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# Thermal and morphometric correlates of the extremely low rate of energy use in a wild frugivorous primate, the Mayotte lemur

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Primates spend on average half as much energy as other placental mammals while expressing a wide range of lifestyles. However, little is known about how primates adapt their rate of energy use in the context of natural environmental variations. Using doubly labelled water, behavioral and accelerometric methods, we measured the total energy expenditure (TEE) and body composition of a population of *Eulemur fulvus* (N = 12) living in an agroforest in Mayotte. We show that the TEE of this medium-sized catheimeral primate is one of the lowest recorded to date in eutherians. Regression models show that individual variation in the rate of energy use is predicted by fat-free mass, body size, thigh thickness and maximum temperature. TEE is positively correlated with increasing temperature, suggesting that thermoregulation is an important component of the energy budget of this frugivorous species. Mass-specific TEE is only 10% lower than that of a closely related species previously studied in a gallery forest, consistent with the assertion that TEE varies within narrow physiological limits. As lemur communities include many species with unique thermoregulatory adaptations, circadian and/or seasonal temperature variations may have constituted a major selective pressure on the evolution of lemur metabolic strategies.

**Keywords** Doubly labeled water, Field metabolic rate, Fattening, Seasonality, Heat stress, Body composition

Animal survival and reproductive success are linked to how individuals manage their energy balance. Because environments provide limited food supply and can be climatically constraining, the allocation of internal resources to major biological functions while maintaining stable energy balance requires energy trade-offs<sup>1-4</sup>. Energy allocation can result in sub-optimal fitness outcomes in dynamic environments, whether natural or anthropogenic, when food resources are unusually limited or climate varies unpredictably, which is characteristic of today's rapidly changing world<sup>5,6</sup>. This problem is particularly acute in frugivorous species, which are exposed to energy stress in the face of marked spatial and temporal variations in fruit resources<sup>7-9</sup>. Attempts at estimating the total energetic costs of physiological and behavioral activity in wild mammals have been mostly restricted to small-sized taxa, including rodents, using the doubly-labelled water (DLW) method<sup>10,11</sup>. In larger-sized taxa (i.e., above 2 kg), the costs are generally indirectly estimated, relying on demographic (e.g., mortality rate, litter size), behavioral (e.g., activity budget, parental care) and physiological (resting metabolic rate or RMR) proxies<sup>1,12-16</sup>. However, even the use of RMR can be misleading as the ratio of total energy expenditure (TEE) to RMR varies considerably depending on the body mass of the species and how much energy is invested in adjustments to the ecological and social environment<sup>17</sup>. Among the few large mammals studied, ungulates and carnivores including seals have been the taxa of choice for TEE measurements. More recently, primates have been the focus of attention in this field. They expend much less energy than other placental mammals, which has led to the development of new metabolic evolutionary scenarios for humans<sup>10,11,18</sup>. However, in order to trace the metabolic evolution

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of primates, we need to better understand the relationship between energy budget, lifestyle and environmental constraints. Studies in human and non-human primates show that TEE is primarily determined by body mass (or fat-free mass), with body mass variation accounting for 97% of the variation in TEE in interspecies comparison, controlling for phylogeny<sup>11,18</sup>. Comparisons of mammalian TEE between seasons, between captivity and the wild, and according to activity levels, have led some authors to conclude that energy expenditure varies only within a narrow physiological range (reviewed in<sup>10,19,20</sup>). This 'constrained total energy expenditure' model, highlighted by<sup>11,21</sup>, is exemplified in ring-tailed lemurs in captivity whose energy expenditure for their mass is 20% higher than that of their wild counterparts<sup>19</sup>. Similarly, it has been estimated that the cost of walking and climbing in active chimpanzees and orangutans would represent only 10 to 20% of their total energy expenditure<sup>22,23</sup>, a result that is somewhat counter-intuitive to the common notion of high locomotion costs associated with foraging over large home ranges. Even human hunter-gatherers do not expend more energy than sedentary Western human populations, once the effects of body mass, age and sex are taken into account<sup>19</sup>. It is argued that the existence of physiological limits to TEE is genetically determined and has been shaped by selective pressures<sup>19</sup>. The major effect of body mass on a species' TEE does not rule out the existence of variation, as comparative measurements of TEE among primates show that species deviate positively or negatively from the allometric regression line linking TEE with body mass<sup>18</sup>. For instance, orang-utans expend very little energy compared to other hominoids and, although the measurements were taken in captivity, the interpretation is that their low metabolic rate enables them to cope with the unpredictable and long-lasting food shortage in the tropical forests of South-East Asia<sup>22</sup>. Unfortunately, to date, the relationship between TEE and environmental constraints has not been formally examined in any non-human primate species (with one exception in a species expressing torpor<sup>24,25</sup>).

Lemurs are an ideal model for investigating this functional relationship because they cope with a hyper-variable environment<sup>26,27</sup>. The selective pressures that have influenced the evolution of lemur socio-ecological traits and metabolism are thought to be unpredictable climates (rainfall variability, cyclones) and habitats with highly variable food resources over time<sup>26</sup>. Contemporary lemur communities include species with unique thermoregulatory characteristics among primates, including heterothermic species (*Microcebus* and *Cheirogaleus* spp., *Haplemur griseus*<sup>28–30</sup>) and homeothermic species that deviate from the standard metabolic model (*Eulemur fulvus*, *E. rufus*). Several of them (*Eulemur rufifrons* × *collaris*, *Lemur catta*) subsist on a limited energy budget, according to measurements with doubly labelled water and, when this is not the case, they are capable of consuming less easily digestible resources (the folivorous *Propithecus* and *Lepilemur*<sup>18</sup>). Moreover, mouse lemurs (*Microcebus murinus*) and other solitary cheirogaleids (*Cheirogaleus* spp.) undergo a fattening period prior to the austral winter<sup>29,30</sup>. There is suspicion from field measurements that a few gregarious lemurs (*Lemur catta*, *Propithecus verreauxi*) also store fat. However, in the latter cases, variations in body fat are deduced from isotopic methods performed on only two individuals (*L. catta*<sup>20</sup>), and from measurements of skinfold thickness (*P. verreauxi*<sup>31</sup>) which would need to be validated for the species<sup>32</sup>.

In the present study, we provide quantitative results on the energetics and body composition of a frugivorous/folivorous lemur (*Eulemur fulvus*) subjected to climatic variability but relative resource stability in an anthropogenic habitat in Mayotte. A previous study in a closely related species (*Eulemur rufifrons* × *collaris*) living in a gallery forest in Madagascar suggested the possibility of fattening and reported a thrifty energy budget using isotopic methods<sup>20</sup>. However, as with all TEE measurements carried out in homeothermic primates, the TEE data from the latter population was not analyzed in relation to environmental factors and did not assess the possibility of seasonal variation.

Here, we applied statistical models to identify morphometric, climatic and astronomic drivers of TEE measured during part of the rainy and dry seasons in Mayotte. The TEE measurements, which explicitly included a seasonal factor for the first time, were supplemented by information on group activity and diet, collected using behavioral methods and accelerometry techniques. Furthermore, to test the existence of metabolic flexibility in taxa known for their ecological adaptability, we relied on the contrast in habitat structure and food supply between our site (an agroforestry system) and the gallery forest of the population of *E. × rufifrons × collaris* previously studied<sup>20</sup>. The comparison seems all the more relevant in that individuals of both species, which reproduce seasonally, were tested at the same time in their reproductive cycle, just before the mating period in the wet season (supplemented by the dry season for the Mayotte lemur).

## Materials and methods

### Ethics

All procedures were carried out in accordance to the ARRIVE guidelines and the guidelines for animal experiments of the European Communities Council Directive of 2010 (2010/63/EU). Captures and DLW experiments were approved by the prefecture of Mayotte (#2020/DEAL/SEPR/274), the Cuvier ethical committee of the MNHN and French Ministry of research (MESRI, APAFIS#27331-20200921173365). Agreements were conditional on a limited number of captures.

### Lemur population description and study area

Brown lemurs are primarily arboreal and (sometimes) terrestrial primates that live in small groups and have a highly seasonal breeding season (birth occurs mainly in September/October in Mayotte). The Mayotte lemur has been introduced on the island during the ninth century from *Eulemur fulvus* populations in northwestern Madagascar. The Malagasy and Mayotte groups form a single clade<sup>33</sup>, so the Mayotte lemur does not merit a sub-level taxonomic distinction. Lemurs are well adapted to the island environmental characteristics, with an estimated population of seven tens of thousands of individuals over 376 km<sup>234</sup>. The lemur groups extend well beyond natural forests to occupy all types of forest, agroforests and agricultural areas with some tree cover. Being part of an on-going program on human-primate relationships in Mayotte, the study took place from March to July 2022 in

an agroforestry plot of several hectares dedicated to fruit tree cultivation (Tsararano; 12°49'53" S, 45°10'22.8" E) where 56 individuals were counted. The wooded area is essentially a system of polycultures, mainly orchards, associated with a fairly present tree cover. It is made up of plots of cultivated (e.g., mango tree, guava, *Cythera* prune, star fruit, avocado trees, edible Annonaceae, *Albizia*, etc.), and native trees and vines (*Saba comorensis*), small banana plantations, spaced by more open areas dedicated to the cultivation of passion fruit, pineapple, papaya, and other edible plants intended for cash crops. From four contiguous groups (out of 5 including 11 to 16 individuals per group) strictly foraging within the agroforest area, we captured a total of 17 adults/subadults during two sessions (March and June, corresponding to the end of the wet season with warm months and the early dry season with cool months, respectively). In Mayotte, sub-adults cannot be distinguished by size from adults (i.e., over 3 years old; N = 72; unpublished data, Laurent Tarnaud) but they tend to play more with infants.

### Climate

The climate is characterized by a wet season lasting from October to April, followed by a 5-month dry season. Average annual rainfall is 1637 mm, with an average minimum temperature of 20.1 °C and an average maximum temperature of 30.6 °C (15-year data since 2011, Coconi/Météo France weather station, 4 km from our study site). We extracted from this database the mean rainfall, minimum T°, maximum T° and mean T° data corresponding to each individual experimental session (see below). The daily climate data (rainfall and temperatures) obtained for the study year (2022) did not show any significant deviation from an average year.

Since *Eulemur fulvus* is active both day and night, depending on nocturnal illumination<sup>35</sup>, astronomical data (sunrise, sunset, moon phases, moonrise and moonset) were gathered from the U.S. Navy website (<https://aa.usno.navy.mil/data/>). We calculated a nocturnal luminosity index based on the phases of the moon and the duration of the moon's illumination during the night<sup>36</sup>.

### Morphometrics

Animals were anesthetized by qualified veterinarians (BQ and BL) with a CO<sub>2</sub> injection rifle using medetomidine (0.1 mg/kg) /ketamine (6 mg/kg; Axience). After darting, the animals were taken to an experimental field station located less than 15 min' walk from the capture site (Fig. S11). Their immobilization was prolonged for handling purposes, under gas anesthesia (2.5% isoflurane) to facilitate rapid recovery. They were weighted and skinfold thickness was measured twice to the nearest 0.1 mm using a sliding caliper (Holtain Tanner/Whitehouse) on 4 body areas known to accumulate fat in lemurs<sup>37</sup>: abdomen, arm, hip and back sites. Summing the means of these measures yielded a composite fat score<sup>38</sup>. Additionally, we measured thigh thickness, which is devoid of adipose tissue and potentially reflect muscle activity<sup>37</sup>. We measured body size as crown-rump length (CRL) with an anthropometer, and calculated the Quetelet index (body mass/crown-rump length<sup>239</sup>). The tail of anaesthetized animals was shaved in different patterns to facilitate individual recognition. The animals were released on the same day and at the same place where they were captured (between 2:45 and 5:00 h after their capture), as soon as they were deemed sufficiently alert after recovery from anesthesia. Monitoring of the released animals (by behavioral observation and telemetry; see below) showed that they were generally able to return to their group quickly, without any apparent social disruption.

### Physiology and behavior

Total energy expenditure per 24 h was measured using doubly labelled water (DLW), as described in<sup>20</sup>. Detailed methods can be found in the Supplementary Methods, but in brief, the animals were captured/recaptured between 1 and 11 March during the rainy season, and between 26 June and 4 July during the dry season. No attempt was made to measure TEE of females in June, during the gestation period. Individual TEE was determined over a 3 to 5-day period depending on opportunities to recapture individuals. A short time interval between capture and recapture posed no apparent problems as the lemurs were rapidly alert after anesthesia. The isotopic equilibration time after injection of the isotopic water was determined at 2-h post-dose. Blood samples were taken from the inguinal vein and analyses were performed using isotope ratio mass spectrometry on distilled blood samples. The 2-point method was used for calculation<sup>40</sup> and the food quotient was set according to the diet, one for the dry season and the other for the wet season (Supplementary Methods). CO<sub>2</sub> production was calculated using Speakman's<sup>41</sup> most widely used Eq. (7.17), valid for small mammals weighing around 2 kg (for other equations, see<sup>42</sup>). Total body water, fat-free mass and fat mass were determined from the 18-oxygen dilution space. Lemurs forage as cohesive groups but in order to recapture them in time, six individuals were fitted with a radio-collar (ATS Europe, Oviedo, Spain; model M2940, 58 g), and one individual from each of the 4 focal groups was fitted with a triaxial accelerometer coupled to a GPS (e-obs GmbH, Grünwald, Germany 2020; collar 1AA, 59 g). One additional accelerometer was used alternately on 5 other lemurs in the focal groups, following successive captures and releases. However, due to the restrictive timetable for injections and blood sampling inherent in the isotopic method and the extreme caution required when shooting, it was not possible to recapture all individuals on time. From the 17 individuals captured, 12 were tested for TEE and body composition (6 males and 3 females in March, and 3 males in June).

### Activity

To determine the time budget, we used 5-min instantaneous and scan sampling<sup>43</sup> on the focal groups, each followed continuously from dawn to dusk (> 150 h of monitoring by observer 1). We began recording group activity shortly after the end of the two capture/recapture sessions. Although the timing of the observations and TEE measurements did not strictly overlap, the behavioral recordings remain broadly indicative of the lemur's general activity budget. Behavioral items were categorized as moving, foraging, feeding, resting, social and miscellaneous. The diet was determined by a second observer following simultaneously the same group as observer

1, by recording the feeding duration (minutes) a given individual devoted to each food item during a 30-min period (focal animal sampling, alternating observations between group members). A total of 234 30-min periods distributed among the focal groups were recorded (wet season:  $N = 144$ , dry season:  $N = 88$ ). Dietary diversity in this study population as in many other *Eulemur*<sup>44–46</sup> is low, so we considered that increasing the monitoring effort would have provided little information on the main foods in this study. In order to assess cathemerality (day and night activity, as is the case in other *Eulemur* populations), we recorded 24-h activity data from each of the accelerometer-fitted individuals ( $N = 4$ , one in each of the focal groups) for the duration of the study.

### Statistical analyses

Energy and body composition data were analyzed cross-sectionally due to the limited number of lemurs captured/recaptured at the two study periods. We first performed a PCA on all 12 morphometric and abiotic variables measured, namely body mass, fat-free mass, fat mass, CRL, Quetelet index, skinfold thickness, thigh thickness, mean rainfall, minimum  $T^{\circ}$ , maximum  $T^{\circ}$ , mean  $T^{\circ}$  and the nocturnal luminosity index. The variables retained for subsequent multiple regression analyses and mixed-effects models contributed substantially to three principal components that explained 87% of the variance in the data. The reduction in the number of correlated morphometric variables was carried out using an informed approach, based on the main recognized factors of individual TEE variation (e.g., fat-free mass<sup>11</sup>). Multiple regression models were then constructed from these selected variables, controlling for non-collinearity (variance inflation factor  $< 5$ <sup>47</sup>). Multiple regression analysis was combined with linear mixed-effects modelling to highlight potential differences between groups. As fixed effects, we entered the morphometric and abiotic variables selected above. As random effects, we entered group identity into the mixed-effects model. We checked the normality of the residuals, the homoscedasticity, and the homogeneity of variance. Behavioral data were pooled to determine an activity budget and diet for the population. The sample size did not allow the data to be split by group, but the groups behaved in much the same way (repeated measures ANOVA with permutation<sup>48</sup>). Members of the same group generally synchronize their movements. We used the R and RStudio softwares (versions 4.2.2 and 2023.09.1<sup>49,50</sup>), packages *FactoMineR*<sup>51</sup> and *Rcmdr2.9-2*<sup>52,53</sup> for the descriptive multivariate analyses, *car*<sup>54</sup>, *effects*<sup>54,55</sup>, *lme4*<sup>56</sup> and *lmerTest*<sup>57</sup> for the multiple regression models and mixed models, and *permuco*<sup>58</sup> for the analyses of variance.

## Results

### Activity budget, cathemeral activity and diet

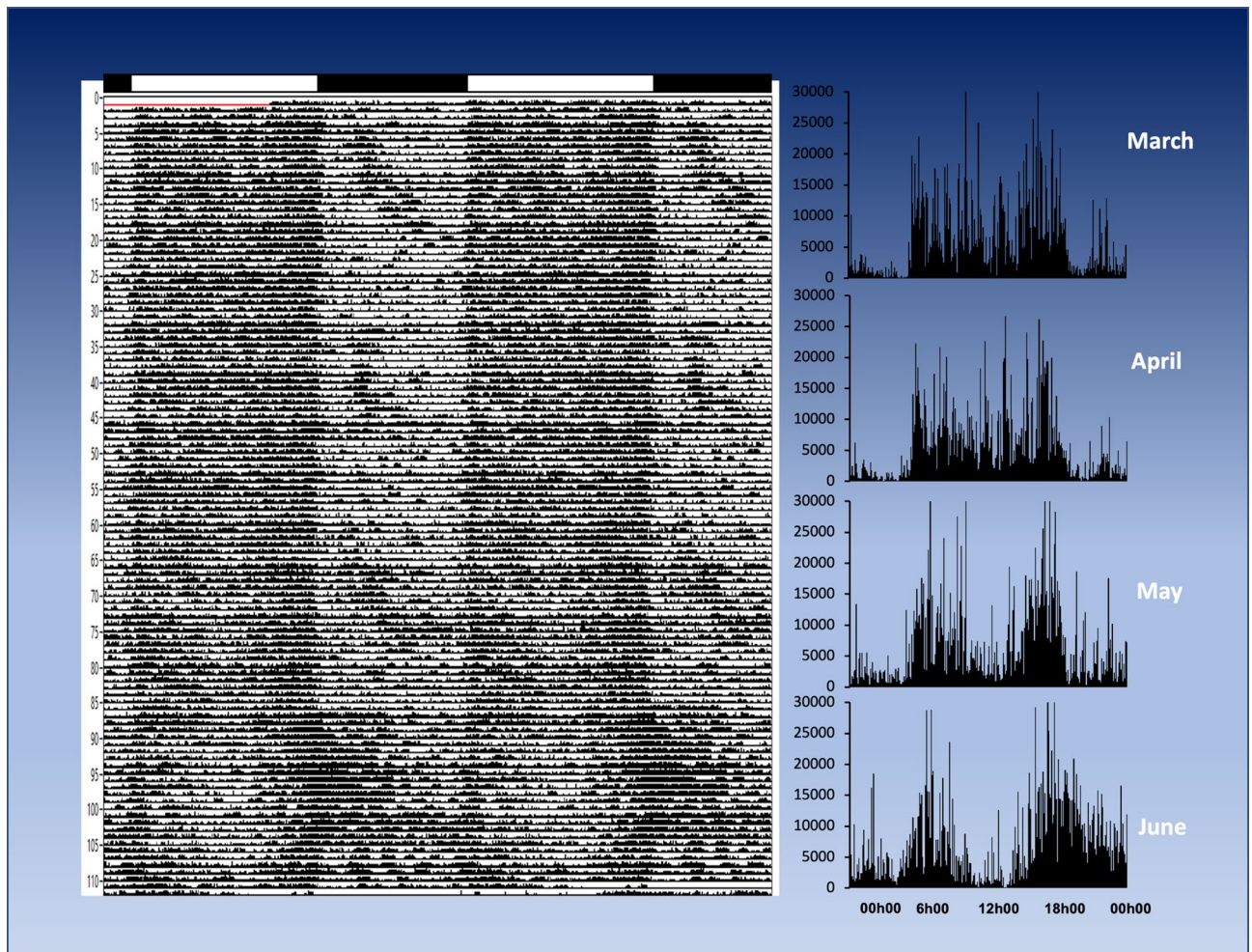
Accelerometry data shows that lemurs are mainly diurnal and are active to a lesser extent at night (Fig. 1). During the daytime period the time allocated to rest is very important (wet month: 44%, dry month: 62%, with no significant difference between groups and seasons,  $p = 0.19$  and  $p = 0.29$ ). The lemurs mainly selected plants grown for their sugar- or fat-rich fruit (88% and 60% of total time spent feeding during the wet and dry seasons, respectively), supplemented by significant leaf matter during dry months (26%). Locomotion for foraging and other purposes accounted for less than 30% of the time budget each season. This, combined with home ranges limited to a few hectares per group (Fig. SI1), indicates a strategy of high energy intake and low foraging costs.

### Morphometrics

No significant sex differences in body mass ( $t = 1.657$ ,  $p = 0.13$ ,  $df = 11$ ) or body size ( $t = 0.718$ ,  $p = 0.49$ ,  $df = 10$ ) were found during the wet months, the only season in which both sexes were captured (Table SI1). In males, body weight decreased by an average of 13% (290 g) between the wet and dry months while body size did not differ (unpaired t-test; body mass:  $t = 2.301$ ,  $p < 0.05$ ,  $df = 15$ ; CRL:  $t = 0.185$ ,  $p = 0.86$ ,  $df = 14$ ). Measurements of skinfold thickness and fat mass proportion (Table SI1 and SI2) indicate that the large seasonal difference in body weight corresponded to a loss of fat mass rather than muscle mass (unpaired t-test, skinfold thickness index:  $t = 6.157$ ,  $p < 0.001$ ,  $df = 15$ ; percent fat:  $t = 2.415$ ,  $p < 0.05$ ,  $df = 10$ ). These data strongly suggest that brown lemurs undergo a fattening period before the dry season. Thigh thickness was positively correlated with fat mass and total body mass, but not with fat-free mass (Spearman's rank correlation;  $p < 0.01$ ,  $p < 0.01$ ,  $p = 0.22$ , respectively).

### Energy expenditure

Detailed physiological and climatic characteristics recorded for each individual during the experimental phase of the study are presented in Table SI2, SI3 and SI4. Mean individual TEE was  $546 \text{ kJ day}^{-1}$  (sd:  $\pm 137 \text{ kJ day}^{-1}$ ;  $N = 12$ ; Table SI3). The TEE of males and females did not differ significantly during the rainy months ( $t = 1.497$ ,  $p = 0.19$ ) but the small sample size may be a limitation to this result. A regression model (model 1) including only the morphometric predictor variables fat-free mass and body size (crown-rump length) explained 56% of the variation in TEE (Table 1). Adding two other morphometric and abiotic factors, thigh thickness and mean maximal temperature (Table SI1 and SI4), increased the fit of the model up to 85% (model 2; Table 1). Fat-free mass was the strongest predictor, with a positive effect, while body size had a negative effect on TEE. The effect of temperature was significant, with each change of one degree Celsius having a fifteen percent impact on total energy expenditure over the range of maximum temperatures recorded during the experiments (27 to 31.5 °C; Fig. 2). Rainfall accounted for a further 3% of the overall fit, but the term was not significant (model 3, Table 1). The addition of the nocturnal luminosity index did not improve the fit of model 3 (adj  $r^2 = 0.88$ ). In the latter case, however, the individual measurements were obtained during sessions where low-light lunar phases, essentially the new moon and the first crescent (Table SI4), are less favorable to the nocturnal activity of these cathemeral lemurs. Linear mixed-effect models including group identity as a random factor yielded non-significant differences with model 2 incorporating only fixed effects ( $p = 0.57$ ; Table SI5).



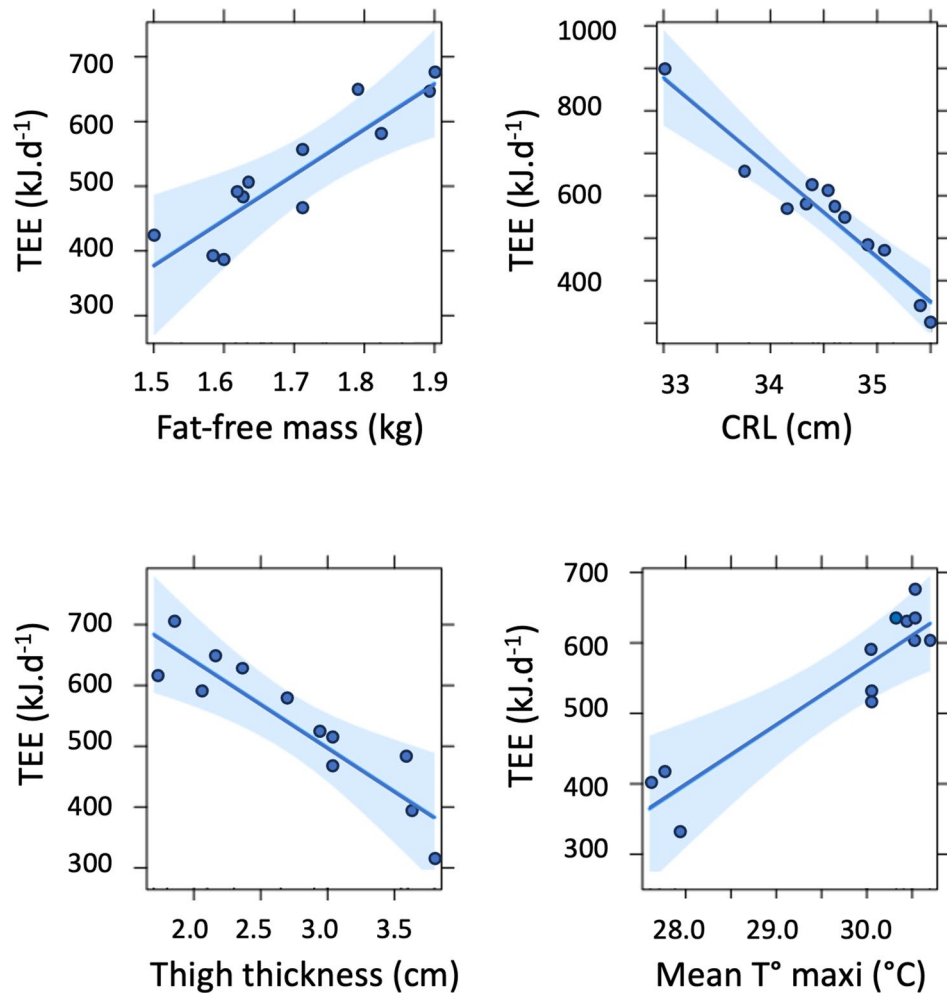
**Fig. 1.** An example of circadian activity rhythm (left) and daily activity profile averaged per month (right) recorded by the accelerometry method. The x-axis of the circadian activity rhythm represents the time of day on two consecutive days. Night and day periods are represented by horizontal black and white bars.

Predictive factor	Model 1				Model 2				Model 3			
	$\beta$	Std. error	t value	P	$\beta$	Std. error	t value	P	$\beta$	Std. error	t value	P
(Intercept)	2048.1	724.8	2.826	*	944.3	533.2	1.774	ns	1750.9	666.8	2.626	*
Fat-free mass (kg)	568.2	220.3	2.579	*	713.5	158.8	4.494	**	617.8	151.3	4.083	**
Crown-rump length (cm)	-68.7	19.4	-3.548	**	-104.5	14.6	-7.176	***	-108.9	13.2	-8.281	***
Thigh thickness (cm)					-139.0	38.3	-3.629	**	-137.1	33.9	-4.036	**
Temperature maxi (°C)					85.0	20.35	4.179	**	66.9	20.9	3.201	*
Cumulative rainfall (mm)									2.3	1.4	1.710	ns
	Adj. $r^2=0.56$ , $df=9$ , $p<0.01$				Adj. $r^2=0.85$ , $df=7$ , $p<0.01$				Adj. $r^2=0.88$ , $df=6$ , $p<0.01$			

**Table 1.** Multiple regression models predicting total energy expenditure.

### Comparison of energy expenditure with other primates and non-primate mammals

The lemurs spent on average  $69 \pm 17\%$  of the energy expenditure predicted by the TEE:mass regression of primates, controlling for phylogeny ( $\log_{10} \text{ TEE (kJ day}^{-1}\text{)} = 0.714 + 0.665 \times \log_{10} \text{ mass (grams)}$ )<sup>18</sup>; Fig. 3). In comparison, the field metabolic rate of adult/subadult brown lemurs (*Eulemur rufifrons* × *collaris*) living in a gallery forest in southern Madagascar (Berenty reserve; calculation from Tables 1 and 2 in<sup>20</sup>) is  $79 \pm 10\%$  of the energy expected for their body mass. The difference between the two lemur populations (based solely on data collected during the same pre-reproductive period, i.e. just before the mating season during the rainy season) is not significant (Student *t*-test on the deviation from the TEE:mass regression,  $t = 1.504$ ,  $p = 0.15$ ,  $df = 18$ ). If we consider not only the wet-season TEE measurements but also the dry-season data for Mayotte lemurs, the difference between species is almost significant ( $t = 2.052$ ,  $p = 0.052$ ,  $df = 22$ ) but remains low, at 12%.

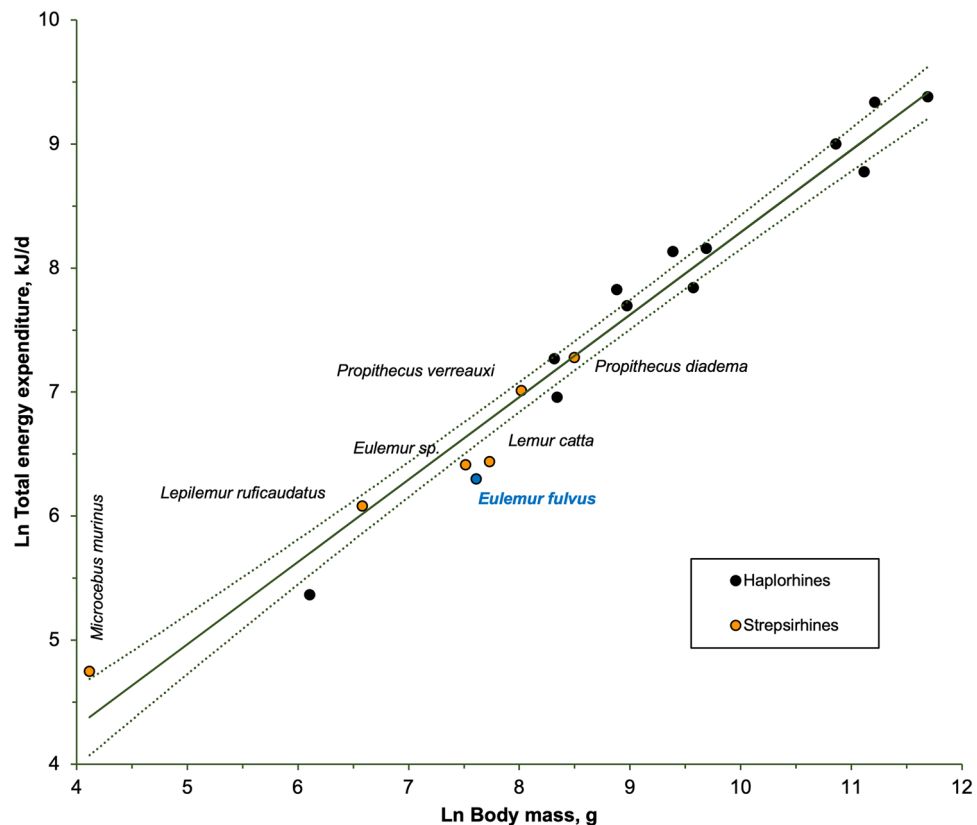


**Fig. 2.** Predictor effect plots of energy expenditure (model 2). Lines and shading in each panel indicate the fitted model and 95% confidence interval, respectively. Dots represent partial model residuals. *TEE* total energy expenditure, *CRL* crown-rump length, *T°* ambient temperature.

Compared with other non-primate placental mammals, the Mayotte lemur and the Berenty lemur are among the eutherians with the lowest rate of energy use, expending only 43% and 50% respectively of the energy expended by a species of similar size (allometric regression, controlling for phylogeny:  $\log_{10} \text{TEE (kJ day}^{-1}) = 0.684 + 0.736 \times \log_{10} \text{mass (grams)}^{59}$ ).

## Discussion

Populations of brown lemurs in Mayotte (Tsararano, *Eulemur fulvus*) and Madagascar (Berenty, *Eulemur rufifrons* × *collaris*) exhibit the lowest TEE recorded for their body mass compared to a set of 18 primate species tested so far with DLW (Fig. 3). It is tempting to conclude that the low field metabolic rate of the brown lemurs studied here is a direct consequence of their lifestyle in a favorable anthropogenic habitat. In fact, their foraging and locomotor activity characteristics do not differ considerably from those of several other *Eulemur* populations. The activity budget and the general typology of the diet are similar between the lemurs of Mayotte and those of Berenty, with a large part of the day spent resting, low dietary diversity and a mainly frugivorous diet supplemented by leaves during the dry season<sup>44,45,60,61</sup>. The brown lemurs of Berenty have larger home ranges<sup>62</sup>, but in southwestern continuous canopy forests in Madagascar, home ranges as low as 1.0 ha have been found, in association with extremely high population densities (*Eulemur rufus*<sup>63</sup>). The broad socio-ecological traits of our lemur population are also similar to those reported in a dry deciduous forest in the south of Mayotte (Saziley): group size and adult sex ratio are comparable to those in the agroforestry plot, and the animals show regular signs of cathemeral activity, with increased nocturnal locomotion during the dry season. In this southern population, the home ranges are also small (< 2 ha), and the poorly diversified diet remains predominantly frugivorous throughout the year<sup>46,64</sup>; see also<sup>65</sup> for more humid habitats). Strikingly, the only other population of *Eulemur* equipped with accelerometers (*Eulemur rufifrons*, Kirindy dry forest, Madagascar) shows a cathemeral activity profile very similar to that found in our study, with predominant daytime activity combined with periods of nocturnal activity circumscribed around the full moon<sup>35</sup>. Finally, variation in climate, mean annual temperature and annual rainfall all fall within the range reported for several *Eulemur* habitats in Madagascar. Accordingly, the



**Fig. 3.** Bi-logarithmic plot of total energy expenditure as a function of body mass in primates, highlighting the low field metabolic rate of the Mayotte brown lemur (blue dot). Each dot represents a species. Orange dots: Strepsirrhines (excepted for the Mayotte brown lemur). Black dots: Haplorrhines. The phylogenetic least square regression line is taken from<sup>18</sup>.

fact that the energy budget of Mayotte lemurs differs little from that of the Berenty population despite variations in habitat structure and composition would confirm the notion of narrow physiological limits for variation in TEE of a species (or of closely related species in the present case). Recent measurements carried out on captive ring-tailed lemurs (*Lemur catta*<sup>66</sup>) show that their TEE differs little from that of their wild counterparts (% deviation from the TEE:mass regression of primates in the ‘Results’ section: 74–81% depending on season versus 71% in Madagascar; calculation from Supplementary data in<sup>20,66</sup>). Brown lemurs in Mayotte and Madagascar are also among the eutherians with the lowest energy budgets. To date, the few other non-torpid large placental mammals with a very low metabolic rate belong to the folivore guild, such as three-toed sloths or giant pandas (e.g., 28% in wild pandas using the equation for non-primate mammals in the ‘Results’ section,<sup>67,68</sup>) and by comparison, other mammals such as koalas expend 51% of the energy expected for their mass (versus 43% and 50% in *Eulemur*; this study). Some believe that cellular metabolic adaptations rather than behavioral adjustments could explain the comparatively low metabolic rates observed in primates<sup>19</sup>. Once phylogenetic group variation is taken into account, fat-free mass is considered one of the main determinants of energy expenditure<sup>11</sup>. In our lemur population, fat-free mass had a strong positive effect on TEE while body size and thigh thickness appeared to be negative predictors of TEE variation. The ‘ideal’ somatic conditions for low energy expenditure therefore seem to be met by animals with low fat-free mass and muscular hind limbs. The fact that thigh thickness had a negative impact on TEE (Table 1) and correlates with fat mass and total body mass (but not with fat-free mass) suggests that adipose individuals need more muscular limbs to support their extra weight, but they could save energy by reducing costly activities such as locomotion.

The fact that body size (CRL) had a negative effect on TEE could be understood in relation to the cost of thermoregulation. Considering the significant effect of ambient temperature on the rate of energy use in this lemur, we might assume that a larger skin surface area, which increases with body size, facilitates cooling by evaporation and leads to lower oxygen consumption. In this respect, the maximum ambient temperatures, which varied between 27 and 31.5 °C during the DLW experimental sessions (Table SI4), were above the thermoneutrality zone recorded in *Eulemur fulvus* (and *E. rufus*; 19–26 °C<sup>69</sup>). During the hottest hours of the day, during the rainy season when temperatures exceed 30 °C (which, in 2022, lasted for at least four months), lemurs display thermoregulatory behavior by resting in the shade of trees and increasing their thermal conductance by adopting relaxed reclining postures and resting against large tree branches, similar to the ‘tree-hugging’ cooling behavior of koalas and sifakas<sup>70,71</sup>. But as they also need to forage to store fat reserves before the dry season and the mating period (in June), in a way comparable to the bulk feeding observed in another *Eulemur*<sup>44</sup>, they remain subject to solar



radiation and potential heat stress<sup>61</sup>; see<sup>68</sup> for a discussion of the neglected risk of hyperthermia). Strikingly, this species deviates from the standard metabolic model in that it shows an extremely depressed metabolic rate (28% of Kleiber) above 30 °C while maintaining its body temperature, and does not increase oxygen consumption when ambient temperatures fall below the thermoneutral zone<sup>69</sup>. This unusual metabolic response, close to that described in sloths<sup>72</sup>, suggests that, for a large part of the year, this homeothermic species incurs high thermoregulatory energy costs, mainly when temperatures are warm. The question may arise as to whether the invoked factor of heat stress is not blurred by the confounding effect of seasonality, the covariates of which are rainfall and food supply. This hypothesis is unlikely since only ambient temperature had an impact on energy expenditure, while rainfall played little role and fruit was available throughout the study due to the temporal staggering of fruit crops. Interestingly, the TEE of captive ring-tailed lemurs living in indoor or outdoor enclosures in the northern hemisphere is slightly higher during the warm season compared with the cold season<sup>66</sup>.

Finally, regarding the link between dietary specialization and metabolism, it should be noted that with the advent of the use of rigorous methods for determining energy expenditure in wild primates, it is now clear that some frugivorous primates (*Eulemur* spp., *Lemur catta*: this study,<sup>20</sup>) rely on energy-saving strategies. This has important implications for scenarios about the evolution of frugivory and primate socioecology, as fruit specialists have long been thought to exhibit high energy input/high energy foraging costs strategies, linked to the search for high quality but spatially and temporally dispersed resources (e.g.,<sup>8</sup>). In fact, the costs of locomotion in primates are probably much lower than expected<sup>22</sup>. Energy-saving strategies in some frugivorous primates have probably been selected when there was a major risk of starvation, resulting from a scarcity of fruit resources over long periods or according to an unpredictable phenological pattern (e.g., in orangutans<sup>22</sup>).

In conclusion, Mayotte lemurs, like Berenty *Eulemur*, display an overall energy-saving strategy compared with other primates, partly linked to a restful lifestyle but mainly a result of physiological adaptations. Regarding the regulation of thermogenesis, brown lemurs do not seem to be as well equipped to withstand high temperatures as they are to react to cool thermal conditions. Their estimated metabolic scope (TEE/RMR), at 2.4 (using 65% of Kleiber<sup>69</sup>), could in this regard be partly the result of a significant allocation of energy resources to thermoregulation. The physiological and behavioral peculiarities of lemurs as a taxonomic group, including heterothermy, a thrifty energy budget and the deviation of certain homeothermic species from the standard metabolic model, suggest that the role of abiotic pressures in the metabolic evolution of this group should be better taken into account, in addition to the drastic dietary constraints often put forward. In the near future, rising ambient temperatures<sup>73</sup> could exacerbate heat stress. To date, little is known about the thermoregulatory capacities of most of these lemur species, although this knowledge is needed to predict their ability to cope with temperature changes.

## Data availability

The data that support the findings of this study are included in the paper or in the online version as supplementary information.

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## Author contributions

B.S., A.Z., S.B., B.Q., B.L. and L.T. conceived and designed this study; B.S., B.Q., B.L., L.T., R.I. and G.C.P. conducted field work; A.Z. carried out laboratory work; B.S., A.Z., B.Q., R.I., G.C.P. and L.T. conducted data analysis; B.S. and L.T. wrote the manuscript; B.Q. and A.Z. reviewed and improved it.

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## Competing interests

The authors declare no competing interests.

## Additional information

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