Timothy M. Eppley, Julia Watzek , Jörg U. Ganzhorn and Giuseppe Donati

Predator avoidance and dietary fibre predict diurnality in the cathemeral folivore Hapalemur meridionalis, *Behavioral Ecology and Sociobiology*, vol. 71, no. 4 (2017)

DOI: 10.1007/s00265-016-2247-3

Predator avoidance and dietary fibre predict diurnality in the cathemeral folivore *Hapalemur meridionalis*

Timothy M. Eppley [a,b,c,*], Julia Watzek [d], Jörg U. Ganzhorn [b], and Giuseppe Donati [c]

[a] Department of Anthropology, University of Texas, Austin, United States of America

[b] Biozentrum Grindel, Department of Animal Ecology and Conservation, University of Hamburg, Hamburg, Germany

[c] Nocturnal Primate Research Group, Department of Social Sciences, Oxford Brookes University, Oxford, United Kingdom

[d] Department of Psychology, Language Research Center, Georgia State University, Atlanta, United States of America

[*]Correspondence:
Timothy M. Eppley
Department of Anthropology
University of Texas
Austin, Texas 78712
United States of America
Tel.: +01 (512) 800-0269
E-mail address: eppleyti@gmail.com

Formatted

Ultimate determinants of *Hapalemur* cathemerality

Abstract

Though numerous mammalian taxa exhibit cathemerality (i.e., activity distributed across 24-h cycle), this includes very few primates, exceptions being species from Aotinae and Lemuridae. Four non-mutually exclusive hypotheses have been proposed to explain ultimate determinants for cathemeral activity in lemurs: thermoregulatory benefits, anti-predator strategy, competition avoidance, and metabolic dietary-related needs. However, these have only been explored in the frugivorous genus *Eulemur*, with some species increasing nocturnality as a possible response to avoid diurnal raptors and to increase their ability to digest fibre during resource scarce periods. Since *Eulemur* lack specialisations for digesting bulk food, this strategy would allow for processing fibres over the full 24-h. The folivorous lemurids, i.e., genus *Hapalemur*, provide a divergent model to explore these hypotheses due to gastrointestinal adaptations for digesting dietary fibre and small body size compared to *Eulemur*. We linked continuous activity data collected from archival tags with observational behaviour and feeding data from three groups of adult *H. meridionalis* from January – December 2013. We tested the effects of thermoregulation, anti-predator, and the weighted proportion of dietary fibre on the daily diurnal/nocturnal activity ratio using a Linear Mixed-Model. Our best-fit model revealed that increased canopy exposure and dietary fibre predicted greater diurnality. Our findings contrast with previous predictions for frugivorous lemurids, proposing a divergent adaptive explanation for folivorous lemurids. We suggest that the need to avoid terrestrial predators, as well as the longer digestive bouts during periods of bulky food, may override cathemerality in favour of diurnality in these bamboo lemurs.

Key words: anti-predator strategy; diel activity; dietary fibre; lunarphilia; southern bamboo lemur; thermoregulation

Significance Statement

Southern bamboo lemurs are active throughout the 24-h cycle, with diurnality increasing with high proportions of dietary fibre, in contrast to other cathemeral primates. They also increase diurnality on days with greater canopy exposure, potentially avoiding nocturnal predators in risky foraging areas. We suggest that folivorous lemurids may require long periods of inactivity to conserve energy and digest dietary fibre, thus limiting activity to periods of optimal foraging efficiency over the 24-h cycle.

Introduction

The strict limiting of activity to either day or night, each representing a contrasting sensorial environment, has had profound consequences on the behavioural ecology of every animal taxon (Enright 1970; Ashby 1972; Charles-Dominique 1975; Aschoff et al. 1982; Halle 2000, 2006). Shifting activity over the 24 h cycle, thus not adhering to a strict diurnal or nocturnal phase, is known as diel activity in the field of animal ecology (Erkert and Cramer 2006; Halle 2006). It is exhibited across many mammalian orders (Serena 1994; Clarke et al. 1995; van Schaik and Griffiths 1996; Flowerdew 2000; Halle and Stenseth 2000; Palomares and Delibes 2000; Zalewski 2000; Brooke 2001; Gilmore et al. 2001; Holley 2001; Curtis and Rasmussen 2002; Taylor and Skinner 2003), despite the challenge of compromising between adaptations for phases of the diel cycle (Martin 1990; Rydell and Speakman 1995; Ankel-Simons and Rasmussen 2008; Prugh and Golden 2014; Santini et al. 2015).

Diel activity patterns are inherently flexible, thus we would expect them to fluctuate according to environmental variation (i.e., a proximate determinant). For example, in most diel species, photoperiodic changes such as sunrise and sunset act as a *zeitgeber* (i.e., an environmental cue that acts as a synchronizing or entrainment agent) by controlling the onset and cessation of activity (Halle 1995, 2000; Taylor and Skinner 2003; Donati and Borgognini-Tarli 2006a; Fernández-Duque and Erkert 2006; Chiesa et al. 2010; Schlichting et al. 2015). While this activity pattern has been shown to be inhibited by negative masking effects, such as a decrease in nocturnal luminosity (Aschoff 1988; Erkert 1989; Horning and Trillmich 1999; Mrosovsky 1999), it is more often the case that activity increases under these low nocturnal light conditions (Orrock et al. 2004; Penteriani et al. 2011; Prugh and Golden 2014). Considering mammalian taxa, ultimate determinants (i.e., adaptive reasons) for diel activity patterns are based on a multitude of non-mutually exclusive explanations, including (1) a thermoregulatory strategy to avoid cold/heat stress (Chiarello 1998; Rezende et al. 2003), (2) anti-predator strategies (Zielinsky 1988; Lode 1995; Gunn et al. 2014), (3) metabolic dietary-related needs (Engqvist and Richard 1991; van Schaik and Griffiths 1996; Halle 2000; Merritt and Vessey 2000), (4) the avoidance of inter-specific competition (Ganzhorn 1989; Kronfeld-Schor and Dayan 1999; Jacob and Brown 2000; Jones et al. 2001), and (5) demographic differences, e.g., group size, age, and/or sex (Beier and McCullough 1990; Wauters et al. 2000; Marcelli et al. 2003; Kaczensky et al. 2006; Zschille et al. 2010). Evidence from primates supports a few of these hypotheses (reviewed in Curtis and Rasmussen 2006; Donati and Borgognini-Tarli 2006b; Donati et al. 2009).

Unlike other mammalian orders, the exhibition of diel activity is rare in Primates (Curtis and Rasmussen 2006), an order where it is more commonly referred to as ‘cathemerality’ (Tattersall 1987). One haplorhine species, *Aotus azarae*, regularly displays a cathemeral activity pattern (Fernández-Duque 2003), while the remaining cathemeral primates are limited to the strepsirrhine family Lemuridae, endemic to Madagascar (Donati and Borgognini-Tarli 2006b). While it has been hypothesized that cathemerality in lemurs is the product of a non-adaptive disequilibrium in a transition from nocturnality to diurnality enabled by the recent extinction of large diurnal raptors and of competitive lemur species (Martin 1972; van Schaik and Kappeler 1993, 1996; Kappeler and Erkert 2003), most evidence lends support for cathemerality likely representing a stable adaptation in lemurs (Curtis and Rasmussen 2006; Kirk 2006; Donati et al. 2007a, 2009, 2013; Eppley et al. 2015a; Santini et al. 2015).

As for the ultimate determinants of cathemerality in lemurs, it is assumed that high climatic seasonality in Madagascar has had a major influence on the evolution of lemur life history traits (Wright 1999; Dewar and Richard 2007). As such, it has been suggested that thermoregulatory stress could potentially affect diel activity patterns (Curtis et al.1999; Mutschler 1999). Though some lemurids display a seasonal shift in activity across habitats without strong temperature seasonality (Andrews and Birkinshaw 1998; Mutschler 1999; Donati and Borgognini-Tarli 2006a; Tarnaud 2006; Donati et al. 2009), the avoidance of extreme temperatures (i.e., both cold and heat) is a common driver for diel activity patterns across many taxa (Greenwood and Metcalfe 1998; Halle and Stenseth 2000; Zielinsky 2000).

Furthermore, activity patterns in part determine the pattern of interactions among predators and prey, playing an important role in the ecology of both (Wolfe and Summerlin 1989; Packer et al. 2011; Penteriani et al. 2011; Prugh and Golden 2014). It is often suggested that a switch to nocturnal foraging represents a predator-avoidance mechanism, reducing risk from diurnal predators (Cowan and Peckarsky 1994; Metcalfe et al. 1999; Reebs 2002; Lang et al. 2006; Orpwood et al. 2006). Considering this strategy, predation has been tentatively linked to lemurid cathemerality as an ultimate determinant (Overdorff 1988; Curtis et al. 1999; Donati et al. 1999; Rasmussen 1999, 2005; Colquhoun 2006, 2007).

A relationship between cathemeral activity and cellulose-rich food with low energy content has been well-documented in small, energy-demanding mammals (Halle 2006). Gut constraints in small mammals with unstructured fermentation chambers may require more or less constant foraging activity to meet energy requirements (Daan and Slopsema 1978). Engqvist and Richard (1991) proposed that the exhibition of cathemeral activity either seasonally or at localized sites by primate species is associated with a shift towards a higher consumption of high fibre, low-quality food. Frugivorous *Eulemur* display an average food-transit time of 3-4 h (Campbell et al. 2004), and ultimately, an extension of foraging across 24 h would allow more time to extract sufficient energy to meet their dietary metabolic demand in animals that lack gastrointestinal adaptations to efficiently digest cellulose (Engqvist and Richard 1991). In fact, several studies of frugivorous primates, e.g., *Eulemur rubriventer* (Overdorff 1988), *E. fulvus mayottensis* (Tattersall 1979; Tarnaud 2006), and *E. collaris* (Donati et al. 2007a, 2009), have linked diel activity to dietary changes and fibrous food, such as leaves (Donati et al. 2016). However, recent evidence of a diel activity pattern in a folivorous primate, the southern bamboo lemur *Hapalemur meridionalis* (Eppley et al. 2015a), adds a layer of complexity surrounding this potential ultimate determinant of lemurid cathemerality. The gastrointestinal tract of these relatively small mammals includes an enlarged, sacculated caeco-colon, which assists in their elevated ability to digest fibre (Martin 1990; Overdorff and Rasmussen 1995; Campbell et al. 2004), allowing for leafy material to be fermented by symbiotic gut microbes across an average food-transit time of 18-36 h, as measured in a closely-related species (Fidgett et al. 1996; Campbell et al. 2000, 2004; Perrin 2013). Thus, the small-bodied folivorous bamboo lemurs, with their elevated digestive capabilities and contrasting dietary guild from other cathemeral strepsirrhines, provide a divergent model with which to determine the role of dietary fibre as an ultimate determinant of this unusual activity pattern among primates.

Here we present systematic 24-h activity pattern data recorded via automatic data-logging tags deployed on *H. meridionalis*, and link these data to our focal observation days. Controlling for proximate factors (i.e., photoperiodic changes and nocturnal luminosity), we aimed to assess which, if any, of three non-mutually exclusive ultimate determinants (i.e., thermoregulatory strategy, anti-predator strategy, and metabolic dietary-related coping mechanism) best explain a cathemeral activity pattern, measured as diurnality (ratio between diurnal and nocturnal activity), in a small-bodied folivorous primate. The competition avoidance hypothesis was not examined due to the minimal occurrence of agonistic interactions between bamboo lemur groups and other lemur species. Furthermore, we did not consider demographic factors as adult *H. meridionalis* group members are often synchronous in their activity pattern. Considering the relatively small body size of southern bamboo lemurs and what has been seen in similar-sized Alaotran gentle lemurs *Hapalemur alaotrensis* (Mutschler 1999), and Azara’s owl monkeys *Aotus azarae* (Fernández-Duque 2003), we predict that high diurnal temperature would inhibit diurnal activity and/or cooler temperature at night would inhibit nocturnal activity. Furthermore, small- to medium-sized lemurs are frequently at risk of predation from diurnal raptors and terrestrial cathemeral or nocturnal mammals (Karpanty and Wright 2007). As *H. meridionalis* are known to utilize sparsely canopied habitats (Eppley et al. 2015b), we predict that the bamboo lemurs will increase their nocturnal activity when feeding in open-canopy habitats and/or increase diurnality when feeding on the ground. Lastly, since the digestive capabilities of *Hapalemur* permit an elevated ability to cope with dietary fibre compared to frugivorous *Eulemur*, we predict that periods of increased dietary fibre will have no effect on bamboo lemurs’ diurnality.

Methods

Study site and species

Data were collected at the Mandena littoral forest (24°95'S 46°99'E) in coastal southeast Madagascar, a protected area of 230 ha of littoral upland forest and interspersed swamps (Eppley et al. 2015b). Observations were conducted on three groups of southern bamboo lemurs (*Hapalemur meridionalis*) (Fausser et al. 2002). These relatively small-bodied primates (1.1 kg) live in small social groups (Eppley et al. 2015c) that are characterized by maintaining a folivorous diet (Eppley et al. 2011, 2016a) and strict territoriality with minimal home range overlap (Eppley et al. 2015b, 2016c).

Ten adult *H. meridionalis* were captured and fitted with external radio-transmitters with an archival tag (ARC400, Advanced Telemetry Systems, Isanti, MN, USA), that recorded a proportional rate of activity every fifteen minutes throughout the duration of the study. For the purpose of this study, however, the data are limited to collared adult individuals from January – December 2013, as this period corresponds to our behavioural observations. Capture and anaesthesia procedures have been previously described in Eppley et al. (2015a). Seven of these individuals were recaptured following the same procedures and data were retrieved manually from the tags.

Astronomical Data

Sunset and sunrise, moonset and moonrise, as well as morning and evening twilight times were obtained from the US Naval Observatory Astronomical Calendar (http://aa.usno.navy.mil/data/docs/RS_OneDay.php) by using the geographical coordinates for Mandena. From these information we were able to calculate both daylength (h) and astronomical twilight (-18° below horizon; Erkert 2011; Eppley et al. 2015a). We then generated a nocturnal luminosity index (NL) through indirect evaluations of moon phase and transit times using the geographic coordinates of Mandena via an ad hoc program, Moon v.2.0 (Curtis et al. 1999), allowing us to estimate the amount of lunar light available over the course of a specific night.

Climatic Data

Climatic factors can be highly variable within coastal southeast Madagascar (Bollen and Donati 2005). Temperature (°C) was recorded in 30-mins intervals throughout the study using Lascar EL-USB-1 data loggers, operated by custom software (EasyLog USB Version 5.45, Lascar Electronics). In 2013, the mean temperature in Mandena was 22.5°C (monthly mean range: 18.5 – 26.7°C), displaying an absolute range between 9.5 – 35.0°C (Eppley et al. 2016b). Precipitation (mm) was measured daily at 6:00h using a rain gauge placed within the study site (Eppley et al. 2015a).

Behavioural Data

From January to December 2013, we conducted full-day focal follows (from sunrise to sunset) for approximately five days a month with three groups (a 4th group was used exclusively for home range calculation). Identification of individuals was made using radio-tracking tags with coloured pendants, with all adult individuals in each group sampled at least once each month.

Due to the differences in habitat and their contrasting floristic structures (Eppley et al. 2015b), we evaluated exposure to diurnal birds of prey by collecting instantaneous point sampling (Altmann 1974) during all activities at 5-min intervals of whether the focal subject was located directly under canopy cover, or if they were exposed (i.e., no canopy directly above the focal). Specifically, we used this daily proportional value as a proxy of risk from aerial predators since the littoral area mostly consists of evergreen trees with little seasonal leaf abscission (Bollen and Donati 2005). Potential diurnal aerial threats to bamboo lemurs present in Mandena include Madagascar harrier-hawk *Polyboroides radiatus*, Henst's goshawk *Accipiter henstii*, and Madagascar buzzard *Buteo brachypterus* (Karpanty 2006; Karpanty and Wright 2007). Given the various hunting strategies of these raptors (Brockman 2003) and that playback experiments of aerial predators have shown *Hapalemur* to descend in the canopy in response to raptor calls (Karpanty and Wright 2007), we considered our canopy exposure method as an acceptable proxy as they should theoretically try to minimize the amount of time they are exposed from above. Additionally, terrestriality is presumed to increase the perceived risk of predation by exposing individuals to potential predators (van Schaik 1983), e.g., fossa *Cryptoprocta ferox* (Donati et al. 2007b), feral dogs (*Canis familiaris*; Eppley et al. 2016a), and Dumeril's boa *Acrantophis dumerili* (Eppley and Ravelomanantsoa 2015). As such, we used the daily proportion of time the southern bamboo lemurs spent on the ground as a proxy for terrestrial predation risk.

Fibre Analysis

Continuous sampling (Altmann 1974) was utilized each time the focal was observed feeding. This included the exact time spent feeding (timed to the second) per food item(s) while noting the plant species, with a new bout recorded if there was a 60 second interval with no feeding. We collected samples of all observed food items ($N = 86$) directly from feeding trees and/or grazing sites on the same day or at the same time the following day. Samples were weighed with an electronic balance (fresh weight), dried in an oven at approximately 40°C for a standard period, and weighed again (dry weight) at the field site. Dry matter specimens were exported to the University of Hamburg and biochemical analyses on all food items were conducted in 2013-2014. Since the argument on possible effects of fibre on cathemerality is based on the assumption that animals need time to extract metabolizable components out of a bulky diet (Donati et al. 2009), we restricted the chemical analyses in the present context to Neutral Detergent Fibre (NDF) and Acid Detergent Fibre (ADF). Both daily weighted proportions of NDF and ADF dry matter were calculated with the proportion of feeding records for each food item as the weighted coefficient (Table 1; Kurland and Gaulin 1987; Eppley et al. 2016a). NDF is composed of non-digestible silica, lignin, cellulose and poorly defined fraction of "hemicellulose". Hemicellulose consists of digestible and non-digestible carbohydrates, cell-wall-bound proteins and possibly digestion-inhibiting tannins. ADF represents the fibre fraction containing cellulose and lignin. Herbivores are assumed to get substantial fractions of energy and nutrients out of hemicellulose, yet its digestion is time-consuming and thus might represent one of the limiting factors of digestion (Rothman et al. 2012). As substantial differences in energy intake are expected in these highly efficient folivorous lemurs depending on whether NDF proportions are mostly digestible or mostly indigestible, we used the difference between NDF and ADF (hereafter called fibre) as a proxy of digestible fibres. Detailed reviews of the procedures and their biological relevance are provided by van Soest (1996), Ortmann et al. (2006), Rothman et al. (2012), and Wallis et al. (2012).

Data Analyses

We considered only full-day focal follows (*N* = 106) of southern bamboo lemurs, that is, we only included data limited to sessions where the focal subject was observed for ≥80% of the day (i.e., as calculated via available daylight per 24-h period), which constituted >1,206 h. We utilized a diurnal-to-nocturnal activity (DN) ratio so as to allow for comparison across taxa (Donati et al. 2013). To determine which factors influenced the DN ratio, we fitted Linear Mixed-effects Models (LMM) in R statistical software (R Development Core Team 2014) using the lmer function of the lme4 package (Bates et al. 2012), with the daily DN ratio as a continuous response variable. We included the following fixed effects: mean temperature (°C), the weighted proportion of fibre in the daily diet, and percentage of terrestriality and canopy exposure (as proxies of predation pressure). In addition, we included as fixed effects the proximate variables of total precipitation (mm), daylength (h), and nocturnal luminosity index (NL). Groups were included as random effect to control for repeated sampling. We then used the ANOVA function to calculate likelihood ratio tests for model comparison, allowing us to determine which model had the best explanatory power by comparing Akaike's Information Criterion (AIC) values for all possible models. *P*-values were obtained with a likelihood ratio test using the afex package (Singmann 2014), developed for R statistical software (R Development Core Team 2014) with significance considered at $P < 0.05$. We tested for the normality of the residuals and the presence of outliers in the LMM using the Kolmogorov-Smirnov test, with data entered for parametric analyses after log transformation as they were not all normally distributed.

Multicollinearity was not an issue for predictors as a correlation matrix of the dependent variable and fixed effects displayed values all less than 0.90 (Cohen et al. 2003; Field 2013). It should be noted that there were a couple large correlations between predictors. In particular, temperature and daylength shared a high degree of variance with each other ($r^2 = 0.53$; Table 2), which limited the amount of variance they can uniquely share with the dependent variable. Despite this high correlation, these variables were not predictive of a change in daily diurnality. Furthermore, terrestrial activity and fibre shared a high degree of variance ($r^2 = 0.59$; Table 2).

Results

From January to December 2013 collar data revealed that bamboo lemurs exhibited a mean (±SD) DN ratio of 4.75 ± 2.48 ($N = 106$; Figure 1). Comparison between daily averages and ranges of the proximate and ultimate factors between low diurnality (< 3.0), intermediate diurnality (3.0 – 5.0), and high diurnal activity (> 5.0) are provided in Table 3.

Our best-fit model (AIC = 284.28, $\chi^2 = 27.53$, $df = 3$, $P < 0.001$) provided a significantly better fit for the data than the null model, and included significant values for one proximate factor (nocturnal luminosity), one anti-predator proxy (canopy exposure), and one dietary related factor (fibre) (Table 4). Specifically, greater nocturnal luminosity increased nocturnal activity (Figure 2a), while both increased canopy exposure (Figure 2b) and the weighted proportion of fibre in the diet were shown to increase bamboo lemur diurnality (Figure 2c). We examined the full model to evaluate the effect of predictors that were not included in the best-fit model (Table 4). Again, only nocturnal luminosity, canopy exposure, and daily proportions of dietary fibre predicted daily diurnality. None of the following fixed effects provided any significant predictive power: temperature (i.e., thermoregulatory proxy), terrestrial activity (i.e., anti-predator proxy), precipitation and daylength (i.e., proximate factors). Indeed, the full model did not provide a significantly better fit for the data than the best-fit model (AIC = 290.27, $\chi^2 = 2.02$, $df = 4$, $P = 0.73$).

Discussion

Our study provides the first systematic examination of determinants of diel activity in a folivorous primate, *H. meridionalis*, thereby allowing previous hypotheses on cathemerality based on mainly frugivorous primates to be tested from an alternative angle. Our results show that canopy exposure and dietary fibre were significant predictors of diurnality. Furthermore, our model revealed that *H. meridionalis* increased nocturnal activity when there was greater nocturnal luminosity (Eppley et al. 2015a). This was not surprising given that moonlight has been shown to be similarly influential to most cathemeral (Charles-Dominique et al. 1980; Wright 1989; Curtis et al. 1999; Donati et al. 2001, 2009, 2013; Fernández-Duque 2003;

Kappeler and Erkert 2003; Donati and Borgognini-Tarli 2006a; Fernández-Duque and Erkert 2006; Schwitzer et al. 2007; Fernández-Duque et al. 2010) and several nocturnal primates (Gursky 2003; Nash 2007)

Thermoregulatory strategy

Ambient temperature was shown to have no influence on bamboo lemur diurnality. Our results are similar to previous studies on the genus *Eulemur* (Andrews and Birkinshaw 1998; Tarnaud 2006; Donati et al. 2009), yet intriguing considering that *Hapalemur* are relatively small-bodied folivores (Tan 1999; Eppley et al. 2011) that do not appear to use torpor (Eppley unpublished data). The activity of the only similarly-sized cathemeral primate studied so far, *Aotus azarae*, is influenced by ambient temperature in Formosa, Argentina, where similar maxima and minima temperatures to Mandena have been recorded (Fernández-Duque 2003). Similarly, limited observations suggest that *H. alaotrensis* avoid high daytime temperatures (Mutschler 1999).

Thermoregulatory strategies appear to be common for many cathemeral non-primate mammals. High ambient temperatures have been shown to constrain diurnal activity in large herbivores, such as Przewalski horse (*Equus ferus przewalskii*) and eastern grey kangaroos (*Macropus giganteus*), thus reducing heat stress by remaining in the shade during the hot daytime and increasing nocturnal activity (Clarke et al. 1995; Berger et al. 1999). In contrast, low ambient temperatures were shown to constrain the activity of herbivorous cururos (*Spalacopus cyanus*, Octodontidae) outside of their burrows during the night (Rezende et al. 2003), while pine martens (*Martes martes*) also significantly decreased their diel activity on cooler days (Zalewski 2000). Furthermore, it is suggested that nocturnal activity of the highly folivorous Atlantic forest maned sloth (*Bradypus torquatus*) is inhibited by lower ambient temperatures (Chiarello 1998). Though it is argued whether or not other small-bodied folivorous lemurs (i.e., *Avahi* and *Lepilemur*) exhibit periodic torpor (Dausmann 2014), our data suggest that southern bamboo lemurs may be tolerant of climatic fluctuations. However, this result may not be extrapolated for all Madagascar as climatic extremes in this coastal region are not as pronounced as in other regions of the island (Bollen and Donati 2005; Dewar and Richard 2007). Therefore this factor may not have been as influential at our study site, which has a monthly mean temperature range of 18.5 – 26.7°C (Eppley et al. 2016b), as compared to the sub-arid south-western forests (daily means: 17.0 and 34.0°C; Andriatsimietry et al. 2009), and the high-altitude eastern rain forests (daily mean of 13.0°C in the austral winter; Blanco et al. 2013).

Anti-predator strategy

As a predator-sensitive behaviour, foraging success is largely determined by the need to minimize predation risk (Schoener 1971; Cowlishaw 1997; Miller 2002), with susceptibility to predation often dependent on the level of exposure of the position of the individual (van Schaik and van Noordwijk 1989; Janson 1998). For example, elephants (*Loxodonta africana*) have been shown to defensively flee in response to human auditory cues (McComb et al. 2014). As such, elephants around Mikumi National Park, Tanzania, are known to raid nearby agriculture fields at night to avoid periods of human activity; however, they decrease crop-raiding on nights of greater lunar luminosity in order to further avoid potential detection (Gunn et al. 2014). Increased terrestrial feeding by *H. meridionalis* in Mandena is due to a greater dietary quality pay-off when the perceived risk of predation was less than or equal to the risk when feeding arboreally (Eppley et al. 2016a). While our model does not support terrestrial activity as influencing changes in diurnality, canopy exposure was found to be a significant factor, i.e., on days when canopy exposure increased southern bamboo lemurs were more diurnal, though against our prediction of avoiding diurnal aerial predation.

The degraded and fragmented habitat matrix of Mandena includes many open-canopy areas, with the majority of these concentrated in the marsh/swamp areas where these lemurs feed heavily on terrestrial food items, such as various grasses and Cyperaceae piths, during diurnal hours (Eppley et al. 2011, 2016a). It has been established that the congener *H. griseus* is a frequent food source for raptors at Ranomafana National Park (Karpanty and Wright 2007), and changes in diel activity are often shown to reduce the perceived risk from diurnal predators (Cowan and Peckarsky 1994; Lang et al. 2006; Orpwood et al. 2006). Conversely, the strategy of these southern bamboo lemurs appears to minimize the potential predation risks associated with exposed nocturnal feeding by focusing terrestrially foraging in open-canopy areas during the day. Despite open canopy areas potentially making bamboo lemurs more susceptible to aerial predation (Grassi 2006), terrestrial foraging in open-canopy areas likely carry a greater perceived risk at night when large terrestrial predators, such as fossa and feral dogs, are more active. In fact, it has been shown that Milne-Edwards' sifaka (*Propithecus edwardsi*) select sleeping sites higher in the canopy at night to avoid detection by terrestrial predators, e.g., fossa (Wright 1998). This potential anti-predator strategy suggests that the marsh/swamp habitat presented higher perceived predation risk at night compared to the littoral forest, while also suggesting that the nutritional benefits gained by foraging in the marsh/swamp may outweigh the risk of predation. However, until more fine-grained data are collected to accurately assess predation rate, these observational proxies are our best approximation.

Metabolic dietary-related needs

Ultimate determinants of *Hapalemur* cathemerality

Contrary to our prediction, daily proportion of dietary fibre (i.e., NDF-ADF) was shown to have a significant influence on the DN activity ratio of *H. meridionalis*. Specifically, diurnality exhibited by *H. meridionalis* decreased on days when the proportion of dietary fibre was low. This is in contrast to what has been observed in cathemeral mammals, such as various small rodents (Halle and Stenseth 2000; Halle 2006) and *Eulemur* (Donati et al. 2007a, 2009). Engqvist and Richard (1991) first suggested that the expansion to 24-hour activity is a consequence of the short food-transit time in frugivorous *Eulemur* and the necessity to refill their stomach to maximize energy extractions when fibre intake increases, i.e. during a seasonal shift to folivory (Tarnaud 2006; Donati et al. 2007a, 2009). This has been observed in many small mammals with a limited capacity for fibre digestion, resulting in a power feeding strategy to maximize overall food intake (Cork and Foley 1991; Halle 2006). The *Hapalemur* genus maintains year-round a folivorous feeding ecology composed largely of bamboos, grasses, and sedges (Overdorff et al. 1997; Mutschler 1999; Tan 1999; Grassi 2002, 2006; Eppley et al. 2011, 2016a), a diet that requires a long food-transit time compared to frugivorous *Eulemur* (Cabre-Vert and Feistner 1995; Fidgett et al. 1996; Campbell et al. 2000, 2004; Perrin 2013). Thus, while the hypothesis put forth by Engqvist and Richard (1991) provides an explanation for *Eulemur* cathemeral activity patterns, it does not explain cathemerality for *Hapalemur*. We propose that bamboo lemur digestive strategies may explain these differences.

Similar to some herbivorous artiodactyls (Polat et al. 2013), herbivorous/folivorous marsupials (Cork and Foley 1991), and folivorous haplorhine primates (Milton 1981, 1998), long resting/digestive bouts may be necessary when bamboo lemurs consume highly fibrous foods. Direct observations, supported by the known long food-transit time which assists in digesting bulk dietary fibre (Overdorff and Rasmussen 1995; Fidgett et al. 1996; Campbell et al. 2000, 2004), suggest that resting bouts of these small lemurids are not interrupted by defecation as frequently as observed in *Eulemur* (Eppley and Donati pers. observ.). Assuming that the ancestral activity pattern of the family Lemuridae is likely to be cathemeral (Curtis and Rasmussen 2006; Tattersall 2008; Donati et al. 2013; Eppley et al. 2015a; Santini et al. 2015), we hypothesize that *Hapalemur* dietary needs may "mask" cathemerality when heavily feeding on high fibre foods, forcing them to become more monophasic. Also, the need to maintain high foraging efficiency on leaves and grass, food categories more often associated with diurnality in primates, may further explain why bamboo lemurs concentrate activity during daylight hours. If our reasoning is correct, bamboo lemurs may have retained cathemerality and the multiple advantages of its flexibility (Curtis and Rasmussen 2006) while adapting it to complement their folivorous specializations. This idea, however, should be considered speculative until more rigorous behavioural and physiological data are collected.

Conclusions

Our data analysis supported both an anti-predatory strategy and metabolic dietary-needs hypotheses as ultimate determinants of cathemeral activity in *H. meridionalis*. The southern bamboo lemurs of Mandena increased diurnal activity when they spent more time in exposed locations, suggesting that open canopy areas are more risky at night compared to during the day. Similarly, the extension of activity into the night decreased as the lemurs ingested more dietary fibre. This is in stark contrast to the dietary strategy of other lemurids that allegedly increase nocturnal activity to cope with increased fibre in their diet (Donati et al. 2016) or are not affected by dietary fibres (Curtis et al. 1999). We suggest that periods of bulky food intake by bamboo lemurs may require long periods of inactivity to digest dietary fibre. Ultimately, these data provide evidence that despite contrasting gastrointestinal morphologies and dietary adaptations among lemurid species, cathemeral activity provides varying adaptive value, as different constraints appear to act simultaneously and/or in different ways depending on the habitat (Curtis and Rasmussen 2006; Donati et al. 2013; Tattersall 2008).

Ethical Statement

This work was supported by the American Society of Primatologists; Conservation International (Primate Action Fund); Idea Wild; Mohamed bin Zayed Species Conservation Fund (Project Number: 11253008); Primate Conservation Inc.; and Primate Society of Great Britain/Knowsley Safari Park. The authors declare that they have no conflict of interest. This research was carried out under the Accord de Collaboration between the Department of Animal Biology of the University of Antananarivo and the Department of Animal Ecology and Conservation of the University of Hamburg, and QIT Madagascar Minerals (QMM). Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de recherché N° 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar. All data were collected in accordance with the ASAB/ABS Guidelines for Use of Animals in Research. It was not possible to record data blind because our study involved focal animals in the field.

Acknowledgments

We thank the Direction du Système des Aires Protégées, and the Ministère de l'Environnement et Forêts of Madagascar for permission to conduct research. We are grateful to Jacques Rakotondranary and Tolona Andrianasolo for obtaining our research permits, and to Katie Hall and Natalie Breden for assistance in the field. We also thank the Environment Team at QMM Rio Tinto for their assistance and provision of logistical support on-site and acknowledge their helpful staff, especially Jean-Baptiste Ramanamanjato, Johny Rabenantoandro, Faly Randriatafika, Laza Andriamandimbiarisoa, David Rabehevitra, Claude Soanary, and Robertin Ravelomanantsoa. Many thanks to Irene Tomaschewski for plant biochemical analyses. We would like to thank Maria van Noordwijk and two anonymous reviewers for their suggestions to improve previous versions of this manuscript.

References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227-266

Andrews JR, Birkinshaw CR (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

Andriatsimietry R, Goodman SM, Razafimahatratra E, Jeglinski JWE, Marquard M, Ganzhorn JU (2009) Seasonal variation in the diet of *Galidictis grandidieri* Wozencraft, 1986 (Carnivora: Eupleridae) in a sub-arid zone of extreme south-western Madagascar. J Zool 279:410-415

Ankel-Simons F, Rasmussen DT (2008) Diurnality, nocturnality, and the evolution of primate visual systems. Am J Phys Anthropol 51:100-117

Aschoff J, Daan S, Groos GA (1982) Vertebrate circadian systems. Springer-Verlag, Berlin

Aschoff J (1988) Masking of circadian rhythms by zeitgebers as opposed to entrainment. In: Hekkens WTJM, Kerkhof GA, Rietveld WJ (eds) Trends in chronobiology: advances in the biosciences. Pergamon Press, Oxford, pp 149-161

Ashby KR (1972) Patterns of daily activity in mammals. Mammal Rev 1:171-185

Bates D, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42

Beier P, McCullough DR (1990) Factors influencing white-tailed deer activity patterns and habitat use. Wildlife Monogr 109:3-51.

Berger A, Scheibe KM, Eichhorn K, Scheibe A, Streich J (1999) Diurnal and ultradian rhythms of behaviour in a mare group of Przewalski horse (*Equus ferus przewalskii*), measured through one year under semi-reserve conditions. Appl Anim Behav Sci 64:1-17

Blanco MB, Dausmann KH, Ranaivoarisoa JF, Yoder AD (2013) Underground hibernation in a primate. Sci Rep 3:1768

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

Brockman DK (2003) *Polyboroides radiatus* predation attempts on *Propithecus verreauxi*. Folia Primatol 74:71-74

Brooke AP (2001) Population status and behaviours of the Samoan flying fox (*Pteropus samoensis*) on Tutuila Island, American Samoa. J Zool 254:309-319

Cabre-Vert N, Feistner ATC (1995) Comparative gut passage time in captive lemurs. Dodo 31:76-81

Campbell JL, Eisemann JH, Williams CV, Glenn KM (2000) Description of the gastrointestinal tract of five lemur species: *Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Hapalemur griseus*, and *Lemur catta*. Am J Primatol 52:133-142

Campbell JL, Williams CV, Eisemann JH (2004) Use of total dietary fiber across four lemur species (*Propithecus verreauxi coquereli*, *Hapalemur griseus griseus*, *Varecia variegata*, and *Eulemur fulvus*): does fiber type affect digestive efficiency? Am J Primatol 64:323-335

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: Luckett WP, Szalay FS (eds) Phylogeny of the primates: a multidisciplinary approach. Plenum Press, New York, pp 69-88

Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E. Pariente GF, Petter Rousseaux A, Petter JJ, Schilling A (1980) Nocturnal Malagasy primates: Ecology, physiology and behavior. Academic Press, New York

Chiarello AG (1998) Activity budgets and ranging patterns of the Atlantic forest maned sloth *Bradypus torquatus* (Xenarthra: Bradypodidae). J Zool 246:1-10

Chiesa JJ, Aguzzi J, Garcıa JA, Sarda F, de la Iglesia H (2010) Light intensity determines temporal niche switching of behavioral activity in deep water *Nephrops norvegicus* (Crustacea: Decapoda). J Biol Rhythm 25:277-287

Clarke JL, Jones ME, Jarman PJ (1995) Diurnal and nocturnal grouping and foraging behaviours of free-ranging eastern grey kangaroos. Aust J Zool 43:519-529

Cohen J, Cohen P, West SG, Aiken LS (2003) Applied multiple regression/correlation analysis for the behavioral sciences, 3rd edn. Erlbaum, Mahwah, New Jersey

Colquhoun IC (2006) Predation and cathemerality: comparing the impact of predators on the activity patterns of lemurids and ceboids. Folia Primatol 77:143-165

Colquhoun IC (2007) Anti-predator strategies of cathemeral primates: dealing with predators of the day and the night. In: Gursky S, Nekaris KAI (eds) Primate anti-predator strategies. Springer, New York, pp 146-172

Cork SJ, Foley WJ (1991) Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defences in temperate and tropical forests. In: Palo RT, Robbins CT (eds) Plant defences against mammalian herbivory. CRC Press, Boca Raton, FL, pp 133-166

Cowan CA, Peckarsky BL (1994) Diel feeding and positioning periodicity of a grazing mayfly in a trout stream and a fishless stream. Can J Fish Aquat Sci 51:450-459

Cowlishaw G (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Anim Behav 53:241-253

Curtis DJ, Zaramody A, Martin RD (1999) Cathemerality in the mongoose lemur, *Eulemur mongoz*. Am J Primatol 47:279-298

Curtis DJ, Rasmussen MA (2002) Cathemerality in lemurs. Evol Anthropol 11(Suppl):83-86

Curtis DJ, Rasmussen MA (2006) The evolution of cathemerality in primates and other mammals: a comparative and chronoecological approach. Folia Primatol 77:178-193

Daan S, Slopsema S (1978) Short-term rhythms in foraging behaviour in the common vole, *Microtus arvalis*. J Comp Phys A 127:215-227

Dausmann KH (2014) Flexible patterns in energy savings: heterothermy in primates. J Zool 292:101-111

Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. Proc Natl Acad Sci USA 104:13723-13727

Donati G, Borgognini-Tarli SM (2006a) 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, Borgognini-Tarli SM (2006b) From darkness to daylight: cathemeral activity in primates. J Anthropol Sci 84:7-32

Donati G, Lunardini A, Kappeler PM (1999) Cathemeral activity of red-fronted brown lemurs *(Eulemur fulvus rufus)* in the Kirindy Forest/CFPF. In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM (eds) New directions in lemur studies. Plenum Press, New York, pp 119-137

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

Donati G, Bollen A, Borgognini-Tarli S, Ganzhorn JU (2007a) Feeding over the 24-h cycle: dietary flexibility of cathemeral collared lemurs (*Eulemur collaris*). Behav Ecol Sociobiol 61:1237-1251

Donati G, Ramanamanjato JB, Ravoahangy AM, Vincelette M (2007b) Translocation as a conservation measure for a threatened species: the case of *Eulemur collaris* in the Mandena littoral forest, south-eastern Madagascar. In: Ganzhorn JU, Goodman SM, Vincelette M (eds) Biodiversity, ecology, and conservation of the littoral ecosystems in southeastern

Madagascar, Tolagnaro (Fort Dauphin). Smithsonian Institution Press, Washington, DC, pp 237-243

Donati G, Baldi N, Morelli V, Ganzhorn JU, Borgognini-Tarli SM (2009) Proximate and ultimate determinants of cathemeral activity in brown lemurs. Anim Behav 77:317-325

Donati G, Santini L, Razafindramanana J, Boitani L, Borgognini-Tarli S (2013) (Un-)expected nocturnal activity in “diurnal” *Lemur catta* supports cathemerality as one of the key adaptations of the lemurid radiation. Am J Phys Anthropol 150:99-106

Donati G, Campera M, Balestri M, Serra V, Barresi M, Schwitzer C, Curtis DJ, Santini L (2016) Ecological and anthropogenic correlates of activity patterns in *Eulemur*. Int J Primatol 37:29-46

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

Enright JT (1970) Ecological aspects of endogenous rhythmicity. Annu Rev Ecol Syst 1:221-238

Eppley TM, Ravelomanantsoa R (2015) Predation of an adult southern bamboo lemur *Hapalemur meridionalis* by a Dumeril’s boa *Acrantophis dumerili*. Lemur News 19:2-3

Eppley TM, Verjans E and Donati G (2011) Coping with low-quality diets: a first account of the feeding ecology of the southern gentle lemur, *Hapalemur meridionalis*, in the Mandena littoral forest, southeast Madagascar. Primates 52:7-13

Eppley TM, Ganzhorn JU, Donati G (2015a) Cathemerality in a small, folivorous primate: proximate control of diel activity in *Hapalemur meridionalis*. Behav Ecol Sociobiol 69:991-1002

Eppley TM, Donati G, Ramanamanjato J-B, Randriatafika F, Andriamandimbiarisoa LN, Rabehevitra D, Ravelomanantsoa R, Ganzhorn JU (2015b) The use of an invasive species habitat by a small folivorous primate: implications for conservation. PLoS ONE 10:e0140981

Eppley TM, Hall K, Donati G, Ganzhorn JU (2015c) An unusual case of affiliative association of a female *Lemur catta* in a *Hapalemur meridionalis* social group. Behaviour 152:1041-1061

Eppley TM, Donati G, Ganzhorn JU (2016a) Determinants of terrestrial feeding in an arboreal primate: the case of the southern bamboo lemur (*Hapalemur meridionalis*). Am J Phys Anthropol DOI:10.1002/ajpa.23034

Eppley TM, Donati G, Ganzhorn JU (2016b) Unusual sleeping site selection by southern bamboo lemurs. Primates 57:167-173

Eppley TM, Ganzhorn JU, Donati G (2016c) Latrine behaviour as a multimodal communicatory signal station in wild lemurs: the case of *Hapalemur meridionalis*. Anim Behav 111:57-67

Erkert HG (1989) Lighting requirements of nocturnal primates in captivity: a chronobiological approach. Zoo Biol 8:179-191

Erkert HG (2011) Chronobiological aspects of primate research. In: Setchell JM, Curtis DJ (eds) Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge, pp 319-338

Erkert HG, Cramer B (2006) Chronobiological background to cathemerality: circadian rhythms in *Eulemur fulvus albifrons* (Prosimii) and *Aotus azarai boliviensis* (Anthropoidea). Folia Primatol 77:87-103

Fausser JL, Prosper P, Donati G, Ramanamanjato J-B, Rumpler Y (2002) Phylogenetic relationships between *Hapalemur* species and subspecies based on mitochondrial DNA sequences. BMC Evol Biol 2:4

Fernández-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

Fernández-Duque E, Erkert HG (2006) Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinian Chaco. Folia Primatol 77:123-138

Fernández-Duque E, de la Iglesia H, Erkert HG (2010) Moonstruck primates: owl monkeys (*Aotus*) need moonlight for nocturnal activity in their natural environment. PLoS ONE 5:e12572

Fidgett AL, Feistner ATC, Galbraith H (1996) Dietary intake, food composition and nutrient intake in captive Alaotran gentle lemurs *Hapalemur griseus alaotrensis*. Dodo 32:44-62

Field A (2013) Discovering statistics using SPSS, 4th edn. Sage, London

Flowerdew JR (2000) Wood mice – small granivores/insectivores with seasonally variable patterns. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer, Berlin, pp 177-189

Ganzhorn JU (1989) Niche separation of seven lemur species in the eastern rainforest of Madagascar. Oecologia 79:279-286

Gilmore DP, Da Costa CP, Duarte DPF (2001) Sloth biology: an update on their physiological ecology, behavior and role as vectors of arthropods and arboviruses. Braz J Med Biol Res 34:9-25

Grassi C (2002) Sex differences in feeding, height, and space use in *Hapalemur griseus*. Int J Primatol 23:677-693

Grassi C (2006) Variability in habitat, diet, and social structure of *Hapalemur griseus* in Ranomafana National Park, Madagascar. Am J Phys Anthropol 131:50-63

Greenwood MFD, Metcalfe NB (1998) Minnows become nocturnal at low temperatures. J. Fish Biol 53:25-32

Gunn J, Hawkins D, Barnes RF, Mofulu F, Grant RA, Norton GW (2014) The influence of lunar cycles on crop-raiding elephants; evidence for risk avoidance. Afr J Ecol 52:129-137

Gursky S (2003) Lunar philia in a nocturnal prosimian primate. Int J Primatol 24:351-367

Halle S (1995) Diel pattern of locomotor activity in populations of root voles, *Microtus oeconomus*. J Biol Rhythm 10:211-224

Halle S (2000) Voles – small graminivores with polyphasic patterns. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer, Berlin, pp 191-215

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

Halle S, Stenseth NC (2000) Activity patterns in small mammals: an ecological approach. Springer, Berlin

Holley AJF (2001) The daily activity period of the brown hare (*Lepus europaeus*). Mammal Biol 66:357-364

Horning M, Trillmich F (1999) Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galapagos fur seals. Proc R Soc B 266:1127-1132

Janson CH (1998) Testing the predation hypothesis for vertebrate sociality: prospects and pitfalls. Behaviour 135:389-410

Jacob J, Brown JS (2000) Microhabitat use, giving-up densities and temporal activity as short and long-term anti-predator behaviors in common voles. Oikos 91:131-138

Jones M, Mandelik Y, Dayan T (2001) Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. Ecology 82:2164-2176

Kaczensky P, Huber D, Knauer F, Roth H, Wagner A, Kusak J (2006) Activity patterns of brown bears (*Ursus arctos*) in Slovenia and Croatia. J Zool 269:474-485

Kappeler PM, Erkert HG (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

Karpanty SM (2006) Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. Int J Primatol 27:239-261

Karpanty SM, Wright PC (2007) Predation on lemurs in the rainforest of Madagascar by multiple predator species: observations and experiments. In: Gursky S, Nekaris KAI (eds) Primate anti-predator strategies. Springer, New York, pp 77-99

Kirk EC (2006) Eye morphology in cathemeral lemurids and other mammals. Folia Primatol 77:27-49

Kronfeld-Schor N, Dayan T (1999) The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. Oecologia 121:123-128

Kurland JA, Gaulin SJC (1987) Comparability among measures of primate diets. Primates 28:71-77

Lambert JE (2002) Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). Int J Primatol 23:1169-1185

Lang AB, Kalko EKV, Romer H, Bockholdt C, Dechmann DKN (2006) Activity levels of bats and katydids in relation to the lunar cycle. Oecologia 146:659-666

Lode T (1995) Activity pattern of polecats *Mustela putorius* L. in relation to food habits and prey activity. Ethology 100:295-308

Marcelli M, Fusillo R, Boitani L (2003) Sexual segregation in the activity patterns of European polecats (*Mustela putorius*). J Zool 261:249-255

Martin RD (1972) Adaptive radiation and behaviour of the Malagasy lemurs. Philos T Roy Soc B 264:320-352

Martin RD (1990) Primate origins and evolution: a phylogenetic reconstruction. Chapman & Hall, London

McComb K, Shannon G, Sayialel KN, Moss C (2014) Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. Proc Natl Acad Sci USA 111:5433-5438

Merritt JF, Vessey SH (2000) Shrews – small insectivores with polyphasic patterns. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer-Verlag, Berlin, pp 235-251

Metcalfe N, Fraser N, Burns M (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. J Anim Ecol 68:371-381

Miller LE (2002) An introduction to predator sensitive foraging. In: Miller LE (ed) Eat or be eaten: predator sensitive foraging among primates. Cambridge University Press, Cambridge, pp 1-17

Milton K (1981) Food choice and digestive strategies of two sympatric primate species. Am Nat 117:476-495

Milton K (1998) Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. Int J Primatol 19:513-548

Mrosovsky N (1999) Masking: history, definitions, and measurement. Chronobiol Int 16:415-429

Mutschler T (1999) Folivory in a small-bodied lemur: the nutrition of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). In: Rakotosamimanana B, Rasamimanana H, Ganzhorn JU, Goodman SM (eds) New directions in lemur studies. Plenum Press, New York, pp 221-239

Nash LT (2007) Moonlight and behavior in nocturnal and cathemeral primates, especially *Lepilemur leucopus*: illuminating possible anti-predator efforts. In: Gursky S, Nekaris KAI (eds) Primate anti-predator strategies. Springer, New York, pp 173-205

Orpwood JE, Griffiths SW, Armstrong JD (2006) Effects of food availability on temporal activity patterns and growth of Atlantic salmon. J Anim Ecol 75:677-685

Orrock JL, Danielson BJ, Brinkerhoff R (2004) Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behav Ecol 15:433-437

Ortmann S, Bradley BJ, Stolter C, Ganzhorn JU (2006) Estimating the quality and composition of wild animal diets—a critical survey of methods. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding ecology in apes and other primates. Cambridge University Press, Cambridge, pp 395-418

Overdorff DJ (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 DJ, Rasmussen MA (1995) Determinants of nighttime activity in ‘diurnal’ lemurid primates. In: Alterman LG, Doyle GA, Izard MK (eds) Creatures of the dark: the nocturnal prosimians. Plenum Press, New York, pp 61-74

Overdorff DJ, Strait SG, Telo A (1997) Seasonal variation in activity and diet in a small-bodied folivorous primate, *Hapalemur griseus*, in southeastern Madagascar. Am J Primatol 43:211-223

Packer C, Swanson A, Ikanda D, Kushnir H (2011) Fear of darkness, the full moon and the nocturnal ecology of African lions. PloS ONE 6:e22285

Palomares F, Delibes M (2000) Mongooses, civets and genets—carnivores in southern latitudes. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer-Verlag, Berlin, pp 119-130

Penteriani V, Kuparinen A, Delgado MdM, Lourenço R, Campioni L (2011) Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. Anim Behav 82:413-420

Perrin MR (2013) The gastrointestinal anatomy of the lesser bamboo lemur, *Hapalemur griseus*, with comments on digestive function. S Afr J Wildl Res 43:79-83

Polat ES, Coskun B, Gurbuz E, Balevi T (2013) The effects of roughage type on the daily patterns of feed intake and eating behaviour in young sheep. Rev Med Vet-Toulouse 164:503–510

Prugh LR, Golden CD (2014) Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. J Anim Ecol 83:504-514

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

Rasmussen MA (2005) Seasonality in predation risk: varying activity periods in lemurs and other primates. In: Brockman DK, van Schaik CP (eds) Primate seasonality: implications for human evolution. Cambridge University Press, Cambridge, pp 105-128

R Development Core Team (2014) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Reebs SG (2002 Plasticity of diel and circadian activity rhythms in fishes. Rev Fish Biol Fisher 12:349-371

Rezende EL, Cortes A, Bacigalupe LD, Nespolo RF, Bozinovic F (2003) Ambient temperature limits above-ground activity of the subterranean rodent *Spalacopus cyanus*. J Arid Environ 55:63-74

Rothman JM, Chapman CA, van Soest PJ (2012) Methods in primate nutritional ecology: A user's guide. Int J Primatol 33:542-566

Rydell J, Speakman J (1995) Evolution of nocturnality in bats: potential competitors and predators during their early history. Biol J Linn Soc 54:183-191

Santini L, Rojas D, Donati G (2015) Evolving through day and night: origin and diversification of activity pattern in modern primates. Behav Ecol 26:789-796

Schlichting M, Grebler R, Menegazzi P, Helfrich-Förster C (2015) Twilight dominates over moonlight in adjusting drosophila's activity pattern. J Biol Rhythm 30:117-128

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369-404

Schwitzer N, Kaumanns W, Seitz PC, Schwitzer C (2007) Cathemeral activity patterns of the blue-eyed black lemur *Eulemur macaco flavifrons* in intact and degraded forest fragments. Endanger Species Res 3:239-247

Serena M (1994) Use of time and space by platypus (*Ornithorhynchus anatinus*: Monotremata) along a Victorian stream. J Zool 232:117-131

Singmann H (2014) afex: Analysis of factorial experiments. R package (Version 0.9-109)

Tan CL (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

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

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

Tattersall I (1987) Cathemeral activity in primates: a definition. Folia Primatol 49:200-202

Tattersall I (2008) Avoiding commitment: cathemerality among primates. Biol Rhythm Res 39:213-228

Taylor WA, Skinner JD (2003) Activity patterns, home ranges and burrow use of aardvarks (*Orycteropus afer*) in the Karoo. J Zool 261:291-297

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120-144

van Schaik CP, Griffiths M (1996) Activity periods of Indonesian rain forest mammals. Biotropica 28:105-112 van Schaik CP, Kappeler PM (1993) Life history, activity period and lemur social systems. In: Kappeler PM, JU Ganzhorn (eds) Lemur social systems and their ecological basis. Plenum Press, New York, pp 241-260

van Schaik CP, Kappeler PM (1996) The social system of gregarious lemurs: lack of convergence with anthropoids due to evolutionary disequilibrium? Ethology 102:915-941

van Schaik CP, van Noordwijk MA (1989) The special role of male *Cebus* monkeys in predation avoidance and its effect on group composition. Behav Ecol Sociobiol 24:265-276

van Soest P J (1996) Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. Zoo Biol 15:455-79

Wallis IR, Edwards MJ, Windley H, Krockenberger AK, Felton A, Quenzer M, Ganzhorn JU, Foley WJ (2012) Food for folivores: nutritional explanations linking diets to population density. Oecologia 169:281-291

Wauters LA (2000) Medium-sized granivores in woodland habitats. In: Halle S, Stensteth NC (eds) Activity patterns in small mammals: an ecological approach. Springer-Verlag, Berlin, pp 131-144

Wolfe JL, Summerlin CT (1989) The influence of lunar light on nocturnal activity of the old field mouse. Anim Behav 37:410-414

Wright PC (1989) The nocturnal primate niche in the New World. J Hum Evol 18:635-658

Wright PC (1998) Impact of predation risk on the behaviour of *Propithecus diadema edwardsi* in the rain forest of Madagascar. Behaviour 135:483-512

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. Yrbk Phys Anthropol 42:31-72

Zalewski A (2000) Factors affecting the duration of activity by pine martens (*Martes martes*) in the Białowieża National Park, Poland. J Zool 251:439-447

Zielinsky WJ (1988) The influence of daily variation in foraging cost on the activity of small carnivores. Anim Behav 36:239-249

Zielinsky WJ (2000) Weasels and martens: carnivores in northern latitudes. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer-Verlag, Berlin, pp 95-118

Zschille J, Stier N, Roth M (2010) Gender differences in activity patterns of American mink *Neovison vison* in Germany. Eur J Wildlife Res 56:187-194

Figure legends

Figure 1 Boxplot displaying the median, quartiles (1st and 3rd), and max/min daily DN activity ratios recorded for each group of *H. meridionalis* (Group 1: *N* = 37 days, Group 2: *N* = 39 days, and Group 4: *N* = 30 days).

Figure 2 Scatter-plot (with trendline and variance) of log DN activity ratio and (a) nocturnal luminosity index, (b) percentage of canopy exposure, and (c) daily proportion of fibre (NDF-ADF) in the southern bamboo lemur diet.