

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

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14

15 **Abstract**

16 Time is considered a resource in limited supply and temporal niche separation is one of the  
17 most common strategies that allows ecologically similar species to live in sympatry.

18 Mechanisms of temporal niche separation are understudied especially in cryptic animals due  
19 to logistical problems in gathering adequate data. Using high-frequency accelerometers

20 attached to radio-collars, we investigated whether the ecologically similar lemurs *Avahi*  
21 *meridionalis* and *Lepilemur fleuretae* in the lowland rainforest of Tsitongambarika, south-

22 eastern Madagascar, show temporal niche separation. Accelerometers stored data with a  
23 frequency of 1Hz for a total of 71 days on three individuals of *A. meridionalis* and three

24 individuals of *L. fleuretae*. We extrapolated motor activity patterns via the unsupervised  
25 learning algorithm expectation maximisation and validated the results with systematic

26 behavioural observations. *Avahi meridionalis* showed peaks of activity at twilights with low  
27 but consistent activity during the day, while *L. fleuretae* exhibited more activity in the central  
28 hours of the night. Both lemur species had their activity pattern entrained by photoperiodic  
29 variations. The pair-living *A. meridionalis* was found to be lunarphilic while the solitary-  
30 living *L. fleuretae* was lunarphobic. We suggest that these activity differences were  
31 advantageous to minimise feeding competition, as an anti-predator strategy, and/or for dietary  
32 related benefits. These findings demonstrate a fine-tuned temporal partitioning in sympatric,  
33 ecologically similar lemur species and support the idea that an activity spread over the 24-  
34 hours, defined here as cathemerality *sensu lato*, is more common than previously thought in  
35 lemurs.

36

### 37 **Significance statement**

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

47

### 48 **Keywords**

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

50

## 51 **Introduction**

52 The exhibition of largely similar habits leads to niche overlap between species, which may  
53 compete if the resources used are in limited supply (La Morgia and Bassano 2009). Three  
54 main niche dimensions - habitat type, temporal differentiation, and food type - have been  
55 shown to be used to reduce niche overlap (Singh et al. 2011). According to the “niche  
56 complementarity hypothesis”, a high overlap in one niche dimension should be compensated  
57 by a low overlap in at least one of the other dimensions (Vieira and Port 2006). Time can be  
58 considered as a resource in limited supply (Halle 2000) and separating the time of activity has  
59 been suggested as one of the most effective strategies for species coexistence (Schoener  
60 1974; Schreier et al. 2009; Schmidt et al. 2013; Scriven et al. 2016). Temporal niche  
61 partitioning has been repeatedly demonstrated as a strategy to reduce competition and allow  
62 coexistence between ecologically similar species in many Orders including Carnivora  
63 (Jácomo et al. 2004; Harrington et al. 2009; Romero-Muñoz et al. 2010), Chiroptera (Adams  
64 and Thibault 2006), Primates (Curtis and Rasmussen 2006; Schreier et al. 2009), Rodentia  
65 (Kronfeld-Schor and Dayan 1999; Castro-Arellano and Lacher 2009), Salmoniformes  
66 (Eloranta et al. 2013), and Squamata (Martínez-Freiría et al. 2010).

67 Activity patterns of animals are endogenously generated by biological clocks and  
68 empowered with mechanisms that allow adaptation to environmental challenges (Refinetti  
69 2016). Activity patterns rely on endogenously fixed rhythms that can be circadian (i.e. over  
70 the 24-h) and circannual (i.e. over the calendar year) (Aschoff 1979). Circadian and  
71 circannual rhythms are shaped by predictable environmental factors, called Zeitgebers, such  
72 as photoperiodic variations, or by less predictable factors that may override the main rhythm,  
73 called masking factors, such as food quality and availability, weather conditions, nocturnal  
74 luminosity, predation, and anthropogenic disturbance (Daan and Aschoff 1982; Halle and  
75 Stensteth 2000; Donati et al. 2009, 2016; Poudel et al. 2015; Brivio et al. 2017).

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

90           In terms of activity patterns, primates were historically classified as diurnal or  
91 nocturnal until the discovery that a lemur species of the genus *Eulemur* exhibited activity  
92 over 24 h (Tattersall 1979). This activity pattern, defined as cathemerality, can provide a  
93 number of ecological advantages such as reduced feeding competition via temporal niche  
94 partition (Curtis et al. 1999; Curtis and Rasmussen 2006), thermoregulatory benefits to avoid  
95 thermal stress (Curtis et al. 1999), reduced predation risk (Donati et al. 1999; Colquhoun  
96 2006), and increased feeding efficiency related to a fibre-rich diet (Engqvist and Richard  
97 1991; Donati et al. 2007, 2009). Different degrees of cathemerality have been observed in  
98 *Eulemur* (c.f. Curtis and Rasmussen 2006), *Hapalemur* (Eppley et al. 2015), *Lemur* (Donati  
99 et al. 2013) in the wild, *Prolemur* (Santini-Palka 1994) and *Varecia* (Bray et al. 2017) in  
100 captivity.

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

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

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

134           Despite the efforts in observing and reporting the temporal activities performed by  
135 these species, a consistent and quantitative approach is needed to clarify the fine-grained  
136 mechanisms of coexistence between the two genera. Recent advances in bio-logging  
137 miniaturised technology, and the use of high-frequency accelerometers in particular, are ideal  
138 for answering research questions related to animal's movement patterns and locomotor  
139 activities in cryptic species for which behavioural observations are problematic (Brown et al.  
140 2013, Chimienti et al. 2016). Accelerometers have been used for many years to study primate  
141 activity patterns (e.g. Kappeler and Erkert 2003, Fernández-Duque and Erkert 2006, Eppley  
142 et al. 2015), although these studies mainly used activity score devices (i.e. the output is a  
143 score and it does not allow complex analysis) with low sampling frequency (usually more  
144 than one minute). High-frequency accelerometers can be used today to extrapolate detailed  
145 activity patterns and classify how animals behave, cost/benefits of movement patterns, and  
146 how they relate to the surrounding environment (Kays et al. 2015; Leos-Barajas et al. 2017;  
147 Patterson et al. 2017).

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

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

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

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

181

## 182 **Materials and methods**

### 183 ***Study site***

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

188

### 189 ***Data collection***

190 We recorded activity data every second for a total of 71 days (7 July 2015-17 September  
191 2015) on three individuals of *A. meridionalis* and three individuals of *L. fleuretae* (two  
192 females and one male from different social groups) via high-frequency accelerometer tags  
193 (Axy-Depth, TechnoSmArt) attached to VHF collars (RI-2D, Holohil Systems Ltd). To attach  
194 the collars, the lemurs were anaesthetised via a dose of 15 ml of Telazol 100mg/ml  
195 (tiletamine HCl and zolazepam HCl; Zoetis Inc.) using a CO<sup>2</sup> air rifle capable of remote  
196 injection for immobilisation (Balestri 2018; Campera 2018). There were no injuries as a  
197 consequence of the captures. The weight of the combined VHF collar and accelerometer tag  
198 with batteries was around 15 g, thus below the 5% threshold of the subjects' weight  
199 recommended for arboreal animals (Wheater et al. 2011). For the validation of the



200 accelerometer data, we recorded activity data (active or inactive) via continuous focal  
201 sampling (Altmann 1974) on six collared individuals for two full nights each. Active  
202 behaviours included feeding, foraging, moving, grooming, and social behaviour. Animals  
203 were recaptured at the end of the study to remove the collars. It was not possible to record  
204 blind data because our study involved focal animals in the field.

205

### 206 *Data analysis*

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

219 We calculated the daily proportion of activity during the day, twilight, and night. As  
220 twilight, we considered the time between the beginning of the morning astronomical twilight  
221 (when the sun is 18° below the horizon before sunrise) and the sunrise, and between the  
222 sunset and the end of evening astronomical twilight (when the sun is 18° below the horizon  
223 after sunset)(Donati et al. 2009). We obtained sunset, sunrise, moon phase, night-length, and

224 beginning and end of astronomical twilights from the U.S. Naval Observatory Astronomical  
225 Almanac (<http://aa.usno.navy.mil/data>) using the coordinates of Ampasy.

226 To evaluate the influence of night-length and moon phase on the activity of *A.*  
227 *meridionalis* and *L. fleuretae*, we ran multiple Generalised Estimating Equation (GEE)  
228 models (Bailey et al. 2013) with proportion of activity (during the day, at twilight, and at  
229 night) or the ND ratio (ratio between nocturnal and diurnal activity) as dependent variables.  
230 We used the ratio to allow comparisons across species and studies since the absolute values  
231 of activity recorded by accelerometers differ from what is recorded via observational  
232 sampling or from other models of accelerometers (Donati et al. 2009; Eppley et al. 2015). For  
233 the ND ratio we included twilight periods within the overall nocturnal activity for  
234 comparative reasons, since twilights are included in the main active phase in most other  
235 studies of cathemerality (Fernández-Duque and Erkert 2006; Donati et al. 2013; Eppley et al.  
236 2015). We used night-length and moon phase as covariates in the model, and individuals as  
237 random factor. We considered days as units of analysis and included an AR1 autocorrelation  
238 structure in the model to control for temporal autocorrelation in the data (Bailey et al. 2013).  
239 We tested several combinations of fit distributions (normal, gamma, inverse gaussian) and  
240 functions (identity, log, power) and chose the model with the lowest Akaike Information  
241 Criterion (AIC) (Burnham and Anderson 2002). The models with a gamma probability  
242 distribution and log link function had the lowest AIC.

243 To determine whether *A. meridionalis* and *L. fleuretae* were active at different times  
244 of the night, we divided the daily activity into 2-h blocks starting from midnight. We then ran  
245 a Repeated Measures (RM) ANOVAs with the activity every 2-h interval as dependent  
246 variable. To determine the difference on activity between *A. meridionalis* and *L. fleuretae*, we  
247 also ran RM ANOVAs with activity during the day, twilight, and night, or the ND ratio as  
248 dependent variable. To determine whether the two species commenced and ended their

249 activity in phase with sunset and sunrise time, respectively, we ran a RM ANOVA with the  
250 difference between activity time and sunset/sunrise. For the RM ANOVAs, we compared  
251 data between *A. meridionalis* and *L. fleuretae* during the same day. Before running the RM  
252 ANOVAs, we tested for normality (Kolmogorov–Smirnov test), sphericity (Mauchly’s test),  
253 and equality of variances (Levene’s test) as underlying assumptions. We performed the tests  
254 via SPSS v25 considering  $P < 0.05$  as level of significance.

255

## 256 **Results**

### 257 ***Influence of night-length and moon phase***

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

270

### 271 ***Daily activity pattern***

272 The 24-h activity pattern of *A. meridionalis* showed two main peaks at 4-6 h and at 18-20 h,  
273 while peaks of activity for *L. fleuretae* were at 2-4 h and at 18-20 h (Fig. 2 and Fig.3). The

274 two species showed a significantly different activity pattern for all the time blocks ( $P <$   
275  $0.001$ ) apart from the time block 14-16 h ( $P = 0.447$ ).

276 *Avahi meridionalis* commenced their activity earlier than *L. fleureate* after sunset  
277 ( $F_{1,70} = 230.69$ ,  $P < 0.001$ ), and ended the activity after *L. fleuretae* before sunrise ( $F_{1,70} =$   
278  $356.87$ ,  $P < 0.001$ ). On average, *A. meridionalis* commenced activity 11.2 (SE 0.9) min after  
279 sunset and ended the activity 10.4 (SE 1.8) min before sunrise, while *L. fleuretae* commenced  
280 activity 42.3 (SE 1.5) min after sunset and ended the activity 108.2 (SE 2.5) min before  
281 sunrise (Fig. 4).

282

## 283 **Discussion**

### 284 ***Temporal niche separation***

285 The ecologically similar lemurs *A. meridionalis* and *L. fleuretae* in the lowland rainforest of  
286 TKG showed different activity patterns that are likely to favour the coexistence of the two  
287 species. The former species showed peaks of activity at twilights with low but consistent  
288 activity during the day, while the latter species showed most activity in the central hours of  
289 the night. Despite its mainly nocturnal and crepuscular activity, *Avahi meridionalis* revealed a  
290 pattern that we define here as cathemerality *sensu lato*, varying from strict nocturnality (ND  
291 ratio: 13.09) to sporadic but even distribution of activity between night and day (ND ratio:  
292 1.12). We consider these woolly lemurs cathemeral on the basis of the following lines of  
293 reasoning. First, on a comparative level the mainly nocturnal *A. meridionalis* had an overall  
294 ND ratio of 3.89 that is similar to the DN activity ratio observed in some cathemeral species  
295 with mainly diurnal activity: 3.98 for southern bamboo lemur *Hapalemur meridionalis*  
296 (Eppley et al. 2015); 4.80 for ring-tailed lemur *Lemur catta* (Donati et al. 2013). Second, the  
297 average motor activity in the resting phase of these woolly lemurs exceeds the 10% threshold  
298 that is explained by occasional sleeping movements, changes of sleeping position,

299 disturbances by conspecifics, ectoparasites, or predatory attacks (Erkert and Kappeler 2004).  
300 Third, taking the definition of cathemerality, that is "The activity of an organism can be  
301 regarded as cathemeral when it is distributed approximately evenly throughout the 24 h of the  
302 daily cycle, or when significant amounts of activity, particularly feeding and/or travelling,  
303 occur within both the light and dark portions of that cycle (Tattersall 1987)" the pattern  
304 observed in *Avahi meridionalis* matches routinely at least the second part of the definition. In  
305 fact, while the distribution of the activity is in average not even between day and night, the  
306 outputs of our accelerometers, as well as opportunistic observations during the day, indicate  
307 that these lemurs engage in locomotor and feeding activity regularly during the daylight  
308 hours. The mainly diurnal lemurids *H. meridionalis* (Eppley et al. 2015) and *L. catta* (Donati  
309 et al. 2013) also show a *sensu lato* cathemerality, with large variations in diurnal/nocturnal  
310 ratio. The activity pattern of the Azara's night monkey, *Aotus azarai*, in the Argentinian  
311 Chaco, the only monkey that exhibits cathemeral activity (Fernández-Duque and Erkert  
312 2006), appears analogous to what we have observed in southern woolly lemurs. It is clear that  
313 while these species concentrate their activity in one phase (nocturnal for *Avahi meridionalis*  
314 and *Aotus azarai*, diurnal for *L. catta* and *H. meridionalis*) they still have some significant  
315 bouts of activity in the other phase that is often dependent on specific abiotic or biotic  
316 conditions (Fernández-Duque 2003; Eppley et al. 2015). Species that show a cathemerality  
317 *sensu stricto* either exhibit a more evenly distributed activity over the 24-hours, at least  
318 seasonally, or they can be either mainly diurnal or mainly nocturnal depending on  
319 environmental conditions and seasons, e.g. the genus *Eulemur* (Curtis and Rasmussen 2006;  
320 Donati et al. 2009, 2016).

321         Temporal niche separation is one of the ecological benefits previously hypothesised to  
322 make cathemerality advantageous in lemurs to reduce feeding competition between species  
323 (Curtis et al. 1999; Curtis and Rasmussen 2006; Donati et al. 2013). Other nocturnal animals

324 were shown to shift towards a more crepuscular activity with some diurnal activity when in  
325 competition with ecologically similar species (Halle 2000; Ziv and Smallwood 2000) or even  
326 conspecifics (Pizzatto et al. 2008). Ecologically similar nocturnal species may also be active  
327 during different parts of the night (e.g. gerbils; Kotler et al. 1993). Although we have no data  
328 to test the causation mechanism of this hypothesis, competition with *L. fleuretae* is a potential  
329 driver of the cathemeral activity observed in *A. meridionalis* at Ampasy. In fact, so far no  
330 evidence of cathemerality was reported in woolly lemurs studied in areas where sportive  
331 lemurs are rare or absent (Harcourt 1991; Norscia and Borgognini-Tarli 2008). The only  
332 previous evidence of diurnal activity in woolly lemurs (mainly vigilance) was reported at  
333 sites where sportive lemurs are present (Warren and Crompton 1997; Thalmann 2001). Until  
334 systematic data over the 24-hours will be available on the two species at other localities,  
335 possible competition between these two folivorous lemurs remains speculative.

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

344         Considering its diet rich in fibres, another possible driver of the flexible activity  
345 pattern observed in *Avahi meridionalis* might be the necessity to maximise food intake over  
346 the 24-h (Engqvist and Richard 1991; Donati et al. 2007, 2009). Despite the adaptation to  
347 folivory in *Avahi* (i.e. midgut fermentation via sacculated caecum and looped colon; Martin  
348 1990), midgut fermentation may reduce the amount of food that can be processed as well as

349 nutrient intake (Campbell et al. 2004). Extra-bouts of feeding activity during the day may  
350 thus be used to maximise nutrient intake over the 24-hours. As a matter of fact, we  
351 opportunistically observed individuals of *A. meridionalis* feeding during the central hours of  
352 the day. This idea also needs to be tested with more fine-grained, year-round data on the  
353 nutritional ecology of these woolly lemurs. For example, the generalist folivore *H.*  
354 *meridionalis* was found to reduce its cathemeral activity during periods of increased fibre  
355 intake and this was related to the prolonged periods of inactivity that fibre digestion may  
356 require (Eppley et al. 2017). Since *A. meridionalis* is also a generalist folivore (Norscia et al.  
357 2012), *Avahi* may show a pattern similar to *Hapalemur*.

358

### 359 ***Influence of photoperiodic variations and moon phase***

360 The activity of *A. meridionalis* and *L. fleuretae* was highly influenced by photoperiodic  
361 variations. This finding confirms that the activity pattern of these nocturnal lemurs is  
362 synchronised with variations of sunset and sunrise (Brockman and Van Schaik 2004).  
363 Malagasy environments are highly seasonal and the influence of photoperiodic variation on  
364 activity patterns of lemurs was reported on a variety of species, e.g. *Eulemur collaris* (Donati  
365 et al. 2009); *E. collaris* X *E. rufus* (Donati et al. 2009); *E. rufus* (Kappeler and Erkert 2003);  
366 *E. mongoz* (Curtis et al. 1999). On the contrary, other researchers found no correlation  
367 between activity profiles in cathemeral lemur species and photoperiodic variation, e.g. *E.*  
368 *macaco* (Colquhoun 1998); *Lemur catta* (Donati et al. 2013); *Hapalemur meridionalis*  
369 (Eppley et al. 2015). Beyond lemurs, seasonal changes in ambient temperature, precipitation,  
370 and food abundance have a stronger effect than photoperiodic variations for owl monkeys in  
371 the Argentinean Chaco (*Aotus azarai*; Erkert et al. 2012), and in other mammals, e.g. crested  
372 porcupines *Hystrix cristata* (Corsini et al. 1995), wild boar *Sus scrofa* (Brivio et al. 2017),  
373 and wood mouse *Apodemus sylvaticus* (Flowerdew 2000). On a theoretical basis, this

374 variation may be the consequence of the different predictability of resources at various sites  
375 (Halle and Stensteth 2000; Rode-Margono and Nekarlis 2013). In fact, TGK as well as nearby  
376 littoral forest sites show a seasonal peak of phenological resources influenced by  
377 photoperiodic variations (Bollen and Donati 2005; Campera 2018; Donati unpub. data), while  
378 sites where the activity is not synchronised by day length tend to show unpredictable  
379 phenological patterns between years (Halle and Stensteth 2000). This link is worth exploring  
380 when more long-term data are available on phenological cycles at Ampasy as well as in other  
381 Malagasy habitats (Bollen and Donati 2005; Wright et al. 2005).

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

391 Temperature may also play a role in shaping the activity profiles of *Avahi*  
392 *meridionalis* and *L. fleuretae* with lower activity during colder months as an energy-saving  
393 strategy. This strategy has been found previously in other lemur species (Kappeler and Erkert  
394 2003; Donati et al. 2009) as well as in other tropical animals (McKechnie and Mzilikazi  
395 2009; Ruf and Geiser 2015). Variation in temperature may also explain why *L. fleuretae*  
396 increases the diurnal activity with the decrease of night-length as animals may have needed to  
397 thermoregulate more by sunbathing as previously reported in other sportive lemurs (Warren  
398 and Crompton 1997; Nash 1998). Phenological patterns, as well as other environmental



399 variables, are dependent on photoperiodic variations (van Schaik et al. 1993) and it is difficult  
400 to isolate single factors. Finally, the reproductive state may have played an important role in  
401 shaping activity patterns (Vieira et al. 2017) since two out of three animals were females and  
402 gave birth around the end of August. This phenomenon may offer another explanation as to  
403 why we found an increase in mean activity starting at the end of August since mothers might  
404 have spent more time allogrooming and nursing their infants, with a consequent increase in  
405 activity while resting, especially during the day.

406 As predicted, the ND ratio of *A. meridionalis* increased while the nocturnal activity of  
407 *L. fleuretae* decreased with the increase in moon luminosity. In contrast to nocturnal  
408 mammals that are usually lunarphobic to reduce predation risk (Nash 2007; Prugh and  
409 Golden 2014), *A. meridionalis* was lunarphilic similar to other cathemeral primates (Erkert  
410 1989; Kappeler and Erkert 2003; Fernández-Duque et al. 2010; Donati et al. 2009, 2013;  
411 Eppley et al. 2015). It has been hypothesised that lunarphilia can be a strategy to reduce  
412 predatory risk by increasing vigilance (Gursky 2003; Prugh and Golden 2014). By living in  
413 pairs *A. meridionalis* may take advantage of more than two eyes to increase vigilance at high  
414 luminosity conditions. In contrast, the alternative strategy, i.e. reducing predation risk by  
415 camouflage and reducing activity at high luminosity conditions, may be a better solution for  
416 solitary animals such as *L. fleuretae* (Starr et al. 2012). The presence at TGK of a full set of  
417 predators, including the main predator of this lemur species, the cathemeral fossa  
418 *Cryptoprocta ferox*, may contribute to the observed lunarphobia of *L. fleuretae* at night. The  
419 fossa, in fact, is expected to be lunarphilic as other large predators since they increase prey  
420 detection at high luminosity conditions (Prugh and Golden 2014).

421 Another advantage of being lunarphilic is the higher foraging efficiency at high  
422 luminosity conditions (Gursky 2003; Donati et al. 2007; Rode-Margono and Nekaris 2014;  
423 Eppley et al. 2015). Such efficiency may be one of the main drivers for the influence of the

424 moon phase on the ND ratio of *A. meridionalis* since this species was not influenced by moon  
425 phase at twilight and at night. On a speculative ground, *A. meridionalis* may spend more time  
426 being active during bright nights and the day (i.e. extend the feeding time over the 24 h) as a  
427 consequence of the limited visibility to discern young high-quality leaves during the new  
428 moon phase. Thus, lunarphilia may represent an advantage for *Avahi* since its visual pigments  
429 appear optimally adjusted to detect young green leaves (Veilleux et al. 2014). In fact, leaf  
430 quality has been shown to be correlated to variation in the green-red and blue-yellow  
431 chromatic differences (Dominy and Lucas 2004).

432

### 433 ***Conclusions***

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

443 The exhibition of a cathemerality *sensu lato* in *A. meridionalis* has implications on the  
444 current hypotheses on the evolution of activity patterns in lemurs (Donati and Borgognini-  
445 Tarli 2006; Donati et al. 2013; Markolf and Kappeler 2013; Santini et al. 2015). The finding  
446 that *A. meridionalis* is cathemeral supports a diurnal ancestor for the Indriidae, thus  
447 strengthening the hypothesis of a secondary nocturnality for *Avahi* (Ganzhorn et al. 1985;  
448 Roos et al. 2004). In this scenario, *Avahi* has evolved nocturnality but retained some ability to

449 be active during the day in a similar way to what has been hypothesised in *Aotus azarai*  
450 (Fernandez-Duque 2003). The findings of this research contribute to the idea that activity  
451 patterns in lemurs are graduated and the more we know about their activity patterns the more  
452 we realise that traditional categorisations are clearly inadequate.

453

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463

#### 464 **Author contributions**

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

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475

476 **Data accessibility**

477 The datasets analysed during the current study are available from the corresponding author on  
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479

480 **Compliance with ethical standards**

481 **Conflict of interest**

482 The authors declare that they have no conflict of interest.

483

484 **Ethical approval**

485 We obtained permission for the field research from the Ministry of Environment and Forest  
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491

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730 **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)  
731 for *Avahi meridionalis* and *Lepilemur fleuretae*. Beta estimates (Standard Error) are parameter estimates of the Generalised Estimating Equation  
732 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  
733 species.

	<i>Avahi meridionalis</i>			<i>Lepilemur fleuretae</i>			F-value
	Activity	Night-length	Moon phase	Activity	Night-length	Moon phase	
	(range) %	Beta (SE)	Beta (SE)	(range) %	Beta (SE)	Beta (SE)	
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**

734 \* 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).