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Bruno Simmen, Hanta Rasamimanana. Energy (Im-)Balance in Frugivorous Lemurs in Southern Madagascar: A Preliminary Study in *Lemur catta* and *Eulemur rufifrons* x *collaris*. *Folia Primatologica*, 2018, 89 (6), pp.382-396. 10.1159/000492570 . hal-02349627

HAL Id: hal-02349627

<https://hal.science/hal-02349627>

Submitted on 5 Nov 2019

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Energy (im-)balance in frugivorous lemurs in southern Madagascar:
a preliminary study in *Lemur catta* and *Eulemur rufifrons x collaris*

Bruno Simmen¹ and Hanta Rasamimanana²

¹ Centre National de la Recherche Scientifique/Muséum national d'Histoire naturelle,
UMR 7206 Eco-anthropologie et Ethnobiologie

² Ecole Normale Supérieure, Université d'Antananarivo, Antananarivo, Madagascar

Short title: Energy intake in wild lemurs

#words: 8332

Corresponding author: Bruno Simmen, Muséum national d'Histoire naturelle, 1 avenue du Petit
Château, 91800 Brunoy, France

E-mail: simmen@mnhn.fr, Phone number: +33 (0)1 60 47 92 33

Abstract

The reproductive cycle of several lemur species is synchronized by photoperiodic changes and is attuned to the seasonal fluctuations of food supply. Irregular periods of food shortage nevertheless occur in Madagascar, which can result in negative energy balance and reduced fitness, especially in frugivorous species. Here, we test if ring-tailed lemurs (*Lemur catta*) and brown lemurs (*Eulemur rufifrons x collaris*) use fat stores to maintain their energy balance in a gallery forest of Madagascar (Berenty Reserve). We assessed the energy intake from weight-based estimates of food intake (mouthful count) and macronutrient contents in the diet during dry and wet months. The metabolizable energy ingested by these frugivorous/folivorous species was high during the late wet season, but was insufficient to meet their energy requirements during the dry season. These preliminary data suggest that these lemurs must store sufficient amount of fat mass during the period of food abundance to meet their maintenance requirements and to cope with the energetic burden of the mating season. Estimates based on models assuming no fibre digestibility during the dry season are consistent with the prediction that brown lemurs should supplement their daytime diet with nighttime feeding in addition to the use of body fat stores.

Key words

metabolic costs, seasonal breeding, energy intake, nutrients, body fat, dry season, primates

Introduction

Species that primarily depend on food resources scarcely or irregularly distributed in time and space like fruit, flowers and animal matter, are at risk of energy imbalance [Oates, 1987; Wright, 1999]. In tropical habitats with unpredictable rainfall and/or a long dry season, frugivorous species have developed opportunistic foraging strategies and shift their diet toward lower quality or fallback food during the lean season [Oates, 1987; Lambert and Rothman, 2015]. In some cases, dietary shifts are accompanied by morphological and physiological adjustments such as changes in the digestive tract size [Munn et al., 2009], basal metabolic rate, and other energy-saving mechanisms such as body fat storage [Muroyama et al., 2006; Canale and Henry, 2010]. Apart from its consequences on survival during the lean season, the storage of body fat could also have evolved to sustain the energy cost of reproduction (e.g., in seasonal breeding mammals or in harsh environments [Brockman and van Schaik, 2005; Canale and Henry, 2010; Garcia et al., 2011; Wells, 2012]). Seasonal body weight changes have sometimes been recorded in wild primates (e.g. [Knott 1998; Richard et al., 2000; Lewis and Kappeler 2005]), but in studies that only measure body mass, it is unclear whether the weight gain reflects fat storage or increased muscle volume [Bercovitch 1987]. It has been argued that, due to their primarily arboreal lifestyle, primates may generally have not relied on body fat storage strategies throughout their evolutionary history [Dittus, 2013]. However, the available data are still too limited to invalidate the existence of fattening in many wild primates. The seasonal increase in body fat has been reported for the first time in semi-free ranging and wild male squirrel monkeys in relation to rainfall cycles and sexual selection [Du Mond & Hutchinson 1967]. High body fat content following periods of high food supply has been reported in Bornean orangutans (*Pongo p. pygmaeus*) living in unpredictable habitats and some strepsirrhine species, especially among the small heterotherm cheirogaleids that enter torpid states during the dry season of Madagascar [Knott, 1998; Fietz and Dausmann, 2006; Génin, 2008; Simmen et al., 2010]. Humans also accumulate fat, a characteristic that was

83 undoubtedly present in early hominins exposed to highly seasonal or volatile environments [Wells,
84 2012]. Obviously, more data are needed to better understand the metabolic adaptations to seasonal
85 energy shortages and to the costs of reproduction in primates, particularly the potential buffer role
86 of fattening.

87 Lemurs provide an interesting case study with regard to the effect of seasonal changes in
88 resource availability and dietary quality on energy balance. Within lemur communities, the scarcity
89 of fruit specialists relative to their African or Asian counterparts has been related to the ecological
90 particularities of Madagascar assumed by some authors, namely unusually low food productions,
91 low protein content of fruits, and fruit scarcity for long periods during the dry season [Fleagle and
92 Reed, 1996; Ganzhorn et al., 2009; Donati et al., 2017]. There is also some evidence that, due to
93 climatic irregularities in some years, lemur communities may experience a fruit shortage during the
94 rainy season beside the dry season [Wright, 1999]. Finally, stochastic and frequent dramatic
95 climatic events such as cyclones occur in Madagascar, which affects individual survival through the
96 loss of food resources [Gould et al., 1999; Dunham et al., 2011; Lewis and Rakotondranaivo, 2011].
97 At an evolutionary time-scale, it would therefore make sense that a range of lemurs has evolved a
98 combination of energy-saving mechanisms, behavioural flexibility and opportunistic feeding
99 strategies. In this respect, a study of body composition and metabolism in sympatric ring-tailed
100 lemurs (*Lemur catta*) and “brown lemurs” (*Eulemur rufifrons x collaris*) living in the subarid south
101 of Madagascar (Berenty Reserve) showed that these seasonal breeding species had large amounts of
102 body fat following the period of greatest food abundance [Simmen et al., 2010], consistent with the
103 hypothesis of a well-defined fattening period just prior to the mating season and the long dry season
104 (see also [LaFleur, 2012]).

105 Given the fragmented nature of available data on the metabolic ecology of these large-
106 sized lemurs in the wild, one aim of the present study is to provide a more in-depth analysis of the
107 risk of energy imbalance incurred by ring-tailed lemurs and brown lemurs in different seasons and
108 food supply contexts. In particular, we analyze whether energy consumption varies according to the

109 timing of the reproductive cycle and is compatible with a fattening process. In order to identify
 110 possible periods of positive and negative energy balance, we estimate metabolizable energy intake
 111 in different seasons and contrast these estimates with total energy expenditure (TEE) measured
 112 previously with doubly labelled water at the same study site in both species (Berenty Reserve
 113 [Simmen et al., 2010]). Finally we discuss whether the cathemeral behaviour (i.e. significant
 114 nocturnal and diurnal activity) reported for these lemurs, one characteristic of the so-called “lemur
 115 syndrome” [Wright, 1999], may be a consequence of insufficient energy intake during daytime or
 116 low ability of these species to digest plant fibres [Engqvist and Richard, 1991; Donati et al., 2007,
 117 2009, 2013; LaFleur et al., 2014]. Based on the seasonal pattern of nocturnality reported for
 118 *Eulemur rufifrons x collaris* at Berenty [Donati et al., 2009] and some activity of *Lemur catta* at
 119 night (Berenty: [Donati et al., 2013]), we made the following predictions: during the dry season, the
 120 two lemurs are not able to meet their energy needs (with possible species differences) by simply
 121 feeding during the day, even accounting for body fat stored during the wet season. In contrast, we
 122 expect that during the period of fruit abundance prior to the mating period and long dry season,
 123 these lemurs maximize their caloric intake, with a large positive energy balance reached through
 124 daytime feeding.

125

126 **Methods**

127 We studied diet composition and seasonal dietary changes in the two lemur species in
 128 1998/1999 [Simmen et al., 2003]. Information on the study site, subjects, behavioural methods and
 129 diets can be found in the 2003 publication. However we give here an overview of the methodology
 130 used to determine diet as, in the present paper, we quantify the daily intake of macronutrients,
 131 secondary metabolites and metabolizable energy using the proportions of plant species and plant
 132 parts in the diet determined in the previous study.

133

134 *Study site and lemur groups*

135 Malaza gallery forest (97 ha) is part of Berenty Private Reserve, Southern Madagascar
 136 (25°0.29'S, 46°19.37'E). The climate is sub-arid with marked, irregular annual rainfall variation
 137 (300-900 mm) and a dry season lasting from April to October [Jolly et al., 2006]. Details on forest
 138 composition and habitat structure in Malaza can be found elsewhere [Jolly et al., 2006; Simmen et
 139 al., 2012, 2014]. At the forest edge, exotic trees species used as foods by some of the focal groups
 140 of lemurs are grown as ornamental plants [Simmen et al., 2003].

141 Ring-tailed lemurs (*Lemur catta*) and “brown” lemurs (*Eulemur rufifrons x collaris*) live in
 142 multi-male, multi-female troops and are primarily frugivore/folivores, supplementing their diet with
 143 flowers (Table 1). There is no significant sex difference of body mass across the populations studied
 144 in the forest areas investigated here (ring-tailed lemurs: 2.3 ± 0.3 kg; brown lemurs: 1.9 ± 0.2 kg;
 145 [Simmen et al., 2010]). Ring-tailed lemurs at Berenty defend relatively small, well-defined home
 146 ranges whereas groups of brown lemurs forage over comparatively larger areas and are less
 147 territorial (Jolly et al., 2006; Pinkus et al., 2006; Tanaka 2007; Simmen, pers. obs.). In the
 148 comparative analysis of diet that we carried out in 1998 and 1999 [Simmen et al., 2003], we studied
 149 3 to 5 groups per lemur species. We selected groups of brown lemurs that foraged within the areas
 150 used by ring-tailed lemur troops. Some focal groups of ring-tailed lemurs foraged inside Malaza
 151 forest, while others lived at the forest edge having access to ornamental plants. Brown lemur groups
 152 were more arboreal than ring-tailed lemurs and were more rarely observed in environments without
 153 tree cover at the forest edge [Simmen et al 2003].

154

155 *Behavioural data collection*

156 Daytime is the only temporal sequence of the nycthemeral cycle during which we can
 157 reliably estimate food and energy intake on a quantitative basis. Therefore, in 1998/1999, we
 158 determined diets from mouthful counts (Hladik 2011; Zinner 1999; Simmen et al., 2017) during
 159 continuous observation of focal individuals (*continuous focal animal sampling*) followed from
 160 dawn to dusk during three periods, following a preliminary survey in December 1997: May-June

161 (early dry season), October-November (late dry season), February-March (late wet season). Due to
 162 the highly synchronized reproductive cycle related to photoperiod changes, breeding occurs
 163 approximately in April-May, gestation lasts until September-October, and lactation until February.
 164 Focal individuals could be approached within a few meters and the visibility generally allowed
 165 close observation of individual feeding activity. The observation sample consisted of 4.0 ± 0.6 full
 166 days of observation on average per species per study period during which only food intake was
 167 recorded (311 hours total observation balanced between the two species and periods). Focal animals
 168 were adult males and females (excluding lactating females), with these identified from their natural
 169 markings or dye spots. Each full-day follow was devoted to one focal animal from one group, but
 170 when the animal was out of sight due to poor visibility conditions, we temporarily shifted to the
 171 nearest individual (adult or large subadult of the same sex). Observation days were spread as much
 172 as possible throughout each study period and alternated between groups of the two species within
 173 intervals generally ≤ 5 days. Daily observations of focal individuals followed during periods up to
 174 14 hours (depending on seasonal photoperiod changes) without major interruption constituted 40%
 175 of total records. We weighed the fresh mass of each food item eaten to convert mouthfuls into
 176 masses of ingested matter. We derived the amount of food eaten for each given day from the sum of
 177 foods consumed by the focal individual (supplemented by the food intake of the alternative
 178 individuals). We averaged daily food intake recorded for each study period and each lemur species.
 179 On this basis, we calculated the relative proportions of the different food items in the seasonal diets
 180 [Simmen et al 2003].

181 The data collected may not be representative of the full feeding repertoire since the
 182 observed sample was small. However, referring to the main studies carried out in the last decades
 183 on the feeding ecology of ring-tailed lemur and brown lemur at the study site, we believe this did
 184 not substantially affect recognition of major food plants in the diet: all studies point out to a
 185 consistently low dietary diversity in both species, while the plant species that contributed most to
 186 their diet in our study were consistent with the top plant species used as foods reported in

187 [Rasamimanana and Rafidinarivo, 1993; Jolly et al. 2006; Pinkus et al. 2006]. This, together with
 188 the observations made during our successive studies at Malaza from 1987 until the present,
 189 suggested that we captured the most prominent features of the dietary characteristics of these
 190 species at the study site. As a result, ≤ 4 plant species accounted for $\geq 75\%$ of the food matter
 191 ingested by each species in each season from a total of 66 food plant spp. (87 food items) and 24
 192 spp. (38 items) consumed respectively by ring-tailed lemurs and by brown lemurs during the study
 193 [Simmen et al., 2003]. The two lemur species typically focused their food choices on *Tamarindus*
 194 *indica*, *Celtis* spp. and other dominant plant species of the gallery forest, supplemented by
 195 *Azadirachta indica*, one common ornamental plant available for groups ranging at the forest edge.
 196 Dietary overlap between the two species was the largest during the early dry season, when these
 197 lemurs used a restricted set of similar plant species as their staple, as found elsewhere [Sussman,
 198 1974; Rasamimanana and Rafidinarivo, 1993]. Table 1 provides an overview of major food
 199 categories in the diet, split by seasons.

200 [Table 1]

201

202 *Chemical assays*

203 We conducted plant sampling and chemical analyses at the same time as the initial
 204 comparative study of the feeding ecology of these species [Simmen et al., 2003; Rothman et al.
 205 2012]. We collected plant samples from feeding trees and dried major food plant samples (62 items;
 206 39 plant species) in an electric field oven (at 50°C) for botanical identification at the National
 207 Museum of Natural History in Paris by experts (Annette Hladik and colleagues) and for chemical
 208 analysis. We obtained samples of major foods from multiple food trees or lianas of the same species
 209 and mixed them to account for within-species variation in chemical content [Rothman et al., 2012].
 210 Since we were primarily interested in estimating the overall diet quality and average daily energy
 211 intake in each season, we blended fruits, flowers and leaves according to their proportion in the
 212 seasonal diets of each lemur species prior to performing the chemical analyses. The mixtures were

213 composed of plant parts that together accounted for 85-100% of the total dry matter consumed by
214 ring-tailed lemurs or brown lemurs during each of the three seasons studied. Although the dietary-
215 mixture method reduces the costs of the chemical analyses, one limitation of the method is that it
216 does not allow for testing the statistical significance of seasonal differences in nutrient and energy
217 intake. Sampling heterogeneous mixtures when the sample contains many different samples and the
218 amount of sample used in each assay is low, also introduces a risk that the food mixture is not
219 representative. To assess the consistency of the results, we performed additional chemical analyses
220 on staple foods separately. We then calculated the weighted mean proportion of nutrients from
221 results obtained on each staple food — that together accounted for $\geq 75\%$ of the total dry matter
222 consumed by the lemurs in each season — and we compared it with the nutrient composition of the
223 dietary mixtures.

224 We determined humidity from portions of plant samples dried at 105°C in the laboratory.
225 We carried out chemical analyses on macronutrients and fibre at the ISHA (Institut Scientifique
226 d'Hygiène et d'Analyses, Longjumeau) following official analytical norms (AFNOR group as a
227 member of ISO). The analyses on the dry powdered samples were performed in duplicate and the
228 results were expressed as mean values with a $\leq 5\%$ difference between the assays for each sample.
229 We determined crude protein ($\text{N} \times 6.25$; Kjeldahl method), crude lipids (HCl hydrolysis and
230 extraction with petroleum-ether), soluble sugars (HPLC), neutral detergent fibre (NDF), and ash
231 (see Simmen et al. [2014] for specific references). We also analyzed phenolic compounds (modified
232 Prussian blue assay [Price and Butler 1977], condensed tannins with acid butanol assay [Porter et
233 al., 1986]), and protein precipitation efficiency (bovine serum albumin-binding property of the plant
234 extract [Asquith and Butler, 1985]) to provide a broader assessment of diet quality beyond
235 macronutrient content. Results for phenolics and condensed tannin concentrations are expressed in
236 relative units as equivalents of a chemical standard (tannic acid and purified quebracho tannin,
237 respectively) and cannot be considered absolute [Rothman et al., 2012].

238

239 *Data analysis*

240 Metabolizable energy intake in each season was the sum of energy provided by readily
 241 digestible energy (i.e. soluble carbohydrates, fat, protein, pectin, and starch) and NDF corrected for
 242 digestibility in food eaten daily averaged for that season. Daily metabolizable energy intake was
 243 calculated in $\text{kJ}\cdot\text{d}^{-1}$ by multiplying the summed kCal eaten daily by 4.18 [Rothman et al., 2012]. The
 244 HPLC assay for soluble sugars does not account for other readily available carbohydrates
 245 potentially present in primate foods, e.g. soluble fibres like pectin and storage compounds like
 246 starch, which could lead to an underestimation of the metabolizable energy value of the diet.
 247 Therefore, we assumed an additional average concentration of 5% of the total dry mass for pectin
 248 and starch, respectively, based on a review of the literature on primate fruits and other tropical fruits
 249 and leaves [Simmen et al., 2017].

250 Similarly wild lemurs' ability to digest NDF is not known but experiments on fibre
 251 digestion in captive *Lemur catta*, *Eulemur* spp. and another large frugivorous lemur, *Varecia*
 252 *variegata*, are helpful for calculating a range of energy intake values derived from microbial
 253 fermentation [Overdorff and Rasmussen, 1995; Campbell et al., 2004a; Schmidt et al., 2005].
 254 Specifically, the NDF digestibility coefficients we used varied according to the fibre content in the
 255 dry matter ingested by our study species. When NDF content in the natural diets was low ($< 25\%$
 256 during the late wet season; table 2), we used a NDF digestibility coefficient at 41% (*Eulemur fulvus*
 257 [Campbell et al., 2004a]). When NDF content was high (up to 46% during the early dry and late dry
 258 season; table 2), we calculated two energy estimates that assume either low or no fibre digestibility
 259 as reported in captivity. In the first estimate, we used a figure at 12% for fibre digestibility, as found
 260 in *Eulemur macaco* fed diets with NDF at 31-35% [Schmidt et al., 2005]). In the second estimate,
 261 we assumed zero fibre digestibility (comparable to the results for *Eulemur fulvus* and *Lemur catta*
 262 fed with large-sized cellulose particles [Overdorff and Rasmussen 1995]) and we calculated
 263 metabolizable energy input based on readily digestible energy only.

264 We estimated the daily metabolizable energy input in each season by first converting the
 265 average dry matter ingested daily into caloric values ($4/9/4 \text{ kCal.g}^{-1}$ for the energy equivalents of
 266 soluble sugars, fat, and protein, respectively). We assumed an energy equivalent of NDF and pectin
 267 at 3 kCal.g^{-1} to account for the energy diverted by gut microbial metabolism [Conklin et al., 2006].
 268 Basically, we used the same range of NDF digestibility coefficients for brown lemurs and ring-
 269 tailed lemurs given similarities in the range of cellulose digestibility in the study reported by
 270 Overdorff and Rasmussen ([1995]; 0 to 21% and 0 to 30%, respectively). Yet, we accounted for a
 271 possibly higher ability of *Lemur catta* to subsist on fibrous foods (see Introduction) when
 272 discussing the relationship between energy intake and energy expenditure. Indeed, *Lemur catta* is
 273 more closely related to the folivorous bamboo lemurs (*Hapalemur* spp.; [Markolf and Kappeler,
 274 2013], it possesses a large and haustrated caecum that may function to improve fibre fermentation
 275 [Campbell et al., 2000], and the overall foliage proportion in their diet is higher than that of brown
 276 lemurs which eat more fleshy fruits [Berenty; Simmen et al., 2003; Pinkus et al. 2006].

277

278 **Results**

279 Table 2 shows the nutrient composition of the seasonal diets (i.e. the dietary mixtures) as
 280 well as the weighted mean concentration of nutrients calculated from the chemical composition of
 281 each staple food. Both types of analyses produced broadly similar results even though the
 282 contribution of food items to the diet differed somewhat between the two analyses. Mature leaves
 283 and unripe fruits of *Tamarindus indica* (Caesalpinioideae), with their high concentrations of NDF
 284 and condensed tannins as well as large protein-precipitation effects, were the staple foods consumed
 285 during the dry months — during the early dry season, they accounted for 60 to 96% of the total
 286 amount of food ingested daily. Consequently, as for other macronutrients and secondary
 287 metabolites, the NDF content of the dry season diet of the two lemur species largely reflected the
 288 chemical composition of this tree species. Brown lemurs had lower dietary proportions of protein
 289 than ring-tailed lemurs during the dry months, while the diet of both species contained large

concentrations of nitrogen-digestibility reducers (bovine serum albumin-binding efficiency and phenolic content; Table 2).

[Table 2]

[Table 3]

At the beginning of the early dry season, both primate species had lower quality diets and reduced metabolizable energy intake compared with the wet season (Fig. 1). During these dry months, the physiological fuel value of the diet was similar between the two species (Table 3), but brown lemurs consumed digestible calories in greater quantity than ring-tailed lemurs because of their greater daily food intake.

During the late wet season when ripe fruit pulps were the staple, soluble carbohydrates accounted for a large proportion of the food matter consumed by both lemur species (table 2). During this period, daily metabolizable energy intake was the highest, with readily digestible energy accounting for a great proportion of total metabolizable energy intake (Fig. 1). As a result, wet season diets were characterized by a higher physiological value (kJ.g^{-1} dry mass) relative to other seasons (Table 3). Interestingly, the contribution of readily digestible energy to overall energy intake was always remarkably high regardless of the digestibility coefficients used to estimate the contribution of fibre to energy input. We found no substantial difference between the two species with regard to this energy fraction (Fig. 1) or the NDF content of their diet at any season (Table 3).

[Figure 1]

Discussion

Although based on a limited sample of feeding observations, our data reveal a large seasonal variation of energy intake, with a broadly similar temporal pattern in the two lemur species (i.e. an increase during the wet season). The high energy consumption found during the wet season

316 is consistent with the hypothesis of a seasonal storage of body fat. In captivity, ring-tailed lemurs
 317 and brown lemurs store fat and undergo seasonal variation in hair metabolism, feeding and activity
 318 of metabolically-active hormones [Pereira and Pond, 1995; Pereira et al., 1999]. These biological
 319 changes are synchronized by the day-length variation, a predictable abiotic cue that allows them to
 320 anticipate the season of food shortage lasting up to 6 or 7 months in their habitats and to adjust their
 321 reproductive cycle accordingly. In our previous study of body composition in ring-tailed lemurs and
 322 brown lemurs at Malaza [Simmen et al., 2010], we observed a high body fat content at about 18%
 323 in both species, without sex differences, at the end of March, before the dry season. This is close to
 324 the body fat percentage found in captive orangutans (approximately 20% [Pontzer et al., 2016a])
 325 and much higher than that of other non-hibernating primates feeding on natural foods (2-5%
 326 [review in Dittus, 2013]). In addition, in the Simmen et al 2010 study, the few individuals captured
 327 from each species showed a large increase in body mass ($17 \pm 4\%$) between the December pilot
 328 study (i.e. after the rains resumed and new leaves and flower buds were available) and when they
 329 were recaptured in March of the following year. Consequently, energy data from different years
 330 indicate a recurring trend in these lemurs of achieving a positive energy balance during the rainy
 331 season. This conclusion as well as the question of whether ring-tailed lemurs and brown lemurs
 332 present an energy imbalance during the dry season can be tested further by contrasting our estimates
 333 of energy intake with the metabolic data previously collected in March/April 2009 in these species
 334 [Simmen et al., 2010], namely total energy expenditure (TEE) and body composition.

335 Energy intake theoretically equates with TEE to sustain a balanced energy budget if
 336 animals do not store fat. TEE was formerly assessed in groups of lemurs that were foraging within
 337 the same forest areas as those studied here. Despite the discontinuity between the studies, energy
 338 intake can be contrasted to energy expenditure values on the basis that TEE is maintained within a
 339 narrow, species-specific physiological range, as discussed by Pontzer et al. [2015]. Indeed, recent
 340 findings in humans [Pontzer et al., 2016b] show that TEE during habitual physical activity cannot
 341 be considered as the sum of each metabolic cost incurred for body maintenance and behavioural

activity (referred to as the additive model). The constrained energy model [Pontzer et al., 2016b], in contrast, is supported by an increasing number of studies in mammals, including primates, which show that TEE (measured with doubly labelled water over an interval of a few days) does not differ substantially between seasons or between captive and wild individuals (TEE or mass-adjusted TEE [Kenagy et al., 1989; Nagy et al., 1999; Pontzer et al., 2014, 2016a; Pontzer, 2015]). In this model, TEE is maintained within a narrow metabolic range because metabolic and behavioural adjustments offset the costs induced by energy-demanding activities such as vigorous physical activity [Pontzer, 2015; Pontzer et al., 2016b]. In *Microcebus murinus*, for example, TEE differs neither between the dry and the wet season in normothermic individuals [Schmid and Speakman, 2000]. Other studies show that gregarious lemurs reduce thermal stress by using behavioural thermoregulation like social huddles and peculiar resting postures and, according to some authors, by performing daylight and nocturnal activity ([Donati et al., 2011; LaFleur et al., 2014; Kelley et al., 2016; Eppley et al., 2017]; but see Fletcher et al. [2012]).

Assuming that the lemurs studied here also maintain their TEE within a narrow metabolic range, the daily energy intake of *Lemur catta* in the early dry season ($\leq 443 \text{ kJ.d}^{-1}$) is less than the total energy expenditure previously measured at $626 \pm 138 \text{ kJ.d}^{-1}$ with doubly labelled water. With large amounts of body fat reserves, however, ring-tailed lemurs could theoretically meet their maintenance energy requirements during most of the dry season: an average of 424 grams of body fat recorded at the end of the wet season [Simmen et al., 2010] is equivalent to a 25-day supply (or 15,800 kJ) for an individual expending 626 kJ.d^{-1} . The energy contained in these fat reserves, combined with the calories obtained from the early dry season diet during daytime, would make it possible to balance the energy needs over a 3-month period. Foraging during the late dry season on the other hand yields energy intake well above requirements (Table 3). In brown lemurs, the calories ingested during daytime in the early dry season ($576\text{-}659 \text{ kJ.d}^{-1}$) and late dry season ($516\text{-}573 \text{ kJ.d}^{-1}$) are barely or not sufficient to meet the energy requirements (TEE: $610 \pm 90 \text{ kJ.d}^{-1}$ [Simmen et al., 2010]). However, the 325 g of fat stored at the end of the wet season [Simmen et al.,

2010] are equivalent to a 20-day energy supply (or 12,100 kJ) for an average individual expending 610 kJ.d⁻¹. In this case, the combination of calories ingested during the dry season with energy stored as body fat is theoretically sufficient to avoid negative energy balance during the whole dry season. Finally, crude protein intake in both species (Table 3) is far above the estimated protein requirements of omnivorous primates (<15% of metabolizable energy; [Oftedal 1991]), especially during the dry season.

We acknowledge that these analyses are solely predictive since our study spanned a short period and we assumed similar digestibility coefficients between wild and captive animals. Also, one potential limitation of our energy throughput analysis is that we compared energy intake with body fat content and energy expenditure measured from different years, using the constrained energy model of Pontzer et al. [2016b]. Further studies should be conducted to assess whether the energy expenditure of these lemurs may vary to a greater extent than this model suggests.

Assuming that our hypotheses are correct, the results are, at first glance, not in agreement with studies that suggest a link between diet and cathemerality (i.e. the nocturnal and diurnal activity). Cathemeral activity in *Eulemur*, it is argued, may be a consequence of the high proportion of fibrous foods in the diet and the inability to extract enough energy from the plant parts consumed during the day [Donati et al., 2007, 2009]. As a result, lemurs are not able to meet their energy needs if they do not supplement their diurnal feeding activity with night-time feeding activity [Engqvist and Richard, 1991].

In fact, our data can be reconciled with the dietary fibre-driven hypothesis on cathemerality to the extent that we probably overestimated energy available from food and adipose tissue. Not all protein ingested and fat substrates can be used as fuel for energy expenditure, and primates, like other mammals, require up to 2.8 g.kg BW⁻¹.d⁻¹ of protein and at least 2% body fat to meet their maintenance costs (Oftedal 1991; NRC 2003; Dittus 2013). Accordingly, in ring-tailed lemurs, the pool of energy available after subtracting these proportions of nutrients (≤ 336 kJ.d⁻¹ from the diet and 14,500 kJ as fat; Table 3) suggests that this species may avoid negative energy balance based

394 on daytime foraging during no more than 2 months at the beginning of the dry season (that is, until
 395 June-July). Brown lemurs, with 490 kJ.d^{-1} as readily digestible energy (assuming zero fibre
 396 digestibility from NDF-rich diets during the dry season; Table 3) plus 10,400 kJ as fat stores, would
 397 be able to balance their energy needs during no more than 3 months (that is, until July-August). In
 398 addition, calculations suggest that daytime energy intake is insufficient for this species at the end of
 399 the dry season, unlike ring-tailed lemurs (Table 3). Yet, these predictions do not account for other
 400 potentially limiting factors. For instance, protein bioavailability is likely diminished by the high
 401 concentrations of tannin and other phenolic compounds in the diet (both species; Table 2). The dry
 402 season diet of *Eulemur* contained a limited concentration of crude protein relative to estimated
 403 requirements of omnivorous primates (as low as 8.5% on a dry matter basis, Table 2, versus 7-16%,
 404 [Ofstedal 1991]) — even though protein intake was far above the estimated requirements ($>26\%$ as a
 405 proportion of metabolizable energy, Table 3, versus $<15\%$, [Ofstedal 1991]). In addition, due to the
 406 timing of reproduction and high energy cost of the breeding season for both males and gestating
 407 females [May-June; Sauther, 1991; Pereira et al., 1999; Rasamimanana et al., 2006; Ostner et al.,
 408 2008], the fat reserves may in fact be depleted shortly after the end of the rainy season. This would
 409 force individuals to distribute their dry season feeding activity over a 24-hour period to balance
 410 their energy needs. In *Eulemur rufifrons x collaris* at Malaza, cathemeral activity is predominantly
 411 observed during the dry season, with a peak in June-July, when food is scarce and the diet is rich in
 412 fibrous foods [Pinkus et al., 2006; Donati et al., 2009]. Systematic observations of *Lemur catta*
 413 using camera traps and direct observation in the wild are limited to the wet season and reveal some
 414 limited activity at night (Berenty: Donati et al., 2013); Tsimananpetsotsa: [LaFleur et al., 2014]).
 415 The nycthemeral activity pattern of this species during the dry season suggests substantial nocturnal
 416 activity, consistent with the hypothesis of a risk of energy imbalance, but the data remain scant
 417 (April-June; [Traina 2001]).

418 In conclusion, our results are in agreement with the hypothesis that lemur species that
 419 primarily feed on scarce and irregular food resources (fruit or insects) have evolved energy-saving

mechanisms including fat storage [Sauther, 1998; Génin, 2008; Simmen et al., 2010]. The risk of nutritional deficiency in these lemurs and other frugivorous lemurs in Madagascar may vary each year due to the erratic climate and irregularities in the fruit supply [Sauther, 1998; Wright, 1999; Dewar and Richard, 2007]. Accordingly we expect that the fat storage process and energy intake may be compromised during unfavourable years and that any major irregularities in the food supply during the wet season will exert a strong selective pressure on the fitness of these lemurs. If the lemurs fail to store enough fat, they could in the short term also rely on the catabolism of muscle tissue, but this hypothesis needs to be explored further. Finally, given the differences in diet, gut morphology and physiology between the two species studied, and partitioning of their ecological niches under conditions of natural coexistence, we expect that ring-tailed lemurs and brown lemurs do not incur the same risk of energy deficiency. During the period of food shortage at Berenty, brown lemurs tend to eat larger quantities of food than ring-tailed lemurs, probably to compensate for the low amount of energy extracted from fibrous foods [Simmen et al., 2003]. Conversely, seasonal changes in the gut microbiota of wild *Lemur catta* [Fogel 2015] indicate possible compensation effect of the gut symbiotic microorganisms to extract metabolizable energy from leaves. The possibility that ring-tailed lemurs obtain more energy per unit weight of food consumed than brown lemurs must be explored further.

437

438 **Acknowledgements**

439 We thank the DeHeaulme family for providing permission to study lemur ecology in the
 440 Berenty Reserve, and the DGDRF in Antananarivo (Ministère des Eaux et Forêts, Madagascar) who
 441 delivered the authorizations to carry out our research program. We thank André Marez for his help
 442 in the chemical assays of secondary metabolites. We are grateful to Shelly Masi who provided
 443 useful comments, to V. Winchester, Anne Mertl-Millhollen and James R. Tysell who edited the
 444 successive drafts of the text, and to three anonymous reviewers. We declare we have no competing
 445 interests.

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