Coping with habitat disturbance: camera-traps reveal cathemerality of Prolemur simus in the community-managed area of Tsaratanana, eastern Madagascar

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Abstract

This study provides new findings on the flexible activity of *Prolemur simus* in an anthropogenically modified habitat in the rural commune of Tsaratanana, eastern Madagascar. Based on camera-trap data, we compared the temporal distribution of activity of one group between the forest edge and the forest core. We also investigated the possible influence of nocturnal luminosity on the activity cycle. The analysis was conducted using Kernel Density estimates and the R package OVERLAP. The distribution across the 24-h cycle confirmed that *Prolemur simus* is cathemeral in the wild. The lemurs displayed three peaks of activity: one during the night and two coinciding with morning and evening twilights. The highest proportions of nocturnal activity occurred at the forest edge and at low moon luminosity suggesting a possible anti-predator and/or human-avoidance strategy. The flexible activity of *Prolemur simus* may contribute to the tolerance of this Critically Endangered species to anthropogenic disturbance.

Introduction

The term 'cathemerality' is used to describe the ability of animals to switch their activity over the diel cycle (i.e. 24h) day. Cathemeral animals do not show either strict diurnal or nocturnal activity, but they distribute it throughout the 24-h period (Tattersall, 1987). Both biotic factors (e.g., predation, food availability, niche partitioning) and abiotic factors (temperature, lunar luminosity) influence this activity pattern (Donati *et al.,* 2016; Halle and Stenseth, 2000). Cathemeral activity is controlled by two main regulatory mechanisms - zeitgebers and masking factors. Zeitgebers - circadian time cues - are described as environmental agents entraining or synchronizing organisms' biological rhythms. Seasonal changes in the light-dark (LD) cycle are thought to be the most powerful zeitgebers (Aschoff *et al.,* 1982). The term 'masking' is used for the stimulatory or inhibitory effects of the environmental factors impacting the endogenous circadian activity pattern e.g., ambient luminance or temperature (Fernández-Duque *et al.,* 2010).

Cathemerality has been widely observed in mammals (Curtis and Rasmussen, 2006; Halle and Stenseth, 2000; van Schaik and Griffiths, 1996) and sporadically in other taxa such as reptiles Tuatara (*Sphenodon punctatus*) (Vermunt *et al.,* 2014) or tropical reef fish **-** *Siganus lineatus* (Fox and Bellwood, 2011). Although common among mammals, this flexibility is not frequent in primates. Routinary cathemerality has been observed predominantly in the Malagasy lemurs, which interestingly display wide diversification in activity patterns (Campera *et al.,* 2019; Curtis and Rasmussen, 2006; Donati *et al.,* 2013, 2016; Santini *et al.,* 2015), but also in a population of owl monkeys, *Aotus azarai* (Fernández-Duque *et al.,* 2010). The origin and evolution of cathemeral activity are still under debate. Most hypotheses consider the cathemeral behavior adaptive (driven by thermoregulation, food quality and availability, predation risk, and feeding competition benefits) (Curtis and Rasmussen, 2006; Donati *et al.,* 2009; Kirk *et al.,* 2006). Cathemerality is considered as one of the lemurs' unusual traits compared to other primates (Wright, 1999). Among the five extant genera of the *Lemuridae* family, cathemeral activity patterns have been observed in *Hapalemur* spp., *Eulemur* spp.**,** *Lemur catta,* and *Prolemur simus* (Donati *et al.,* 2009; 2013; Eppley *et al.,* 2015; LaFleur *et al.,* 2014; Tan, 1999). Recent studies based on data from accelerometers also revealed that southern woolly lemur *Avahi meridionalis*, previously thought to be strictly nocturnal, exhibits low but consistent bouts of diurnal activity (Campera *et al.,* 2019).

Since 2009, several groups of greater bamboo lemurs (*Prolemur simus*) living in the forest patches of the rural commune of Tsaratanana are monitored within the 'Bamboo lemur' program developed by L'Association Française pour la Sauvegarde du Grand Hapalémur - Helpsimus (Helpsimus, 2020). The site does not have an official status of protection but benefits from a community-based management. This setting provides a great opportunity to test the flexibility of cathemeral lemurs in response to anthropogenic changes (Donati *et al.,* 2016). Using camera trap data, this study aims to determine the temporal activity pattern of one of the groups monitored in the area. Most of our knowledge on the activity pattern of wild greater bamboo lemurs come from the Ranomafana National Park where these lemurs have been observed to have peaks of activity at dawn and dusk as well as during the night regardless of lunar phases (Tan, 2000). However, no detailed descriptions of the pattern are available and comparisons with other studies on cathemeral lemurs are difficult. Likewise, studies from captivity showed these lemurs to have several peaks of activity at dawn, dusk, night, and day (Brunon, unpublished data; Santini-Palka, 1994) but extending these results to wild animals is complicated.

This study aims to provide data on greater bamboo lemurs' activity pattern outside of the protected zone in a degraded and anthropogenically-modified habitat. Moreover, we aim to compare the temporal distribution of the activity of a wild group in two contrasting zones – the edge and core of the forest fragment. Finally, we investigate the possible influence of the nocturnal luminosity on the activity of this species. We predict that greater bamboo lemurs in non-protected areas will show more activity distributed during the night when in close proximity to human settlements.

Materials and Methods

This study was carried out between April and July 2018 in the forests fragment surrounding fokotany Sahofika (*fokontany* – the smallest administrative subdivision in Madagascar), located in the rural commune of Tsaratanana, south-eastern Madagascar. Located in the Ifanadiana district, around 390 km south-east of the capital Antananarivo and close (around 4 km) to the Ranomafana National Park, the study area lies in an unprotected zone. The forest patches surrounding Sahofika include degraded secondary forest dominated by bamboo - *Valiha diffusa* (named locally '*vologasy*') - and agricultural land (predominantly rice) (Rakotoarinivo *et al.,* 2017).

The data were collected by the volunteer and local guides working for the Association Française pour la Sauvegarde du Grand Hapalémur - Helpsimus. Photos and videos were recorded by three camera traps installed in three different locations of the forest fragment of Sahofika which lies within the home range of one of the groups of greater bamboo lemurs monitored by Helpsimus (group 5 which in 2018 consisted of a total of 54 individuals; Helpsimus annual report 2018) (Fig. 1). The First camera (camera A), set from 4th April to 25th May 2018, was located in the core of the forest fragment within an area where the canopy cover is dense and human disturbance is low. The second camera (camera B), set from 4th April to 25th May 2018, was located near a rice field at the edge of the forest fragment with less canopy cover and more exposure to human activity. The third camera (camera C), set from 4th April to 10th July 2018, was set up near the top of a hill within the core of the forest fragment, with a view of the horizontal branch used by the lemurs. All cameras (model: Coolife Hunting Camera with Night Vision Motion Sensor) were active 24h/day. When triggered by movement the devices recorded a picture followed by a 5-second video. Each capture recorded the date, time, and temperature.

A minimum time interval of 30 minutes was used to minimize the nonindependence of consecutive photographs (Gerber *et al.,* 2012; Linkie and Ridout, 2011). Kernel density estimation was used in order to determine the temporal activity pattern of the lemurs over the 24-h cycle. The statistical analysis was conducted using the program R version 4.0.0 (R Core Team, 2020). The R package OVERLAP (Meredith and Ridout, 2020) was used to calculate the kernel density function for all independent samples (Ridout and Linkie, 2009). Times of the captures were converted into radians as this package uses trigonometric functions for fitting density curves. The function *densityPlot()* was then used to fit the kernel density function for a given data set and plot it (Meredith and Ridout, 2020). As in previous research on cathemeral primates, ranges of the sunrise and sunset times, as well as astronomical morning and evening twilight at the study area, were marked on the plot (Erkert and Cramer, 2006). Sunrise, sunset, and nocturnal luminosity index (NII) were calculated via the software MOON version 1.0 (implemented by R. M Thomas 1998) using the geographical coordinates of one of the camera-traps locations (Donati and Borgognini-Tarli, 2006). To compare the temporal distribution of greater bamboo lemurs' activity between contrasting fragment zones: fragment edge – next to the rice fields (Camera B), and fragment core (camera A and C) – a coefficient of overlap was estimated using the same package. The coefficient of overlap (Δ), ranging from 0 (no overlap) to 1 (full overlap) is defined as the area under both of the density curves. The estimator of the coefficient of overlap, Δ_1, was used due to the small sample size (N < 50). A confidence interval of 95% was used in generating 10,000 bootstrap samples (Ridout and Linkie, 2009).

Each independent sample captured by camera traps was categorised as diurnal or nocturnal. The activity that occurred between the beginning of the morning astronomical twilight, when the sun is 18^{O} below the horizon before sunrise, and the end of astronomical evening twilight when the sun is 18^{O} below the horizon after the sunset, was considered diurnal. The activity that occurred between the end of astronomical evening twilight when the sun is 18^{O} below the horizon after the sunset and the beginning of the morning astronomical twilight when the sun is 18^{O} below the horizon before sunrise was categorized as nocturnal (Donati and Borgognini-Tarli, 2006). Nocturnal captures were divided into three categories - according to the value of the Index of luminosity (NII) which ranged between 0 – 54% during the whole study period: category 1- low luminosity 0 – 18%, category 2 - medium luminosity 19 – 36%, and category 3 - high luminosity 37 – 54%. The frequency of nocturnal captures was calculated within each category. To determine the possible interaction between nocturnal luminosity and activity, a chi-square test was used to compare the observed nocturnal captures with a hypothesized even frequency across luminosity index values. Non-parametric statistical tests were conducted using IBM SPSS Version 25.0.

Results

This study resulted in 199 active camera trap days, of which 126 independent photographic captures of the greater bamboo lemurs (74 were classified as diurnal and 52 as nocturnal). During the study period, sunrise ranged between 05:58 AM and 06:28 AM, while sunset varied between 05:15 PM and 05:47 PM. The beginning of the astronomical morning twilight ranged between 04:45 AM and 05:15 AM, the end of the evening astronomical twilight ranged between 06:28 PM and 07:00 PM. The length of the day varied from 10.84 to 11.82 hours. Kernel density estimates of activity across the 24-h cycle confirmed lemurs' cathemerality (Fig. 2). The group of greater bamboo lemurs displayed three peaks of activity: one during the night and two coinciding with morning and evening astronomical twilights. Nocturnal activity increased after 11:00 PM with the highest density occurring between 01:00 AM and 02:30 AM. Subsequently, animals increased their activity from 05:00 AM with the peak occurring at 6:30 AM. Lemurs' lowest activity was recorded during the morning and central hours of the day, between 09:00 AM and 12:00 (noon). The maximum activity occurred in the evening between 05:00 PM and 07:00 PM.

The comparison of the activity pattern between two contrasting forest zones – fragment edge (77 independent photographic captures obtained from camera B) and fragment core (49 independent photographic captures obtained from cameras A and C) is shown in Figure 3. Calculations of the coefficient of overlap showed low overlap between the distribution of the activity within two zones ($\Delta_1 = 0.34$; obtained confidence intervals lower: 0.22 upper: 0.47). In the fragment core the lemurs were more active during the day with two peaks of activity, the highest peak occurring between 6:00 AM and 07:30 AM and the second between 01:00 PM to 06:00 PM. In the edge, the activity of the lemurs was mainly at twilights and nocturnal with three peaks of activity, between 05:30 PM and 08:00 PM, 00:00 (midnight) and 03:00 AM, and between 05:00 AM to 07:00 AM.

We found significant differences in the distribution of nocturnal captures across NII categories ($\chi2$ (2, N = 52) = 45.5, $p < 0.001$). Data are skewed towards the lower range of the luminosity index. The frequency of the nocturnal captures was highest within the low index of luminosity - 77%. Just 17% of nocturnal captures were observed at medium luminosity and only 6% of nocturnal captures occurred at high luminosity (Fig. 4).

Discussion

This study supports previous observations of greater bamboo lemurs' flexible activity, and it represents the first systematic record of the cathemeral activity of this species in the field. Our results are in line with a preliminary study of the diurnal activity pattern of two groups of greater bamboo lemurs living in the forests around Vohitrarivo, also monitored by Helpsimus (Rakotoarinivo *et al.,* 2017). Although Rakotoarinivo *et al*. suggest a bimodal pattern of activity for these lemurs, the study was based on direct diurnal observations, thus peaks of activity at night were not observed. Our results are also in agreement with the previous report from captive animals, where *Prolemur simus* have been observed to have three or four peaks of activity at dawn, dusk, night, and day (Santini-Palka, 1994). The study group in our study showed two peaks of activity corresponding with astronomical morning and evening twilights, indicating that sunrise and sunset likely work as zeitgebers. Interestingly, greater bamboo lemurs were also observed to have a third, lower peak of activity during the night.

A low overlap of the activity between the fragment core and the fragment edge indicates a significantly different temporal distribution of activity by the study group. Cameras located in the forest core recorded more diurnal activities, whereas the camera at the edge of the forest fragment, close to the rice fields, recorded much more nocturnal activities. A possible reason behind this contrasting activity distribution may be related to an anti-predator strategy. Predation is thought to have a major influence on primates' ecology (Stanford, 2002; Willems and Hill, 2009) and it contributes to changes in primates' activity patterns (Colquhoun, 2006). For example, cathemeral brown lemurs (*Eulemur* spp.) have been shown to increase their nocturnal activity in anthropogenic habitats where encounters with local people or domestic animals are more likely to happen (Donati *et al.,* 2016). In our study area, greater bamboo lemurs have been observed several times to crop feed on rice fields (Helpsimus, unpublished). Although there is no evident conflict between lemurs and humans at our study site, local people keep dogs, which represent a threat for the lemurs (Anderson, 1986; Roullet pers. com). The core zone of the forest may thus be perceived as safer for the lemurs. Such temporal strategy of predator-avoidance to minimize predation risk during crop feeding has been also observed in chimpanzees at Kibale National Park. Chimpanzees have been found crop feeding in the maize after sunset and during the new moon nights (Krief *et al.,* 2014). However, our conclusions are based on only three cameras which resulted in a low sample size. Further, long-term studies are needed to confirm these results.

In contrast with other cathemeral lemurs, which increase activity with higher luminosity at night, greater bamboo lemurs were more active during nights with low luminosity. An increase of nocturnal activity of collared brown lemurs (*Eulemur collaris*), blue-eyed black lemurs (*Eulemur flavifrons),* red-fronted lemurs *(Eulemur rufifrons)*, and southern bamboo lemur *(Hapalemur meridionalis)* is always associated with an increased percentage of the illuminated lunar disc and nocturnal luminosity (Donati and Borgognini-Tarli, 2006; Kappeler and Erkert, 2003; *E*ppley *et al.,* 2015; Schwitzer *et al.,* 2007). An opposite pattern of decreasing the nocturnal activity during full moon nights (also known as lunarphobia) has been observed in other cathemeral mammals e.g., European badger (*Meles meles)* (Cresswell and Harris, 1988) and the binturong *(Arctictis binturong)* (Prugh and Golden, 2014). Within the primates, nocturnal pygmy loris (*Xanthonycticebus pygmaeus)* and bengal slow loris (*Nycticebus bengalensis*) also decrease their activity on a night with increased luminosity (Rode-Margono and Nekaris, 2014; Rogers and Nekaris, 2011). Since the forest where this bamboo lemur group lives is open and partially degraded, it is possible that better visibility at low luminosity levels allows these lemurs to navigate while minimizing the risk of predation, especially if this is caused by non-forest predators like domestic dogs (Mella-Mendez *et al.,* 2019).

Cathemerality is a flexible response that may change according to ecological conditions. In our preliminary study, cathemeral *Prolemur simus* have shown their plasticity by adjusting their activity pattern to local conditions. Due to the small sample size used for the analysis of the overlap of activity patterns, our data must be taken with caution and conclusions can only be confirmed by future long-term studies. However, our results suggest that this threatened and unique species is able to cope with some degrees of anthropogenic disturbance. Over the past ten years, the number of known populations of *Prolemur simus* has increased as a result of discovering them in unexpected locations, often scattered in non-protected areas. These areas have been the focus of intensive community-based conservation efforts (Rakotoarinivo *et al.,* 2017; Rakotonirina *et al.,* 2013; Rakotonirina and Chamberlan, 2014; Randriahaingo *et al*., 2014; Ravaloharimanitra *et al.,* 2013a, 2013b, 2017). The population of greater bamboo lemurs monitored by Helpsimus in the area of this project is likewise increasing (Helpsimus., unpublished data) as well as the cultivated area in the region. Actions that may facilitate the survival of these lemurs within forest patches, e.g., building footbridges above the crop fields, are essential to sustain the growing population of this Critically Endangered primate.

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Figure Legends

Fig. 1. Location of the three camera traps (camera A, B, and C) in the forest fragment of fokotany Sahofika, Madagascar.

Fig. 2. Density estimates of activity pattern of *Prolemur simus* based on camera-trap data from the forest fragment of Sahofika, Madagascar. Dot dashed lines present a range of the beginning morning and evening astronomical twilight in the study area. Dotted lines present a range of sunrise and sunset. The actual data is presented at the foot of the graph.

Fig. 3. Overlap of the density estimates of *Prolemur simus* activity pattern between two contrasting forest zones – fragment edge and fragment core. Dot dashed lines present a range of the beginning morning and evening astronomical twilight in the study area. Dotted lines present a range of sunrise and sunset.

Fig. 4. Frequency of the nocturnal captures within three categories of the index of luminosity (NII).