at different nocturnal illumination levels is presented in figure 3a and reveals a trend towards increased activity with increasing nocturnal illumination in galagos from $I = 0.1–0.5$. However, when $I \approx 0$, at new moon, activity levels are higher than at most other illumination levels. The results of the least-squares regression analysis demonstrate that the species' mean travel speed is not a significant function of nocturnal illumination ($r^2 = 0.022$, $F_{(1, 50)} = 1.15$, $p = 0.289$). Analysis of data for males (fig. 3b) reveals a similar picture to that for the species as a whole, but in this case activity is a significant function of nocturnal illumination ($r^2 = 0.118$, $F_{(1, 33)} = 4.42$, $p = 0.043$). Figure 3c shows data for males excluding nights during the mating season and during freezing temperatures and reveals a highly significant relationship between activity and nocturnal illumination ($r^2 = 0.362$, $F_{(1, 28)} = 15.92$, $p < 0.001$). This may represent the baseline (masking or direct) effect of nocturnal illumination on male activity, excluding two further overriding behavioural effects, with freezing temperatures inhibiting activity and the breeding season enhancing activity [Erkert and Cramer, 2006]. Figure 3d shows the relationship for females, which exhibits a negative trend that is not significant ($r^2 = 0.114$, $F_{(1, 14)} = 1.80$, $p = 0.201$), but provides an explanation as to why the species as a whole exhibits no apparent relationship between activity and nocturnal illumination levels, with any discernible effect of nocturnal illumination on the species' activity being cancelled out by intersexual differences.
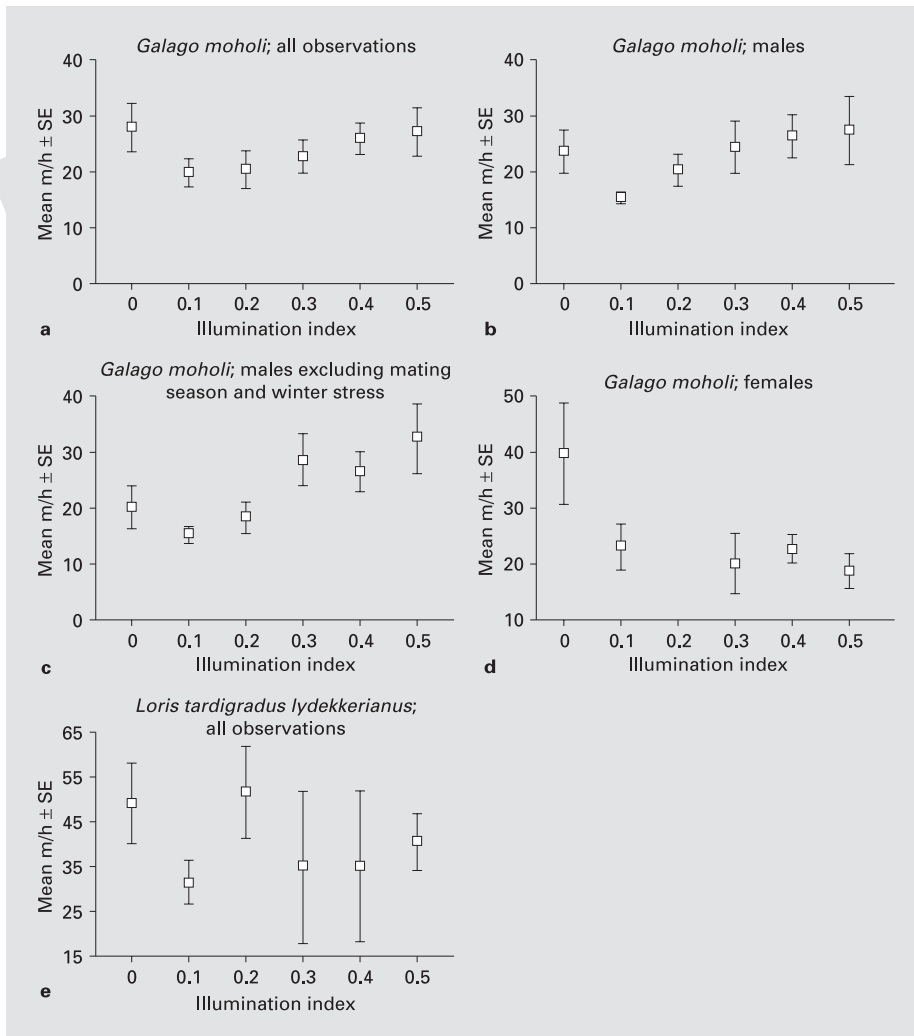
**New moon**

p = 0.001

20th–21st March 1977
| | |
|---|---|
| SS | 18:16 |
| MS | 18:40 |
| ATW | 19:32 |
| ATW | 04:53 |
| SR | 06:08 |
| MR | 07:26 |
| $I = 0$ | MTS = 7 m/h |
| TW | MTS = 26 m/h |

**First quarter**

p = 0.476

7th–8th May 1976
| | |
|---|---|
| MR | 12:45 |
| SS | 17:33 |
| ATW | 18:51 |
| MS | 00:35 |
| ATW | 05:12 |
| SR | 06:30 |
| $I = 0$ | MTS = 7 m/h |
| $I > 0$ | MTS = 22 m/h |
| TW | MTS = 18 m/h |

**Full moon**

p = 0.997

6th–7th January 1977
| | |
|---|---|
| SS | 18:58 |
| MR | 19:36 |
| ATW | 20:26 |
| ATW | 03:56 |
| SR | 05:24 |
| MS | 07:04 |
| $I > 0$ | MTS = 24 m/h |
| TW | MTS = 36 m/h |

**Last quarter**

p = 0.520

11th–12th February 1977
| | |
|---|---|
| SS | 18:49 |
| ATW | 20:10 |
| MR | 00:10 |
| ATW | 04:29 |
| SR | 05:50 |
| MS | 13:50 |
| $I = 0$ | MTS = 13 m/h |
| $I > 0$ | MTS = 28 m/h |
| TW | MTS = 32 m/h |

**2**

**Fig. 3.** The effect of nocturnal illumination on year round activity in *G. moholi* (**a**; all observations), *G. moholi* males (**b**), *G. moholi* males excluding mating season observations and observations when the animals were experiencing winter stress (**c**), *G. moholi* females (**d**) and *L. tardigradus lydekkerianus* (**e**).

**Fig. 2.** The effect of hourly nocturnal illumination on male *G. moholi* activity at Mosdene, South Africa, during the four main moon phases: new moon (**a**), first quarter (**b**), full moon (**c**) and last quarter (**d**). P = Phase; SS = sunset; MS = moonset; ATW = astronomical twilight; SR = sunrise; MR = moonrise; MTS = mean travel speed; TW = twilight.

A different picture can be drawn for the lorises. Bearder et al. [2001] showed that lorises altered their activity during the light moon, significantly increasing both foraging and travel. The increase in foraging was related to the capture of quick moving and higher quality prey, which require more hunting time, and which can be seen better during the lighter moon phases. The staple diet of lorises is ants [Nekaris and Rasmussen, 2003], which were consumed all year long during all moon phases, and in greater quantities when light levels were low. The feeding location, in terms of vulnerability to predators, did not alter with the moon phase; this, in combination with few potential predators at the site, suggested that lorises at this locality did not face high predation pressure. No explanation was offered for the significant change in increasing travel during the light moon by Bearder et al. [2001], but influence of predation at this site was thought most likely to be minimal.

We have reanalysed the travel data for slender lorises, considering also their travel speed. The average travel speed for all lorises (n = 92) was 34.3 ± 21 m/h. Adult males (n = 46) travelled an average of 36.9 ± 26.8 m/h, with adult females (n = 46) travelling at an average speed of 31.8 ± 21.4 m/h. The analysis of mean travel speed at different nocturnal illumination levels is presented in figure 3e and reveals no relationship between activity and illumination ($r^2$ = 0.002, $F_{(1, 29)}$ = 0.06, p = 0.815). The discrepancy between these results and those noted above can be accounted for by the stealthy nature of slender loris locomotion, with relatively slow locomotion taking up more time in their activity budgets than is represented by actual distance covered. As an instantaneous sampling regime was adopted, pauses in locomotion are not reflected in sample points, but are revealed when looking at distances travelled. These results accord with the foraging results given by Bearder et al. [2001]; in a relatively predator-free environment, lorises do not alter their movement patterns according to moonlight.

Lunar periodic modulation of activity rhythm has been observed in a number of nocturnal and cathemeral primates and other mammals, while in others it is seen to be absent (table 1). The results for *G. moholi*, with intersexual differences essentially cancelling each other out, indicate that nocturnal mammals living in more dispersed social systems should be investigated in detail before any conclusion is reached as to whether or not nocturnal illumination affects their activity. When nocturnal primates are compared to other small-bodied mammals, there is a trend for primate activity to increase with higher nocturnal illumination, while other mammals avoid moonlight. Although the loris case may seem to contradict this, the importance of vision is related to finding higher quality mobile prey when the moon is up. These factors would appear to suggest that vision plays an important role in primate behaviour and ecology by comparison to other similar-sized mammals and will be discussed in more depth below.

### Diurnal Activity in Nocturnal Strepsirhines

Nocturnal primates usually seek a safe retreat where they sleep during the day, but they may sometimes wake up and become active [Pariente, 1979]. In the case of *G. moholi,* for example, animals become active in five different circumstances. First, individuals become alert and move away in response to disturbance by a potential predator [Bearder et al., 2001]. Second, animals become active in response to ad-

**Table 1.** Overview of selected field studies on mammals assessing the effect of moonlight on nocturnal activity, and showing the different types of classification of moon phase employed

| Family | Genus | Source | Moon phase classification | Effect of moonlight |
|---|---|---|---|---|
| **Order: Primates** | | | | |
| Cebidae | *Aotus* | Erkert [1974, 1976]; Fernandez-Duque [2003, 2006] | new moon, waxing moon, full moon, waning moon | increases activity |
| | *Aotus* | Wright [1989] | week centered on new moon, week centered on full moon and waxing or waning half moon | |
| Galagidae | *Galago* | Nash [1986] | week centered on new moon, week centered on full moon and waxing or waning half moon | |
| | *Galago* | Bearder et al. [2001] | moon absent, half moon, full moon | |
| Tarsiidae | *Tarsius* | Niemitz [1984] | moon absent, moon present | |
| Lemuridae | *Eulemur* | Colquhoun [1998] | week centered on new moon, week centered on full moon and waxing or waning half moon | |
| | *Eulemur* | Donati et al. [1999, 2001] | new moon, full moon | |
| | *Eulemur* | Donati and Borgognini Tarli [2006] | nocturnal illumination index | |
| | *Eulemur* | Kappeler and Erkert [2003] | new moon, waxing moon, full moon, waning moon | increases activity |
| | *Eulemur* | Overdorff and Rasmussen [1995] | moon absent, half moon, full moon | no effect |
| | *Eulemur* | Curtis et al. [1999] | nocturnal illumination index | |
| Megaladapidae | *Lepilemur* | Nash [2000] | new moon, full moon | |
| Cheirogaleidae | *Microcebus* | Nash [2000] | | |
| Lorisidae | *Loris* | Bearder et al. [2001] | new moon, full moon | no effect |
| **Order: Chiroptera** | | | | |
| Phyllostomatidae | *Artibeus* | Erkert [1974, 1976] | new moon, waxing moon, full moon, waning moon | decreases activity |
| | *Phyllostomas* | Erkert [1974, 1976] | new moon, waxing moon, full moon, waning moon | decreases activity maximum activity; moon waxing |
| Pteropididae | *Rousettus* | Erkert [1974, 1976] | new moon, waxing moon, full moon, waning moon | decreases activity maximum activity; moon waning |
| **Order: Rodentia** | | | | |
| Heteromyidae | *Dipodomys* | Kaufman and Kaufman [1982] | starlight – moonlight, moonlight + cloud cover, moonlight – cloud cover | decreases activity |
| | *Dipodomys* | Lockard and Owings [1974] | moon absent, moon present | decreases activity on a seasonal basis |
| | *Dipodomys* | O'Farrell [1974] | moon phase recorded but no classification provided | decrease activity to varying degrees; less so in small cryptic species |
| | *Perognathus* | O'Farrell [1974] | | |
| | *Microdipodops* | O'Farrell [1974] | | |
| | *Peromyscus* | O'Farrell [1974] | | |
| Muridae | *Reithrodontomys* | O'Farrell [1974] | | decrease activity to varying degrees; less so in small cryptic species |
| | *Onychomys* | O'Farrell [1974] | | |
| | *Neotoma* | O'Farrell [1974] | moon phase recorded but no classification provided | |
| | *Mesocricetus* | Erkert [1974, 1976] | new moon, waxing moon, full moon, waning moon | no effect |
| Hystricidae | *Hystrix* | Alkon and Saltz [1988]; Corsini et al. [1995] | continuous scale measuring 12 phases of the lunar cycle | decreases activity on a seasonal basis |
| **Order: Carnivora** | | | | |
| Mustelidae | *Mustela* | Halle [2000] | moon phase recorded but no classification provided | decreases activity |

verse weather conditions. They sometimes move into the sun in the early morning, or during winter days, and return to the shade as the sun gets higher. They also move from an exposed to a sheltered sleeping place in response to heavy rainfall [Bearder, 1969]. Third, individuals that are unable to find sufficient insects and gum during the night, for example when these foods are frozen during mid-winter, are seen searching for food by day [Bearder and Doyle, 1974]. Fourth, an alternative response to winter food shortages is to end nocturnal activity and return to a sleeping place up to 7 h earlier than usual and become active again before sunset to collect gum that is no longer frozen [Bearder and Martin, 1980b]. Finally, there are examples of individuals who adjust their activity cycles to suit daytime provisioning in captivity [Anderson, pers. comm.]. In each of these cases the behaviour of the animals was indistinguishable from their behaviour under the cover of darkness. On one occasion, for example, they were seen to travel some 80 m between sleeping trees in broad daylight, grooming themselves, licking gum and leaping several metres between small supports and jumping along the ground.

Although no observations have been made of slender loris daytime feeding behaviour, grey slender lorises *(L. l. lydekkerianus* and *L. l. nordicus)* may also move up to 300 m when disturbed at their sleep sites by potential predators. This shows that even specialist nocturnal primates can be sufficiently flexible in their sensitivity and perception to permit diurnal activity, yet there is also variation. Diurnal activity appears to be relatively rare in most lorises and, among galagos, some species are evidently more inclined to avoid daylight than others. *Galagoides thomasi* in Cameroon, for example, returned earlier to their sleeping sites and left later than sympatric *Sciurocheirus alleni*, *Euoticus elegantulus* and *Galagoides demidovii* [Bearder and Honess, pers. obs.].

## An Assessment of the Visual Capabilities of Nocturnal Specialists

Other studies of the activity and movement patterns of nocturnal strepsirhines point to the fact that they are strongly visually oriented animals [Charles-Dominique, 1977; Pariente, 1979]. They possess excellent night vision that enables them to navigate, locate prey and negotiate varied supports by sight. Experimental studies have demonstrated that they do not sniff their way along scent trails [Charles-Dominique, 1977] and the habit of wiping urine onto the palms of the hands and soles of the feet in *Otolemur* and *G. moholi*, for example, has been linked primarily to enhancing grip [Welker, 1974; Harcourt, 1981]. Indeed, vision is not only paramount in enabling strepsirhines to move through the environment (*G. moholi* remain immobile if placed in a completely dark room [Bearder, 1969]), but there is circumstantial evidence that visual acuity is much greater than might be expected for the eyes of nocturnal specialists.

### Structure of the Retina
Rohen and Castenholz [1967] note that reports of diurnal activity in the bushbaby genera *Galagoides*, *Euoticus* and *Otolemur* correspond with the presence of a weakly developed area centralis. There is also evidence of a small population of cones in the retina of *Otolemur garnettii* (1–3%) [Petry and Harosi, 1990; Wikler and Rakic, 1990]. Cones are also reported for *Otolemur crassicaudatus*, *Nycticebus cou-*

*cang* and *Loris tardigradus* [Wolin and Massopust, 1970; Deegan and Jacobs, 1996]. They appear to be of one type only, similar to those found in owl monkeys *(Aotus)*, having a photopigment with peak sensitivity in the middle to long wavelengths (545 nm) [Dartnall et al., 1965; Petry and Harosi, 1990; Deegan and Jacobs, 1996]. The lack of short wavelength cones in both *O. crassicaudatus* and *Aotus* indicates that these species do not have colour vision, although the tapetum lucidum may play a role in this respect (see below). Nevertheless, both species possess a gene for short wavelength cone pigmentation (that has lost its function) suggesting that they may be derived from ancestral forms that had colour vision and were dichromatic [Deegan and Jacobs, 1996]. Short-wavelength cones are common in the retinas of most primates [Jacobs and Deegan, 1993] including diurnal/cathemeral lemurs *(L. catta, Eulemur fulvus)*, which also have a middle-to-long wavelength pigment indistinguishable from that of the bushbaby [Jacobs and Deegan, 1993]. Deegan and Jacobs [1996] point out that the presence of some cones, in addition to rods, expands the spectral window available to bushbabies and owl monkeys and allows greater powers of discrimination based on spectral differences. The spectral composition of moonlight is approximately equivalent to that of sunlight, but both are modulated in a forest environment when the light passes through the canopy [Pariente, 1974; Erkert, 1989]. Therefore, cones might well serve a valuable function in nocturnal species and would also help them to shift between scotopic to photopic conditions (i.e., to be cathemeral).

Although detailed research in this area is still incomplete, there are a number of additional observations that suggest a dominant and flexible role for vision in nocturnal strepsirhines, just as in all other primates. These include comparisons of facial markings, evidence for visual recognition between conspecifics at night, variation in the colour of tapetal reflections and observations of behaviour when different species are exposed to white light.

### Facial Markings

The contrasting light and dark facial markings that are characteristic of several primates, carnivores and birds have been interpreted as anti-glare devices [Kingdon, 1992; Ortolani, 1999], cryptic disguise [Kingdon, 1992; Pariente, 1979], a deterrent to predators by increasing the apparent size of the eyes [Pariente, 1979] and status signalling [Whitfield, 1987; Kingdon, 1992]. They also have the potential to carry information about the identity of the species, and even the individual, when the animals approach each other at night [Becker et al., 1999]. Although research on this aspect is limited, a broad comparison of facial patterns across nocturnal species in which vision plays an important role indicates that their facial markings are species-typical [Bearder, 1999; Nekaris and Jayewardene, 2003]. For example, the great majority of species within the primate families Lorisidae, Cheirogaleidae and Megaladapidae have distinctive patterns of facial markings that enable a careful observer to distinguish between species (fig. 4a) and between individuals (fig. 4b) by sight. The characteristic masks of owl monkey species and many diurnal or cathemeral lemurs may well perform the same function. Patterns of light and dark fur on the face are also characteristic of the smaller diurnal New World monkeys where there is a predominance of dichromatic vision [Hershkovitz, 1977] and they are undoubtedly analagous to the distinctive, and often more colourful facial markings of trichromatic Old World primates in playing an important role in individual recognition
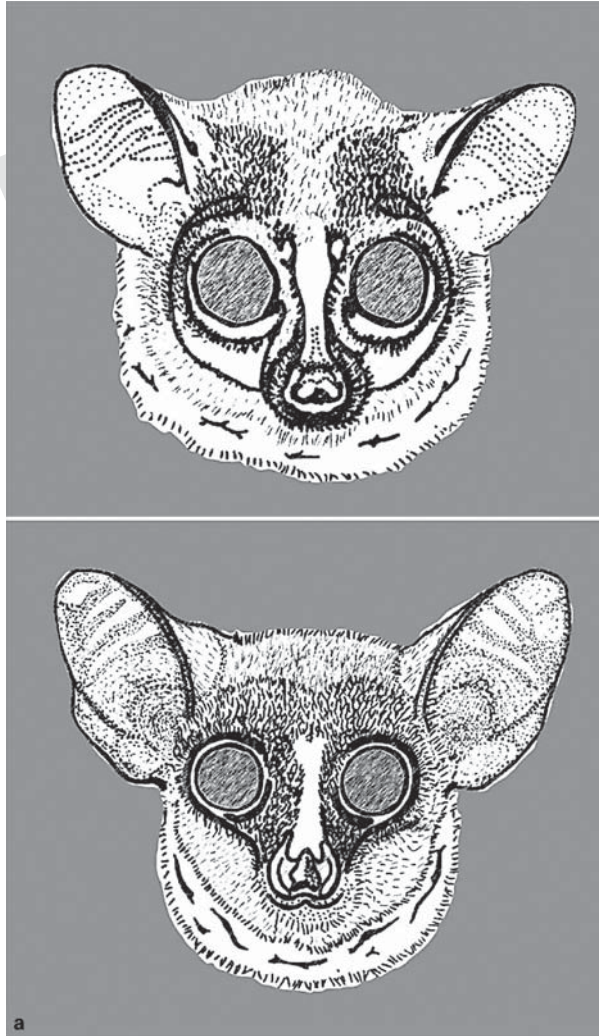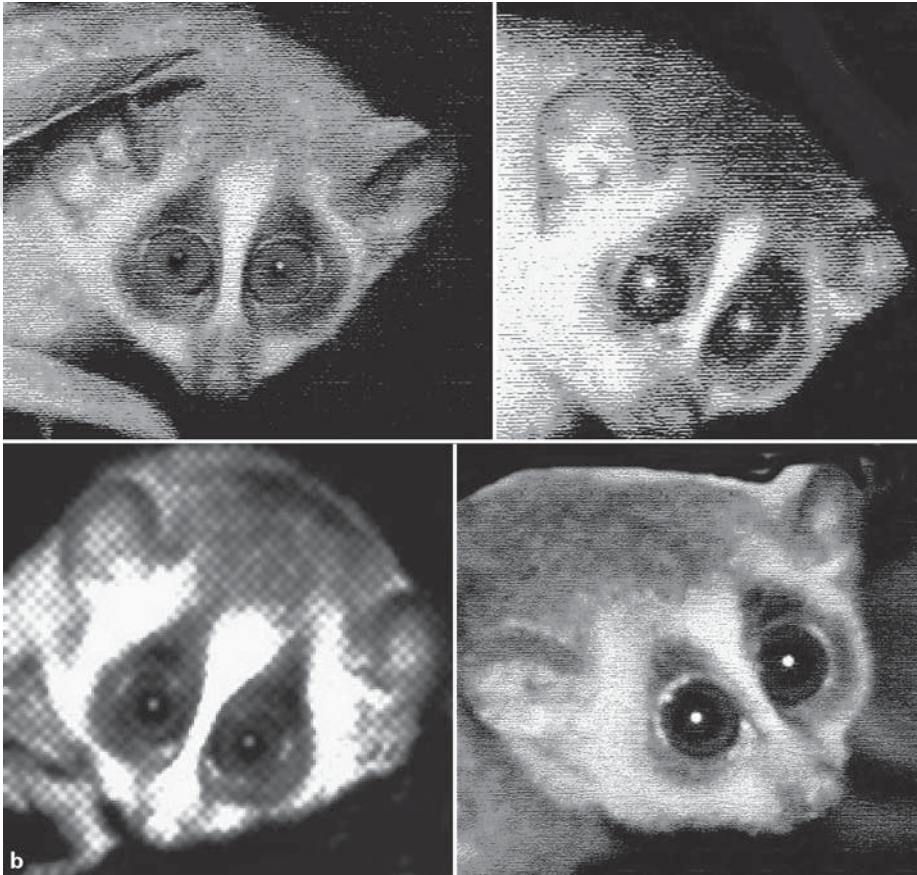
**Fig. 4.** Tracings from photographs showing differences in the pattern of facial markings in *G. demidovii* (above) and *G. thomasi* (below) (**a**) and four *L. tardigradus* studied at Ayyalur Interface Forestry Division, rasterized to maximize individual facial patterns (**b**). The shape of the ears, length of muzzle, width of preauricular hair zone, circumocular patches, and interocular stripe width all contribute to facial variation.

[Kingdon, 1980, 1988]. Individual and species-typical facial patterns are also implicated for other mammals, particularly carnivores such as badgers, polecats, raccoons, civets, genets and most cats [Müller, 2002; Neal and Cheeseman, 1996; Heilbrun et al., 2003]. Distinctive facial markings are also seen in many of the possums and some visually-oriented rodents and antelopes, and species-specific differences are found in the face patterns of owls [Bearder, pers. obs.] as well as between indi-

viduals in other birds, e.g. turnstones [Whitfield, 1986, 1987], Bewick swans [Scott, 1978], ospreys [Bretagnolle et al., 1994] and ruffs, queleas and house finches [Dale et al., 2001]. Facial markings are inconspicuous or absent in species that rely more on their senses of smell or hearing, for example most rodents, lagomorphs, bats, mongooses and some nocturnal primates (e.g., *Perodicticus* and *Arctocebus*).

### Visual Recognition at a Distance

The 2-year radio tracking study of lesser galagos in open woodland, outlined above, provided many opportunities to witness interactions between tagged individuals when they met at night (n = 375). All-night follows of single individuals at close range enabled the observer to monitor differences in the response of the focal animal to others of known age and sex. Social interactions had previously been studied in detail in captivity, where rank order between strangers was quickly established with the aid of scent, and subsequent encounters followed highly predictable patterns corresponding to relative dominance and subordination [Bearder, 1974]. The usual sequence of events when two individuals approached each other in the wild was that one gave a distinctive call ('explosive cough') while they were between 5 and

20 m apart, indicating that it was subordinate. In the encounter that followed, the animal that had called would invariably retreat (usually to the base of a tree or onto the ground) and give calls of anxiety or alarm if chased [Bearder, 1969]. Less frequently, when the focal animal came close to another, it might look towards it but not approach. In the few remaining cases, when the other was a dominant rival, the subject would move behind the trunk of a tree and remain there till the adversary had moved away. These observations do not prove that galagos could recognize each other by sight, but the fact that they recognized when to give a submissive call showed that they could accurately predict the relative status of each individual they met from a distance of up to 20 m, presumably based on vision. There was no indication of sniffing at the time of first approach, although any subsequent interaction was invariably accompanied by olfactory checking at close range and by sniffing of branches where the other had been sitting.

Similar results were found in the open habitat occupied by slender lorises. Lorises slept in groups of up to 7 individuals, with whom they might share amicable interactions throughout the night [Nekaris, 2003b]. In fact, positive interactions such as grooming, playing and feeding together comprised up to 52% of an animal's activity budget [Nekaris, 2001]. Vocal communication in lorises often served as a spacing mechanism, advertising an animal's whereabouts and thus helping to avoid confrontation, which is limited [Nekaris, 2000; Bearder et al., 2001]. In a network of relatively small overlapping ranges, animals came together often, in what were deemed as neutral interactions. These neutral interactions (n = 144) generally were comprised of seeing one another from a distance, and glancing back and forth at one another. Although scent marking sometimes accompanied staring, no vocalizations were made between individuals known to be members of the same sleeping group, and they appeared to be able to distinguish one another, even when over 50 m apart. Conversely, occasions when non-group members approached each other (n = 26) were accompanied by intense staring and vocalizing from a distance of 30–50 m. These encounters usually began with two animals fixing gazes at one another, and moving their heads from side to side. They would then begin a fierce 'whistling' bout. Although scent may play a role at such a distance, the fixed staring suggests again the importance of the facial mask in recognising non-group members, and indeed the individually distinctive face markings were used by the observer to distinguish individuals [Nekaris, 2003a].

### The Significance of the Tapetum Lucidum

Anatomical comparisons of visual capabilities between mammals in general show clearly that species are fine-tuned to the demands of different habitats and activity rhythms [Pariente, 1979; Wikler and Rakic, 1990; Dusenbery, 1992; Jacobs, 1993; Ahnelt and Kolb, 2000; Silveira, 2004]. Differences in the size and curvature of the retina and lens, and the relative density of cone and rod cells have been found between nocturnal and diurnal species [Kirk, 2006], with cathemeral species having intermediate arrangements. Less information is available on the structure and function of the reflective layer behind the retina, the tapetum lucidum [Pirie, 1959; Pariente, 1976; Nicol, 1981; Schwab et al., 2002]. The structure of the tapetum varies according to the species, due to different arrangements of granules in the pigmentary epithelium. The particular shape and arrangement of the granules has been related to etho-ecological conditions, reflecting the wavelengths most relevant to the species'

ecology [Pariente, 1976; Schwab et al., 2002]. In theory, the reflection of light back through the retina effectively doubles the stimulation of the retinal cells, since the incoming light passes directly back to its source [Dartnall et al., 1965; Ollivier et al., 2004]. Different species of mammals exhibit different coloured eye-shine when white light from a headlamp is used to locate them at night and this is also influenced by the angle of the eye. The reflection from the eyes of herbivores is usually white; carnivores tend to have green or blue reflections, whereas the eye-shine of strepsirhine primates in Africa and Asia is predominantly red, and that of lemurs is yellow or orange. In addition, African strepsirhines that live sympatrically, vary in the relative degree of red reflection. For example, in the rainforests of Cameroon, the tapeta of *G. demidovii* and *S. alleni* appear ruby red, those of *Euoticus pallidus* pink, *Perodicticus potto* reflects more orange and *G. thomasi* crimson [Bearder, pers. obs.]. These colour differences probably relate to the wide range of pigments and techniques used to provide tapetal reflectance noted by Schwab et al. [2002], including pigmented reflecting crystals and structural colours. The fact that each of these species utilizes the shared habitat in a different way [Charles-Dominique, 1977; Ollivier et al., 2004] points to the functional significance of these differences.

### Reactions to Torchlight

Added to this, each species reacts differently when exposed to red or white light from a torch or spot-lamp. Most nocturnal species probably do not detect light towards the red end of the spectrum as they do not possess separate medium and long wave-length cones with peak sensitivities in the green and red, respectively, that characterize diurnal trichromats [Jacobs and Deegan, 1993] and can usually be observed by means of red light without disturbance [Southern, 1955]. Mysore slender lorises froze at the sight of white light, and on one occasion a female with her infants refused to return to her sleeping site and showed signs of acute stress with prolonged exposure to white light [Nekaris, 2003b]. Red slender lorises *(Loris tardigradus tardigradus)* fold up their ears and make stress faces when exposed to white light [Nekaris, pers. obs.]. Interestingly, red slender lorises showed immense sensitivity to light, ceasing social behaviour in the presence of flashlights of any colour, and only coming together to groom after a red light had been turned off. Some nocturnal lemurs (e.g., *Microcebus murinus*) will turn their heads away from white light almost immediately, but often blink at it briefly before doing so. Other nocturnal lemurs such as *Cheirogaleus medius*, *Lepilemur* spp. and *Avahi* spp., as well as cathemeral *Eulemur* spp. do not appear disturbed and will stare into the light without blinking [Curtis, pers. obs.; Müller, pers. comm.]. Similarly, some galagos remain undisturbed even when exposed to white light. For example, *O. crassicaudatus* will stare without blinking, whereas the sympatric *G. moholi* immediately looks away, appears confused and attempts to escape [Charles-Dominique and Bearder, 1979]. The possible causal and functional significance of such species-typical differences has yet to be explored – including the possibility of some degree of colour vision [see review by Jacobs, 1993].

## A Review of Nocturnal Vision and the Evolution of Cathemerality

Charles-Dominique [1975] argues convincingly that the ancestral state for mammals was probably nocturnal, as a result of competition with early birds in the developing flowering forests of the Palaeocene. This stems from the fact that the fossil record of early mammals indicates that they were relatively small and insectivorous, and would thus have occupied similar feeding niches to birds. Early birds and mammals avoided competition by being active during the day and at night, respectively. Most authors consider that the earliest primates were also nocturnal [Martin, 1990; Ross, 1996, 2000; Heesy and Ross, 2001]. Since most forest birds are relatively small (due to the constraints of flight), there would have been an ecological opportunity for mammals to out-compete them for daytime niches by increasing their body size, bringing new structural and energetic advantages into play. Most large mammals that cannot easily hide retain the ability to be active by day or night and can therefore be classified as cathemeral [Curtis and Rasmussen, 2006]. In the special case of arboreal mammals, most are either fully diurnal or fully nocturnal, in association with larger and smaller body size respectively [Nowak, 1991]. This pattern is probably related to the fact that both diurnal and nocturnal species are able to find safe sleeping places in the trees; but larger size has the disadvantage that it is harder to find suitable refuges from birds of prey and other predators while asleep during the day, thus leading to the selection against nocturnality in larger primates. The larger size of diurnal primates reduces the range of predators able to catch them, and predation is further offset by their tendency to form groups [van Schaik, 1983; Wrangham, 1987; Janson, 1992]. Such constraints and opportunities set the scene for the evolution of cathemerality in primates.

In his broad review of the role of vision in prosimian behaviour, Pariente [1979] concludes by stating that the eyes of most living primates, including those that are nocturnal specialists, are able to operate effectively during daylight. This suggests a degree of plasticity that would permit fairly rapid transition from nocturnal to diurnal life. While the earliest mammals were probably more reliant on the senses of smell and hearing, the early primates became increasingly reliant on the sense of vision and associated developments of visual areas of the nervous system. Pariente proposes that early primate ancestors may have needed to see well both by day and by night, leading to a dual-purpose eye at the very outset, which subsequently became more limited in one direction or another because of specific specialisations. Our results also demonstrate that even extant nocturnal primates (with strong twilight zeitgebers) are able to become active during the day on a facultative basis in relation to critical circumstances such as extreme food shortages, cold temperatures, rainfall and disturbance by potential predators. It is therefore likely that a less specialized nocturnal ancestor would also have had this flexibility and would have exploited it when necessary. Any ecological opportunities that extended the advantages, or reduced the disadvantages, of becoming more diurnal would have selected for compromises in anatomy and physiology towards a more cathemeral type. In this scenario, cathemerality is seen as a staging post from nocturnality to diurnality, but it could equally work in the opposite direction, as presumably in the cases of *Avahi* and *Aotus*, which are regarded as secondarily nocturnal.

Assuming that a relatively small nocturnal species was the ancestral form for both haplorhines and strepsirhines, it is clear that the evolution of diurnality has progressed in very different ways in the two groups. Haplorhines largely lost the ability to operate at night and became increasingly dependent on acuity of vision at the expense of their other senses. Diurnal strepsirhines, on the other hand, developed a parallel capacity for fine discrimination and colour vision (albeit not as highly developed as in haplorhines). Like haplorhines, this was associated with an increase in body size, a shift towards greater reliance on plant foods and a greater tendency to form groups, but they retained a suite of characteristics associated with nocturnal sensitivity. These include relatively large eyes and ears, a reflective tapetum lucidum, a well-developed sense of smell, a moist nose and associated Jacobsen's organ, and somewhat smaller brains compared to haplorhine primates of the same body size. The key question concerns the circumstances that may account for these differences.

One answer is that the ancestral form that gave rise to diurnal lemurs was already highly specialized towards a nocturnal life compared to a less specialized nocturnal ancestor for the haplorhines. A second and complementary answer may lie in the fact that the early evolution of the two groups took place under very different environmental conditions, one in biologically diverse tropical rainforests and the other in the less species-rich and highly seasonal habitats of sub-tropical Madagascar. Finally, it has been suggested that the time-scale for the evolution of diurnal activity in the two groups was very different. Van Schaik and Kappeler's [1996] 'evolutionary disequilibrium' hypothesis argues that the recent extinction of large-bodied lemurs and diurnal raptors on Madagascar, as a result of human colonization, could have triggered movement into diurnal niches by specialised nocturnal species, with cathemerality as a transitional stage.

The extent of specialization in sensory anatomy of nocturnal, diurnal and cathemeral lemurs makes it highly unlikely that the transition from nocturnal to diurnal life has been a recent one. If, on the other hand, the earliest primates that colonized Madagascar had already been highly adapted for nocturnal activity, their diurnal descendants would have built upon this basic design without losing those characteristics that remained useful. According to this interpretation, the major difference between the sensory and perceptual abilities of diurnal lemurs and anthropoid primates is because they are the end products of evolution from very different starting points – specialized and less specialized nocturnal ancestors, respectively.

It can be further argued that the relatively stable conditions of the mainland tropical rainforests would have selected for an ability to survive in the face of intense competition, leading to increased specialization in diurnal primates and little ability to operate at night. On the other hand, the more unstable environmental conditions and less intense competition in Madagascar would tend to select for a more flexible response (hence cathemerality), either due to necessity or increased opportunity. Both sets of conditions are strongly indicated. The southerly latitude of Madagascar has not changed appreciably during the evolution of mammals and its inhabitants exhibit universal deep-rooted adaptations to reproductive seasonality compared to species living closer to the equator. Its distance from the mainland ensured that it was colonised by relatively few mammalian orders and there is also a paucity of birds. Consequently, primates evolving on Madagascar would have been exposed to stress factors (e.g., seasonal food shortages and extreme weather

conditions) shown to force nocturnal specialists away from their preferred activity cycle. In addition, there would have been opportunities that fostered increased flexibility of movement by day or night (e.g., absence of direct competitors for food and absence of specific predators). Island life could arguably also have led to a greater significance of periodic local catastrophes such as fire, floods or hurricanes which, again, would tend to promote flexibility [Wright, 1999]. This interpretation is strengthened by the present day distribution of primate species that exhibit cathemeral activity. Cathemeral lemurs and the one cathemeral owl monkey all live in relatively unstable, seasonally variable habitats [Curtis and Rasmussen, 2002; Fernandez-Duque, 2003].

### Conclusions and Future Research

Our survey of the visual capabilities of nocturnal primates shows a much greater variation in types of vision than is generally supposed. It is no longer adequate to study the visual anatomy and associated physiology and behaviour of a few species and assume that others will be the same. The increasing appreciation of the diversity of nocturnal primates is indicated by the burgeoning of previously unrecognized species and genera [Yoder et al., 2001; Grubb et al., 2003]. Subtle but distinct differences between even closely related species in characteristics such as eye-shine colour, facial markings, tapetal structure and retinal anatomy, point to the possibility of major distinctions between genera. Further work is required to elucidate a number of questions raised in this initial overview. These include: (1) Which aspects of facial markings are being used by the animals in recognising species as opposed to individuals? (2) What is the functional significance of differences in tapetal reflection and reaction to white torchlight? (3) Are there differences in visual anatomy that correlate with differences in food selection such as fast- or slow-moving prey? (4) What is the extent of activity throughout the 24-hour cycle across a range of species that are generally considered strictly diurnal or nocturnal, and how is this influenced by ambient light?

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