Temporal niche separation between the two ecologically similar nocturnal primates *Avahi meridionalis* and *Lepilemur fleuretae*.

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Abstract

Time is considered a resource in limited supply and temporal niche separation is one of the most common strategies that allows ecologically similar species to live in sympatry. Mechanisms of temporal niche separation are understudied especially in cryptic animals due to logistical problems in gathering adequate data. Using high-frequency accelerometers attached to radio-collars, we investigated whether the ecologically similar lemurs *Avahi meridionalis* and *Lepilemur fleuretae* in the lowland rainforest of Tsitongambarika, south-eastern Madagascar, show temporal niche separation. Accelerometers stored data with a frequency of 1Hz for a total of 71 days on three individuals of *A. meridionalis* and three individuals of *L. fleuretae*. We extrapolated motor activity patterns via the unsupervised learning algorithm expectation maximisation and validated the results with systematic behavioural observations. *Avahi meridionalis* showed peaks of activity at twilights with low but consistent activity during the day, while *L. fleuretae* exhibited more activity in the central hours of the night. Both lemur species had their activity pattern entrained by photoperiodic variations. The pair-living *A. meridionalis* was found to be lunarphilic while the solitary-living *L. fleuretae* was lunarphobic. We suggest that these activity differences were advantageous to minimise feeding competition, as an anti-predator strategy, and/or for dietary related benefits. These findings demonstrate a fine-tuned temporal partitioning in sympatric, ecologically similar lemur species and support the idea that an activity spread over the 24-hours, defined here as cathemerality *sensu lato*, is more common than previously thought in lemurs.

Significance statement

Ecologically similar species may exhibit temporal niche partitioning and separate their peaks of activity when co-occurring in an area. We show for the first time that the mainly nocturnal genus *Avahi* can exhibit high crepuscular activity with low but consistent bouts of activity (up to 44.6% of daily activity) during the day. We defined this activity as cathemerality *sensu lato* as opposed to the cathemerality *sensu stricto* observed in *Eulemur* sp. We suggest that this flexible activity may be advantageous for the species to minimise feeding competition and predatory pressure, and/or to provide dietary-related benefits. This finding in the secondary nocturnal genus *Avahi* supports the idea that activity patterns in lemurs are graduated and traditional categorisations are inadequate.

Keywords

Niche partitioning, cathemeral, diel, Madagascar, bio-logging, accelerometer

Introduction

The exhibition of largely similar habits leads to niche overlap between species, which may compete if the resources used are in limited supply (La Morgia and Bassano 2009). Three main niche dimensions - habitat type, temporal differentiation, and food type - have been shown to be used to reduce niche overlap (Singh et al. 2011). According to the "niche complementarity hypothesis", a high overlap in one niche dimension should be compensated by a low overlap in at least one of the other dimensions (Vieira and Port 2006). Time can be considered as a resource in limited supply (Halle 2000) and separating the time of activity has been suggested as one of the most effective strategies for species coexistence (Schoener 1974; Schreier et al. 2009; Schmidt et al. 2013; Scriven et al. 2016). Temporal niche partitioning has been repeatedly demonstrated as a strategy to reduce competition and allow coexistence between ecologically similar species in many Orders including Carnivora (Jácomo et al. 2004; Harrington et al. 2009; Romero-Muñoz et al. 2010), Chiroptera (Adams and Thibault 2006), Primates (Curtis and Rasmussen 2006; Schreier et al. 2009), Rodentia (Kronfeld-Schor and Dayan 1999; Castro-Arellano and Lacher 2009), Salmoniformes (Eloranta et al. 2013), and Squamata (Martínez-Freiría et al. 2010).

Activity patterns of animals are endogenously generated by biological clocks and empowered with mechanisms that allow adaptation to environmental challenges (Refinetti 2016). Activity patterns rely on endogenously fixed rhythms that can be circadian (i.e. over the 24-h) and circannual (i.e. over the calendar year) (Aschoff 1979). Circadian and circannual rhythms are shaped by predictable environmental factors, called Zeitgebers, such as photoperiodic variations, or by less predictable factors that may override the main rhythm, called masking factors, such as food quality and availability, weather conditions, nocturnal luminosity, predation, and anthropogenic disturbance (Daan and Aschoff 1982; Halle and Stensteth 2000; Donati et al. 2009, 2016; Poudel et al. 2015; Brivio et al. 2017).

Photoperiodic variation is an important Zeitgeber, especially for animals that, by living far from the equator, experience seasonal variations in daylength and climate (Brockman and van Schaik 2004). The endogenous clock is influenced by light that synchronises activity to the photoperiod; thus, activity is usually strongly affected by the annual variation in sunrise and sunset time (Erkert 1989; Reppert and Weaver 2002). The activity of nocturnal prey species may be further affected by the intensity of nocturnal illumination due to its correlation with predation risk (Beier 2006; Prugh and Golden 2014). At high luminosity conditions, nocturnal prey species may decrease their activity to reduce predation risk (lunarphobia; Nash 2007; Saldaña-Vásquez and Munguía-Rosas 2013; Upham and Haffner 2013) or increase their activity to maximise foraging efficiency and predators' detection (lunarphilia; Gursky 2003; Rode-Margono and Nekaris 2014; Brivio et al. 2017). The choice of one of these two strategies or more often a gradient between them is determined by the balance between associated costs (increased vulnerability to predation) and benefits (improved detection of food and predators) (Prugh and Golden 2014).

In terms of activity patterns, primates were historically classified as diurnal or nocturnal until the discovery that a lemur species of the genus *Eulemur* exhibited activity over 24 h (Tattersall 1979). This activity pattern, defined as cathemerality, can provide a number of ecological advantages such as reduced feeding competition via temporal niche partition (Curtis et al. 1999; Curtis and Rasmussen 2006), thermoregulatory benefits to avoid thermal stress (Curtis et al. 1999), reduced predation risk (Donati et al. 1999; Colquhoun 2006), and increased feeding efficiency related to a fibre-rich diet (Engqvist and Richard 1991; Donati et al. 2007, 2009). Different degrees of cathemerality have been observed in *Eulemur* (c.f. Curtis and Rasmussen 2006), *Hapalemur* (Eppley et al. 2015), *Lemur* (Donati et al. 2013) in the wild, *Prolemur* (Santini-Palka 1994) and *Varecia* (Bray et al. 2017) in captivity.

The sympatric lemur genera *Avahi* (Indriidae) and *Lepilemur* (Lepilemuridae) are ideal models to study temporal niche separation in strepsirrhines, since they are both nocturnal, mainly folivorous, and have a comparable body mass (Thalmann 2001). Both species are exceptional since folivory in nocturnal primates is rare as colour vision is thought to be important in these species to discern leaves with higher protein content (Dominy and Lucas 2004). Furthermore, these lemurs have a relatively small body mass (ranging from 560 to 1210 g; Razafindratsima et al. 2018), which is at the lower limits for folivory in primates (Lehman 2007). Previous studies demonstrated the presence of scramble competition and mechanisms of niche separation between *A. occidentalis* and *L. edwardsi* in the deciduous forest of Ampijoroa, where both genera occur at high density (Warren and Crompton 1997, Thalmann 2001). Since folivorous primates as well as frugivorous ones are known to experience scramble competition driven by resource variations in quality, availability, and spatial distribution (Snaith and Chapman 2007), this ecological pressure is likely to be present between *Avahi* and *Lepilemur* species.

The genus *Avahi* is considered strictly nocturnal, although its ancestors have been hypothesised to be diurnal and its nocturnality is considered secondary (Ganzhorn et al. 1985; Roos et al. 2004). Recent findings suggested that the strength of selection to maintain SWS1 opsin gene for colour vision in *Avahi* is similar to what has been found in diurnal primates (Veilleux et al. 2014). This adaptation is considered a retention from diurnal ancestors and *Avahi* may have experienced consistent selection to retain dichromatic colour vision throughout its evolutionary history (Veilleux et al. 2014). Thus, *Avahi* possesses some visual adaptations that may facilitate activity in dim light conditions. Also, *Avahi* was reported several times to be active occasionally during the day (Ganzhorn et al. 1985; Warren and Crompton 1997). This pattern suggests that this lemur might exhibit diurnal activity in certain conditions, although the extent of this activity has never been explored systematically.

The sportive lemurs *Lepilemur* spp. are considered strictly nocturnal (Nash 2007), although some species have been reported to show a high level of vigilance and grooming during daytime (Charles-Dominique and Hladik 1971; Warren and Crompton 1997; Seiler et al. 2013). Sportive lemurs were also reported to rest in sunny spots near sleeping sites (Warren and Crompton 1997; Nash 1998). Considering these reports, the question arises on whether in certain environmental conditions, or in conditions of high competition with *Avahi* (Warren and Crompton 1997), sportive lemurs may reveal some flexibility in their activity pattern.

Despite the efforts in observing and reporting the temporal activities performed by these species, a consistent and quantitative approach is needed to clarify the fine-grained mechanisms of coexistence between the two genera. Recent advances in bio-logging miniaturised technology, and the use of high-frequency accelerometers in particular, are ideal for answering research questions related to animal's movement patterns and locomotor activities in cryptic species for which behavioural observations are problematic (Brown et al. 2013, Chimienti et al. 2016). Accelerometers have been used for many years to study primate activity patterns (e.g. Kappeler and Erkert 2003, Fernández-Duque and Erkert 2006, Eppley et al. 2015), although these studies mainly used activity score devices (i.e. the output is a score and it does not allow complex analysis) with low sampling frequency (usually more than one minute). High-frequency accelerometers can be used today to extrapolate detailed activity patterns and classify how animals behave, cost/benefits of movement patterns, and how they relate to the surrounding environment (Kays et al. 2015; Leos-Barajas et al. 2017; Patterson et al. 2017).

We aim to investigate, using high-frequency accelerometers, whether the southern woolly lemur *A. meridionalis* and the Fleurette’s sportive lemur *L. fleuretae* show temporal niche partitioning in the lowland rainforest of Tsitongambarika (TGK), south-eastern

Madagascar. The TGK forest has a high density of both *A. meridionalis* and *L. fleuretae* (Balestri 2018) and this may entail a certain degree of contest competition, thus favouring activity avoidance as a mechanism for niche separation (Schreier et al. 2009). In addition, we test whether nocturnal luminosity and photoperiodic variations have a role in controlling activity patterns of these two lemur species. The lowland rainforest of TGK represents an ideal location to test the influence of these Zeitgebers and masking factors on nocturnal primates. First, TGK is the southernmost rainforest in Madagascar and thus it is exposed to significant photoperiodic variation (from 10.6 to 13.7 h). Second, this lowland rainforest is characterised by a strong seasonality in terms of young leaf availability (Campera 2018). In particular, we predict:

1) That *A. meridionalis* and *L. fleuretae* have peaks of activity at different times of the night to reduce contest competition. Based on the abovementioned visual adaptations of *Avahi* (Veilleux et al. 2014), we expect *A. meridionalis* to be more active during the brighter segments of the night, i.e. twilights or full moon nights. We also expect woolly lemurs to expand their activity during the daylight hours, since diurnal bouts may represent an ecological advantage to reduce feeding competition with *L. fleuretae* (Curtis et al. 1999; Curtis and Rasmussen 2006);
2) Night-length to be a predictor of the activity of both *A. meridionalis* and *L. fleuretae*. Animals are in fact expected to synchronise the activity with sunset and sunrise variations (two-oscillator model of circadian rhythmicity; Pittendrigh and Daan 1976) to reduce daily energy expenditure (Baldellou and Adam 1998) and to avoid overheating (Erkert 2000). We thus expect both species to increase the intensity of their nocturnal activity in short nights since they have less time to meet their energy requirements (Corsini et al. 1995; Brivio et al. 2017);

3) *Lepilemur fleuretae* to be lunarphobic since it has a solitary social system and it is expected to use a cryptic strategy to minimise the risk of being detected by predators at night. Conversely, *A. meridionalis* is expected to be lunarphilic to increase foraging efficiency and predator detection considering the advantages provided by the abovementioned visual adaptations and the pair-living social system (Prugh and Golden 2014).

Materials and methods

Study site

The study was conducted at the Ampasy research station (S 24° 34' 58'', E 47° 09' 01''), a valley of around 3 km^2 located in the northernmost portion of the TGK Protected Area. The TGK forest represents one of the last large expanses of lowland rainforest in Madagascar. See Campera et al. (2017) for a detailed description of the study area.

Data collection

We recorded activity data every second for a total of 71 days (7 July 2015-17 September 2015) on three individuals of *A. meridionalis* and three individuals of *L. fleuretae* (two females and one male from different social groups) via high-frequency accelerometer tags (Axy-Depth, TechnoSmArt) attached to VHF collars (RI-2D, Holohil Systems Ltd). To attach the collars, the lemurs were anaesthetised via a dose of 15 ml of Telazol 100mg/ml (tiletamine HCl and zolazepam HCl; Zoetis Inc.) using a CO^2 air rifle capable of remote injection for immobilisation (Balestri 2018; Campera 2018). There were no injuries as a consequence of the captures. The weight of the combined VHF collar and accelerometer tag with batteries was around 15 g, thus below the 5% threshold of the subjects' weight recommended for arboreal animals (Wheater et al. 2011). For the validation of the accelerometer data, we recorded activity data (active or inactive) via continuous focal sampling (Altmann 1974) on six collared individuals for two full nights each. Active behaviours included feeding, foraging, moving, grooming, and social behaviour. Animals were recaptured at the end of the study to remove the collars. It was not possible to record blind data because our study involved focal animals in the field.

Data analysis

From the raw data collected with the accelerometers, we calculated dynamic acceleration and amplitude, intended as standard deviation of the dynamic acceleration, by using the package "plotrix" for R software over a smoothing factor of 10 seconds (Chimienti et al. 2016). A time window of 10 s was chosen considering that we were generally interested in overall activity patterns. The integrated variables were analysed via the package "Rmixmod" for R software using the unsupervised learning algorithm (i.e. algorithm that group accelerometer data without the need of training datasets into different clusters based on statistical functions) Expectation Maximisation (EM) (Biernacki et al. 2003). To test the efficiency of this method in detecting activity and inactivity, we compared the data obtained via the EM algorithm with simultaneous behavioural observations. The algorithm had a correspondence of 98.6-99.4 % (N = 3 individuals) and 98.2-99.3 % (N = 3 individuals) with the inactive behaviour detected via behavioural observations for *A. meridionalis* and *L. fleuretae*, respectively.

We calculated the daily proportion of activity during the day, twilight, and night. As twilight, we considered the time between the beginning of the morning astronomical twilight (when the sun is 18° below the horizon before sunrise) and the sunrise, and between the sunset and the end of evening astronomical twilight (when the sun is 18° below the horizon after sunset)(Donati et al. 2009). We obtained sunset, sunrise, moon phase, night-length, and beginning and end of astronomical twilights from the U.S. Naval Observatory Astronomical Almanac (http://aa.usno.navy.mil/data) using the coordinates of Ampasy.

To evaluate the influence of night-length and moon phase on the activity of *A. meridionalis* and *L. fleuretae*, we ran multiple Generalised Estimating Equation (GEE) models (Bailey et al. 2013) with proportion of activity (during the day, at twilight, and at night) or the ND ratio (ratio between nocturnal and diurnal activity) as dependent variables. We used the ratio to allow comparisons across species and studies since the absolute values of activity recorded by accelerometers differ from what is recorded via observational sampling or from other models of accelerometers (Donati et al. 2009; Eppley et al. 2015). For the ND ratio we included twilight periods within the overall nocturnal activity for comparative reasons, since twilights are included in the main active phase in most other studies of cathemerality (Fernández-Duque and Erkert 2006; Donati et al. 2013; Eppley et al. 2015). We used night-length and moon phase as covariates in the model, and individuals as random factor. We considered days as units of analysis and included an AR1 autocorrelation structure in the model to control for temporal autocorrelation in the data (Bailey et al. 2013). We tested several combinations of fit distributions (normal, gamma, inverse gaussian) and functions (identity, log, power) and chose the model with the lowest Akaike Information Criterion (AIC) (Burnham and Anderson 2002). The models with a gamma probability distribution and log link function had the lowest AIC.

To determine whether *A. meridionalis* and *L. fleuretae* were active at different times of the night, we divided the daily activity into 2-h blocks starting from midnight. We then ran a Repeated Measures (RM) ANOVAs with the activity every 2-h interval as dependent variable. To determine the difference on activity between *A. meridionalis* and *L. fleuretae*, we also ran RM ANOVAs with activity during the day, twilight, and night, or the ND ratio as dependent variable. To determine whether the two species commenced and ended their activity in phase with sunset and sunrise time, respectively, we ran a RM ANOVA with the difference between activity time and sunset/sunrise. For the RM ANOVAs, we compared data between *A. meridionalis* and *L. fleuretae* during the same day. Before running the RM ANOVAs, we tested for normality (Kolmogorov–Smirnov test), sphericity (Mauchly's test), and equality of variances (Levene's test) as underlying assumptions. We performed the tests via SPSS v25 considering $P < 0.05$ as level of significance.

Results

Influence of night-length and moon phase

The three individuals of *A. meridionalis* had their peaks of activity at twilight (Fig. 1). The median ND ratio was 3.89 (range = 1.12-13.09). The activity of *A. meridionalis* during the day, at twilight, and at night increased when night-length decreased, while the ND ratio was not influenced overall by night-length (Table 1). The activity of *A. meridionalis* during the day increased and the ND ratio decreased with the decrease of moon luminosity, while there was no effect of moon luminosity on the activity at twilight and at night. The three individuals of *L. fleuretae* had their peaks of activity at night (Fig. 1). The median ND ratio was 7.12 (range = 1.57-584.61). The activity of *L. fleuretae* during the day, at twilight, and at night increased when night-length decreased, while the ND ratio was not influenced overall by night-length (Table 1). The activity of *L. fleuretae* during the day, the activity at twilight, and the ND ratio decreased, and the nocturnal activity increased with the decrease of moon luminosity.

Daily activity pattern

The 24-h activity pattern of *A. meridionalis* showed two main peaks at 4-6 h and at 18-20 h, while peaks of activity for *L. fleuretae* were at 2-4 h and at 18-20 h (Fig. 2 and Fig.3). The two species showed a significantly different activity pattern for all the time blocks ($P < 0.001$) apart from the time block 14-16 h ($P = 0.447$).

Avahi meridionalis commenced their activity earlier than *L. fleureate* after sunset ($F_{1,70} = 230.69$, $P < 0.001$), and ended the activity after *L. fleuretae* before sunrise ($F_{1,70} = 356.87$, $P < 0.001$). On average, *A. meridionalis* commenced activity 11.2 (SE 0.9) min after sunset and ended the activity 10.4 (SE 1.8) min before sunrise, while *L. fleuretae* commenced activity 42.3 (SE 1.5) min after sunset and ended the activity 108.2 (SE 2.5) min before sunrise (Fig. 4).

Discussion

Temporal niche separation

The ecologically similar lemurs *A. meridionalis* and *L. fleuretae* in the lowland rainforest of TGK showed different activity patterns that are likely to favour the coexistence of the two species. The former species showed peaks of activity at twilights with low but consistent activity during the day, while the latter species showed most activity in the central hours of the night. Despite its mainly nocturnal and crepuscular activity, *Avahi meridionalis* revealed a pattern that we define here as cathemerality *sensu lato*, varying from strict nocturnality (ND ratio: 13.09) to sporadic but even distribution of activity between night and day (ND ratio: 1.12). We consider these woolly lemurs cathemeral on the basis of the following lines of reasoning. First, on a comparative level the mainly nocturnal *A. meridionalis* had an overall ND ratio of 3.89 that is similar to the DN activity ratio observed in some cathemeral species with mainly diurnal activity: 3.98 for southern bamboo lemur *Hapalemur meridionalis* (Eppley et al. 2015); 4.80 for ring-tailed lemur *Lemur catta* (Donati et al. 2013). Second, the average motor activity in the resting phase of these woolly lemurs exceeds the 10% threshold that is explained by occasional sleeping movements, changes of sleeping position, disturbances by conspecifics, ectoparasites, or predatory attacks (Erkert and Kappeler 2004). Third, taking the definition of cathemerality, that is "The activity of an organism can be regarded as cathemeral when it is distributed approximately evenly throughout the 24 h of the daily cycle, or when significant amounts of activity, particularly feeding and/or travelling, occur within both the light and dark portions of that cycle (Tattersall 1987)" the pattern observed in *Avahi meridionalis* matches routinely at least the second part of the definition. In fact, while the distribution of the activity is in average not even between day and night, the outputs of our accelerometers, as well as opportunistic observations during the day, indicate that these lemurs engage in locomotor and feeding activity regularly during the daylight hours. The mainly diurnal lemurids *H. meridionalis* (Eppley et al. 2015) and *L. catta* (Donati et al. 2013) also show a *sensu lato* cathemerality, with large variations in diurnal/nocturnal ratio. The activity pattern of the Azara's night monkey, *Aotus azarai,* in the Argentinian Chaco, the only monkey that exhibits cathemeral activity (Fernández-Duque and Erkert 2006), appears analogous to what we have observed in southern woolly lemurs. It is clear that while these species concentrate their activity in one phase (nocturnal for *Avahi meridionalis* and *Aotus azarai*, diurnal for *L. catta* and *H. meridionalis*) they still have some significant bouts of activity in the other phase that is often dependent on specific abiotic or biotic conditions (Fernández-Duque 2003; Eppley et al. 2015). Species that show a cathemerality *sensu sticto* either exhibit a more evenly distributed activity over the 24-hours, at least seasonally, or they can be either mainly diurnal or mainly nocturnal depending on environmental conditions and seasons, e.g. the genus *Eulemur* (Curtis and Rasmussen 2006; Donati et al. 2009, 2016).

Temporal niche separation is one of the ecological benefits previously hypothesised to make cathemerality advantageous in lemurs to reduce feeding competition between species (Curtis et al. 1999; Curtis and Rasmussen 2006; Donati et al. 2013). Other nocturnal animals were shown to shift towards a more crepuscular activity with some diurnal activity when in competition with ecologically similar species (Halle 2000; Ziv and Smallwood 2000) or even conspecifics (Pizzatto et al. 2008). Ecologically similar nocturnal species may also be active during different parts of the night (e.g. gerbils; Kotler et al. 1993). Although we have no data to test the causation mechanism of this hypothesis, competition with *L. fleuretae* is a potential driver of the cathemeral activity observed in *A. meridionalis* at Ampasy. In fact, so far no evidence of cathemerality was reported in woolly lemurs studied in areas where sportive lemurs are rare or absent (Harcourt 1991; Norscia and Borgognini-Tarli 2008). The only previous evidence of diurnal activity in woolly lemurs (mainly vigilance) was reported at sites where sportive lemurs are present (Warren and Crompton 1997; Thalmann 2001). Until systematic data over the 24-hours will be available on the two species at other localities, possible competition between these two folivorous lemurs remains speculative.

As alternative but not mutually exclusive hypothesis to competition, since woolly lemurs are pair living primates that do not use tree holes during the resting time and that are at high risk of predation for their small size, their cathemerality could also be the result of an anti-predator strategy (Warren and Crompton 1997; Seiler et al. 2013). According to this idea, vigilance would make up a large percentage of diurnal activity budgets to help the animals escaping day active predators. This hypothesis has been used to explain diurnal activity in other nocturnal primates, such as *L. sahamalazensis*, where individuals have been seen to rest vigilant at the entrance of their tree holes to spot for raptors attacks (Seiler et al. 2013).

Considering its diet rich in fibres, another possible driver of the flexible activity pattern observed in *Avahi meridionalis* might be the necessity to maximise food intake over the 24-h (Engqvist and Richard 1991; Donati et al. 2007, 2009). Despite the adaptation to folivory in *Avahi* (i.e. midgut fermentation via sacculated caecum and looped colon; Martin 1990), midgut fermentation may reduce the amount of food that can be processed as well as nutrient intake (Campbell et al. 2004). Extra-bouts of feeding activity during the day may thus be used to maximise nutrient intake over the 24-hours. As a matter of fact, we opportunistically observed individuals of *A. meridionalis* feeding during the central hours of the day. This idea also needs to be tested with more fine-grained, year-round data on the nutritional ecology of these woolly lemurs. For example, the generalist folivore *H. meridionalis* was found to reduce its cathemeral activity during periods of increased fibre intake and this was related to the prolonged periods of inactivity that fibre digestion may require (Eppley et al. 2017). Since *A. meridionalis* is also a generalist folivore (Norscia et al. 2012), *Avahi* may show a pattern similar to *Hapalemur*.

Influence of photoperiodic variations and moon phase

The activity of *A. meridionalis* and *L. fleuretae* was highly influenced by photoperiodic variations. This finding confirms that the activity pattern of these nocturnal lemurs is synchronised with variations of sunset and sunrise (Brockman and Van Schaik 2004). Malagasy environments are highly seasonal and the influence of photoperiodic variation on activity patterns of lemurs was reported on a variety of species, e.g. *Eulemur collaris* (Donati et al. 2009); *E. collaris X E. rufus* (Donati et al. 2009); *E. rufus* (Kappeler and Erkert 2003); *E. mongoz* (Curtis et al. 1999). On the contrary, other researchers found no correlation between activity profiles in cathemeral lemur species and photoperiodic variation, e.g. *E. macaco* (Colquhoun 1998); *Lemur catta* (Donati et al. 2013); *Hapalemur meridionalis* (Eppley et al. 2015). Beyond lemurs, seasonal changes in ambient temperature, precipitation, and food abundance have a stronger effect than photoperiodic variations for owl monkeys in the Argentinean Chaco (*Aotus azarai*; Erkert et al. 2012), and in other mammals, e.g. crested porcupines *Hystrix cristata* (Corsini et al. 1995), wild boar *Sus scrofa* (Brivio et al. 2017), and wood mouse *Apodemus sylvatiscus* (Flowerdew 2000). On a theoretical basis, this variation may be the consequence of the different predictability of resources at various sites (Halle and Stensteth 2000; Rode-Margono and Nekaris 2013). In fact, TGK as well as nearby littoral forest sites show a seasonal peak of phenological resources influenced by photoperiodic variations (Bollen and Donati 2005; Campera 2018; Donati unpub. data), while sites where the activity is not synchronised by day length tend to show unpredictable phenological patterns between years (Halle and Stensteth 2000). This link is worth exploring when more long-term data are available on phenological cycles at Ampasy as well as in other Malagasy habitats (Bollen and Donati 2005; Wright et al. 2005).

One of the possible explanations for the increase in activity with the decrease of night-lengths is that animals had a shorter time to meet their energetic requirements (Corsini et al. 1995; Brivio et al. 2017). The increase of activity in *Avahi meridionalis* and *Lepilemur fleuretae* at TGK with the decrease of night-length may also be the consequence of the diet change during periods of food abundance. In particular, *L. fleuretae* was found to feed on flowers of *Albizia* sp. that are mainly available in September (Campera 2018). Feeding on flowers may require longer distances travelled and higher activity levels than feeding on leaves, and this might partially explain the strong effect of photoperiodic variation on the activity patterns in *L. fleuretae*.

Temperature may also play a role in shaping the activity profiles of *Avahi meridionalis* and *L. fleuretae* with lower activity during colder months as an energy-saving strategy. This strategy has been found previously in other lemur species (Kappeler and Erkert 2003; Donati et al. 2009) as well as in other tropical animals (McKechnie and Mzilikazi 2009; Ruf and Geiser 2015). Variation in temperature may also explain why *L. fleuretae* increases the diurnal activity with the decrease of night-length as animals may have needed to thermoregulate more by sunbathing as previously reported in other sportive lemurs (Warren and Crompton 1997; Nash 1998). Phenological patterns, as well as other environmental variables, are dependent on photoperiodic variations (van Schaik et al. 1993) and it is difficult to isolate single factors. Finally, the reproductive state may have played an important role in shaping activity patterns (Vieira et al. 2017) since two out of three animals were females and gave birth around the end of August. This phenomenon may offer another explanation as to why we found an increase in mean activity starting at the end of August since mothers might have spent more time allogrooming and nursing their infants, with a consequent increase in activity while resting, especially during the day.

As predicted, the ND ratio of *A. meridionalis* increased while the nocturnal activity of *L. fleuretae* decreased with the increase in moon luminosity. In contrast to nocturnal mammals that are usually lunarphobic to reduce predation risk (Nash 2007; Prugh and Golden 2014), *A. meridionalis* was lunarphilic similar to other cathemeral primates (Erkert 1989; Kappeler and Erkert 2003; Fernández-Duque et al. 2010; Donati et al. 2009, 2013; Eppley et al. 2015). It has been hypothesised that lunarphilia can be a strategy to reduce predatory risk by increasing vigilance (Gursky 2003; Prugh and Golden 2014). By living in pairs *A. meridionalis* may take advantage of more than two eyes to increase vigilance at high luminosity conditions. In contrast, the alternative strategy, i.e. reducing predation risk by camouflage and reducing activity at high luminosity conditions, may be a better solution for solitary animals such as *L. fleuretae* (Starr et al. 2012). The presence at TGK of a full set of predators, including the main predator of this lemur species, the cathemeral fossa *Cryptoprocta ferox*, may contribute to the observed lunarphobia of *L. fleuretae* at night. The fossa, in fact, is expected to be lunarphilic as other large predators since they increase prey detection at high luminosity conditions (Prugh and Golden 2014).

Another advantage of being lunarphilic is the higher foraging efficiency at high luminosity conditions (Gursky 2003; Donati et al. 2007; Rode-Margono and Nekaris 2014; Eppley et al. 2015). Such efficiency may be one of the main drivers for the influence of the moon phase on the ND ratio of *A. meridionalis* since this species was not influenced by moon phase at twilight and at night. On a speculative ground, *A. meridionalis* may spend more time being active during bright nights and the day (i.e. extend the feeding time over the 24 h) as a consequence of the limited visibility to discern young high-quality leaves during the new moon phase. Thus, lunarphilia may represent an advantage for *Avahi* since its visual pigments appear optimally adjusted to detect young green leaves (Veilleux et al. 2014). In fact, leaf quality has been shown to be correlated to variation in the green-red and blue-yellow chromatic differences (Dominy and Lucas 2004).

Conclusions

We found a clear temporal niche separation between the ecologically similar lemurs *A. meridionalis* and *L. fleuretae*, with the former more active at twilight and showing a low but consistent activity during the day and the latter more active in the central hours of the night. Year-round data, however, are now necessary to understand whether this temporal niche separation is consistent throughout the year or just a seasonal strategy. It is important to stress that causal links are difficult to demonstrate since it is unknown how the activity pattern of one species would change in the absence of the other. The observed activity patterns of the two species are in fact further explained by an opposite response to environmental factors, such as moonlight.

The exhibition of a cathemerality *sensu lato* in *A. meridionalis* has implications on the current hypotheses on the evolution of activity patterns in lemurs (Donati and Borgognini-Tarli 2006; Donati et al. 2013; Markolf and Kappeler 2013; Santini et al. 2015). The finding that *A. meridionalis* is cathemeral supports a diurnal ancestor for the Indriidae, thus strengthening the hypothesis of a secondary nocturnality for *Avahi* (Ganzhorn et al. 1985; Roos et al. 2004). In this scenario, *Avahi* has evolved nocturnality but retained some ability to be active during the day in a similar way to what has been hypothesised in *Aotus azarai* (Fernandez-Duque 2003). The findings of this research contribute to the idea that activity patterns in lemurs are graduated and the more we know about their activity patterns the more we realise that traditional categorisations are clearly inadequate.

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Author contributions

MCa, MB, GD conceived and designed research. MCa, MB conducted the research. MCa, MCh, GD analysed and interpreted the data. MCa, GD led the writing of the manuscript. MB, MCh, VN, KAIN revised the manuscript critically for important intellectual content. All authors gave final approval for publication.

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Data accessibility

The datasets analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

We obtained permission for the field research from the Ministry of Environment and Forest of Madagascar (XX/16/MEEMF/SG/DGF/DAPT/SCBT.Re). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of Oxford Brookes University following the "Guidelines on the observation, handling and care of animals in field research"

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Table 1: Median activity (range) during the day, at twilight, and at night, and median ND ratio (i.e. ratio between nocturnal and diurnal activity) for *Avahi meridionalis* and *Lepilemur fleuretae*. Beta estimates (Standard Error) are parameter estimates of the Generalised Estimating Equation models with night-length and moon phase as covariates. F-value indicate the result of the RM ANOVA test for the difference between the two species.

	Avahi meridionalis			***Lepilemur fleuretae***			
	Activity (range) %	**Night-length Beta (SE)**	**Moon phase Beta (SE)**	**Activity (range) %**	**Night-length Beta (SE)**	**Moon phase Beta (SE)**	**F-value**
Diurnal	14.0 (3.7-32.7)	-0.30 (0.14)*	-0.19 (0.02)**	9.1 (0.1-31.3)	-0.39 (0.07)**	0.11 (0.05)*	5.35*
Twilight	66.0 (21.4-83.2)	-0.20 (0.04)**	-0.02 (0.03)	39.3 (9.1-75.8)	-0.48 (0.05)**	0.10 (0.02)**	1024.93**
Nocturnal	50.9 (26.7-71.6)	-0.24 (0.09)**	0.05 (0.04)	70.6 (47.3-96.1)	-0.24 (0.04)**	-0.11 (0.02)**	492.00**
ND	3.9 (1.1-13.1)	-0.00 (0.03)	0.23 (0.05)**	7.1 (1.6-584.6)	0.25 (0.18)	-0.47 (0.06)**	471.00**

* $P < 0.05$; ** $P < 0.01$

Figure 1: Variation of activity of *Avahi meridionalis* (above) and *Lepilemur fleuretae* (below) during the day, at twilight, and at night. Means and standard errors for successive moon phases from 07/07/2015 to 17/09/2015 are shown. Black circles indicate new moon phases.

Figure 2: Daily activity of *Avahi meridionalis* (black line) and *Lepilemur fleuretae* (grey line). Hourly distribution of activity (mean and standard error) of three individuals of *A. meridionalis* and *L. fleuretae* over the 24-h from 07/07/2015 to 17/09/2015. Sunset: 17:17-17:46; evening astronomical twilight: 18:37-19:02; morning astronomical twilight: 4:32-5:16; sunrise: 5:47-6:36.

Figure 3: Daily activity patterns of two neighbouring individuals, one *Lepilemur fleuretae* and one *Avahi meridionalis*, for a lunar cycle.

Figure 4: Difference between the end of activity and sunrise (above) and between the beginning of activity and sunset (below). Data are daily means and standard errors in three individuals of *Avahi meridionalis* (black line) and three individuals of *Lepilemur fleuretae* (grey line).