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Vertical Clingers and Sleepers¹: Seasonal Influences on the Activities and Substrate Use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar

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Key Words

Activity budget · Diet · Field study · Seasonality · Substrate use

Abstract

Lepilemur leucopus was the subject of an 11-month field study at Beza Mahafaly Special Reserve, Madagascar. Radio-tracking provided point samples of activities and foods eaten for the 5 subjects (4 males, 1 female) across the hot, wet season and the cool, dry season. Across all seasons and animals, about 50% of the time was spent resting and/or self-grooming and about 30% of the time feeding. The majority of foods eaten were leaves and species diversity of the diet was low. During the cooler season, all 5 subjects rested significantly more and travelled significantly less than in the warmer season. Across seasons, feeding time did not change significantly. This species appears to cope with a poor quality diet through inactivity which increases during times of thermoregulatory stress. Substrates used were primarily more vertical and of small (<5 cm) diameter. Substrates did not change markedly across seasons.

Introduction

Lepilemur is a particularly interesting genus because it combines small adult body size (446–1,000 g, depending on species) with a diet high in leaves [1]. This puts it, along with *Avahi*, at the lower limit of body size for folivorous primates [2]. Until recently, the only intensive study of *Lepilemur* that was readily available was that of Hladik and Charles-Dominique [3–5]. It was conducted on *Lepilemur leucopus* over a period of approximately 2 months at Berenty, in the southeast of Madagascar. The study period, September–October, was at the driest, but not the coldest, time of the year. The diet of *Lepilemur* was composed primarily of leaves and flowers. Flowers of

¹ Thanks to Judith Masters for this most appropriate description of *Lepilemur*.

the dominant species (*Alluaudia*) were used when leaves were least available. The authors described *Lepilemur* at this site as a 'vertical clinger and leaper'. They suggested that *Lepilemur* copes with a low quality diet and small body size by a combination of low rates of activity, small ranges, a digestive tract with a large hindgut (especially the caecum, which may be adapted to bacterial fermentation or otherwise specialized for digestion of plant structural carbohydrates), and the reingestion of feces (caecotrophy). However, the only quantified data presented to support the claim of a low activity rate came from a single night follow of a single male. No quantified data were presented on substrate use. This team also reports on *Lepilemur* diet from the Marosalaza Forest in western Madagascar [6]. A figure in that report suggests that approximately a quarter of the diet was based on fruit, and mentions that seeds were found in feces, but no other quantified data on diet are presented. In neither study were animals radio-collared for aid in following.

A less accessible study by Russell [7] was subsequently carried out from July–October at the same site at Berenty. The study period encompassed a cool, wet period (July–August) and a warm (not hot, i.e. over 30°C), dry period (September–October) and is the only study which addresses possible seasonal effects on *Lepilemur* behavior. Russell quantified activities, but did not have radio-tracked animals, so he had difficulty staying with his subjects. He argues that *Lepilemur* is not clearly caecotrophic and that it is not more inactive than other lemurs. However, his definition of 'inactive' was restricted to animals at rest, *with eyes closed*. He separated this from 'awake' (animals sitting at rest but with eyes open). It is unclear if his comparative conclusion is warranted (see below). Feeding time was 91% on leaves, 6% on flowers and fruit, and the remainder on latex and bark. The diet was low in diversity: 51% of feeding time was on the leaves of *Alluaudia procera*. Quantified data on substrate use were not presented.

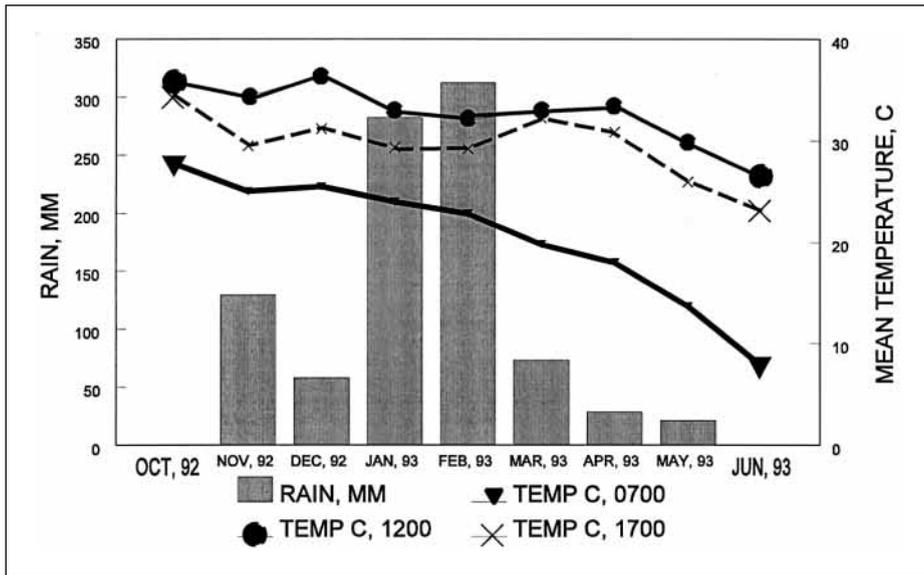
More recently, Ganzhorn [8] has analyzed the quality of the diet of *Lepilemur* and *Avahi* where they are sympatric and in potential competition as members of the folivore guild. Leaves eaten by *Lepilemur* at sites where *Avahi* is present are of lower quality than those eaten by *Avahi* and are of lower quality than those eaten by *Lepilemur* where *Avahi* is absent. No quantified data on activity budgets or substrate use are presented. Warren and Crompton [9] showed that *Lepilemur*, compared to *Avahi* and other arboreal leaping prosimians, moved very little, which minimized energy costs of locomotion. They also report that *Lepilemur* used a diet primarily of low-quality leaves.

If energy minimization is the strategy of *Lepilemur*, it is expected that it would especially reduce activity in the coldest part of the year, when thermoregulation for this small animal might be most difficult. This study will compare data from two seasons of a study of *L. leucopus* at Beza Mahafaly Special Reserve in southwest Madagascar, a highly seasonal habitat. The effect of season on activity budgets, diet, and substrate use will be examined with quantified data based on focal observations aided by radio-tracking of subjects.

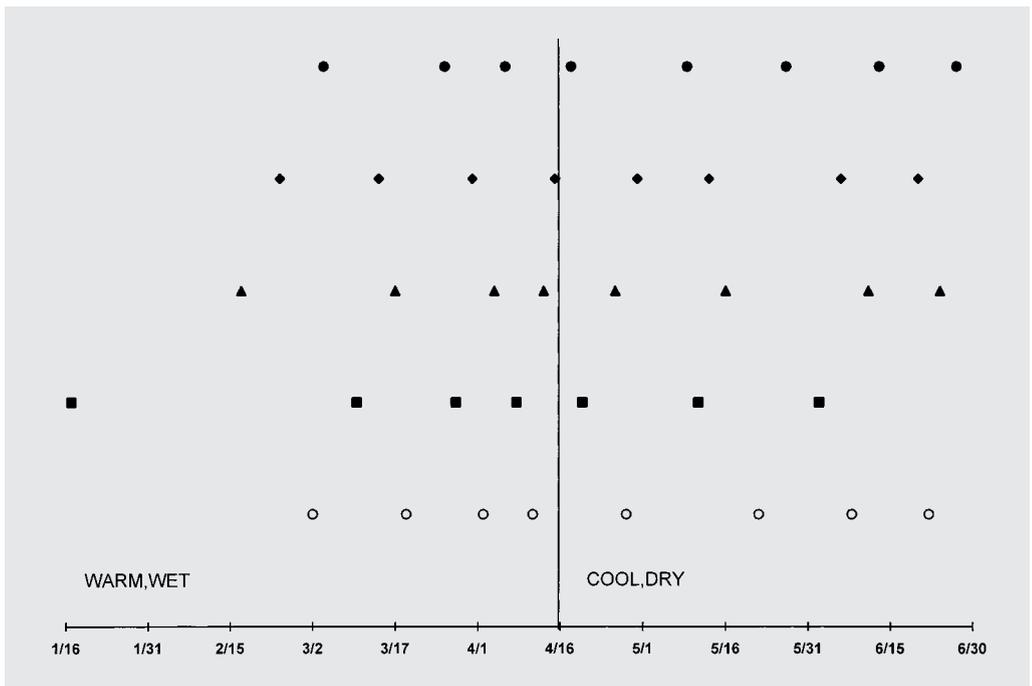
Methods

Study Site and Seasons

The study was done in parcel 1 of the Beza Mahafaly Special Reserve, which is a xerophytic strip of riverine deciduous and semideciduous vegetation dominated by *Tamarindus indica* (kily)



a



b

Fig. 1. **a** Rainfall and temperature (recorded at three times each day), monthly means during the study period. **b** Dates of observations on each subject during each season (female, open circles; males solid symbols with each symbol representing one male). Note (1) two observations of 1 male (squares) in December (3rd and 27th) are not shown, and (2) the horizontal scale range is different from figure 1a.

[10–14]. This is a highly seasonal environment in the driest region of Madagascar. Annual rainfall is highly variable and most rain falls between October and March. The area around the reserve averages 720 mm per year [10]; during another study in October 1987–November 1988, 522 mm of rain fell at the site in a year [14]. During the night, the austral summer minimum temperatures are as low as 21 °C and sink to as low as 3 °C in the austral winter [10]. The total rain between October through May during the study was 906 mm, considerably more than in other years. Changes in rainfall and temperature during the study period are illustrated in figure 1a. Temperatures during the night are best represented by the temperatures recorded at 07.00 h. Since night-time temperatures fell gradually but most sharply in April and main *Lepilemur* foods began to show signs of leaf drop in mid-April, it was somewhat arbitrary as to when to split observations into the ‘warm/wet’ season and the ‘cool/dry’ season. April 15, 1993 was used as the end date for the ‘warm/wet’ season, since this date best equalized the samples between seasons (see below, fig. 1b).

Subjects

The 5 subjects (Ss) included 4 males (520–700 g, median 655 g) and 1 female (585 g). All subjects’ ranges were in the part of parcel 1 nearest the river, where trees were the tallest. Neither identification of an animal’s sex nor individual identification was possible without trapping and artificial marking. Of the 12 Ss ever trapped, 9 were males and 3 were females. Ss were trapped by blow-darting or removing them by hand from a sleeping place during the morning daylight hours. While sedated (telozol or ketamine used), each was fitted with a collar carrying a Telonics radio-tracking transmitter and a tag of colored, reflective beads for individual visual identification. The transmitter also had a small piece of reflective tape applied, which facilitated seeing the animal at night, especially when the S was high in trees. The reflective markers were under the animal’s chin and small, only visible when ‘hit’ with a bright light from below, so it is unlikely they would have assisted predators (e.g. owls) seeing Ss. A variety of body measurements and biological samples were collected upon capture. Animals were returned to their trapping site within 4–6 h of being caught. The entire collar-transmitter package weighed 15–20 g, less than 4% of the animals’ body weight. Attempts to use a back-pack harness were not successful and should not be attempted in the future.

Observation Methods

Observations were conducted between December 3, 1992 and June 27, 1993. Prior to and during the early part of this period (September–November, 1992) considerable time was spent working out methods of capturing animals, of securely attaching radio-tracking transmitters, and in observing unmarked animals. Radio-tracking permitted location of the sleeping site during the day and, if the *Lepilemur* was not in a sleeping hole or a dense tangle of vines, it enabled the observer to see the animal and determine if it was alone. However, the bead identification tag was often invisible under the animal’s chin, as it slept hunched in a ball. At night, animals were followed with a white-headlamp by the author and her assistant. The animals habituated to being followed and observed very quickly, especially if the central, brightest part of the lamp beam was kept off the subject. Focal animal follows were carried out from the time the animal left its sleeping place at dusk to midnight. This was standardized as a stopping time, since a variety of logistical factors precluded all-night follows. In the one all-night follow detailed by Charles-Dominique and Hladik [3], a *Lepilemur* male at Berenty covered 44% of its meters of travel and performed 61% of its time feeding for the night by midnight. Observations on each subject (8–9 follows, about 50 h per S) were spaced approximately equally through time and across seasons (fig. 1b). Observations were frequently disrupted by the higher than usual rainfall, which commonly fell at night.

During focal follows, the position of the animal in its range, its activity, and its positional behavior were recorded at 5-min interval instantaneous scans. The activities were categorized in this analysis as REST (animal alone, not moving, eyes open or closed, including self-grooming), TRAVEL (animal moving within or, more usually, between crowns), FEED (picking, handling, ingesting or clearly chewing food), or OTHER (all else, including all social behavior, vocalizing, and otherwise, mainly excreting). If possible the item fed on was noted. The height, diameter and angle of the support the animal was on was noted. Even with radio-tracking it was easy to lose sight of the animal when it moved. Time out of sight varied with the category of behavior (percent of scans: activity:

11%, height of substrate 14%, angle of substrate 22%, diameter of substrate 24%). This variation was because eye-shine permitted estimation of height and activity but not diameter and angle of support.

Because of the difficulty in seeing the items being fed on at each 5-min interval, feeding was also scored in a 1/0 fashion across each 5-min interval. If two different items were fed on in the same interval, each was given 0.5 score. This was very rare as *Lepilemur* tended to sit for a long time feeding in one place, then leave and feed elsewhere. There was a high positive correlation between the percent of scans where feeding occurred and the percent of 5-min intervals in which feeding occurred across all observations (Pearson's $r=0.78$, $d.f.=40$, $p<0.01$). Consequently, the 1/0 scores are viewed as good estimators of the relative (but not absolute) time spent feeding on different items in each season.

Analysis and Data Presentation

For every S, scores were prepared each season which represented the proportion of good observation time (not total time in focal follow) in each behavior category or using each support category for the three support variables. Since there were only five Ss, the only nonparametric test which could achieve significance at $p<0.05$ was a one-tailed Wilcoxon matched pairs signed-rank test (and only if all 5 Ss changed in the same way between seasons). Only two of the variables had clear one-tailed predictions: it was expected that animals would rest more in cooler weather and, consequently, travel less. Other changes in behavior were expected between the seasons, but it was less clear which direction such changes would take. Consequently, these data are presented for descriptive purposes and the degree of consistency in patterns of change across Ss will be noted.

Results

Seasonal Changes in Activity Budgets

It was predicted that *Lepilemur* would minimize energy expenditure in the cooler season. For all 5 Ss, REST significantly increased and TRAVEL significantly decreased in the cool/dry season as compared to the warm/wet season (table 1). No consistent pattern of behavioral changes occurred across all 5 Ss for the behavior categories of FEED or OTHER.

Diet and Seasons

All Ss ate leaves almost exclusively. These came primarily from *Tamarindus indica* (kily), *Euphorbia tiruculli*, and various vines (primarily *Marsdenia* sp. and *Pentopetia androseifolia*, both of the Asclepiadaceae). New leaves of kily and of *Euphorbia* were eaten, but not to the exclusion of mature leaves. The *Euphorbia* grew with jointed stems, the growing tips of which carried the tiny leaves (when they were present). It was primarily these 'tips' which were eaten. The only non-leaf food seen eaten was *T. indica* flowers (fig. 2). The only indication of fruit eating came in one of 69 fecal specimens examined; it contained many seeds. These seeds resembled those of Cucurbitaceae.

Ss showed considerable individual differences in the most frequent foods used. This appeared to be related to the specific foods abundant in each S's range. For example, one male had particularly large 1/0 feeding scores on *Euphorbia tiruculli*; his range contained a large stand of these trees. Two foods did show consistent feeding differences across seasons. All five Ss ate more *T. indica* leaves and fewer *Marsdenia* sp. leaves in the hot/wet season as compared to the cool/dry season. Two of the major foods, *Marsdenia* and *Euphorbia*, were high latex producers. *Marsdenia* had very large leaves (about the size of a person's hand, local name 'bokabe' translates as 'big leaf')

Table 1. Seasonal differences in behavior and substrate use – median (and range) of percent good observations

		Season	
		cool/dry	warm/wet
Behavior	feed	31 (18–35)	35 (16–40)
	rest*	54 (50–70)	44 (42–66)
	travel*	10 (9–11)	15 (13–17)
	other	5 (2–7)	5 (3–6)
Support category	category interval		
Height, m	0–5	9 (9–35)	7 (0–29)
	> 5–10	39 (26–61)	40 (22–45)
	>10–15	36 (23–46)	46 (28–75)
	>15–20	3 (1–12)	8 (0–11)
Angle, degrees above horizontal	0–20	13 (4–17)	14 (4–17)
	21–40	21 (14–28)	24 (18–29)
	41–60	35 (25–41)	29 (22–39)
	61–90	37 (23–44)	38 (24–39)
Diameter, cm	0–5	67 (11–73)	74 (50–78)
	> 5–10	19 (13–22)	20 (13–33)
	>10–15	7 (4–15)	5 (3–7)
	20–50	4 (2–17)	5 (1–9)

* Significant at $p < 0.05$, one-tailed, $n = 5$ (Wilcoxon signed rank-marked pair tests).

and was available most of the year, in contrast to the smaller leaved vines which were eaten, which were losing their leaves at the start of the cooler season.

Dietary diversity also did not change consistently across the seasons for all Ss. Using the percent of 1/0 feeding scores on the top three food items to estimate diversity, three Ss increased diversity in the cool/dry season and two Ss decreased it (median, range: hot/wet 76%, 73–86%; cool/dry 82%, 75–83%). The percent of scores devoted to the single most eaten species was higher in the cool/dry season than in the warm/wet season for three Ss and lower for two Ss (median, range: hot/wet 39%, 27–62%; cool/dry 51%, 27–65%). In the warm season, the single most eaten species by each S was *Marsdenia* (2 Ss), *Euphorbia* (2 Ss) or kily flowers. Those most eaten in the cool season were *Marsdenia* (3 Ss) and *Euphorbia* (2 Ss).

Substrate Use in Relation to Activity and Season

The first examination of substrate use aggregates the data across all behavior categories (table 1). No pattern of changes in substrate use with seasons occurred consistently across all Ss for any of the substrate use categories (height, angle, or diameter). In general, substrate heights between 5 and 15 m were most frequently used. In this part of the forest, maximum tree heights were about 20 m. More oblique and vertical support angles were used much more than more gently sloped and horizontal supports. By far the greatest preponderance of time was spent on small diameter supports.

Given that behaviors changed with season, it is necessary to see if any shift of substrate use was due to specific activities being associated with specific substrate use

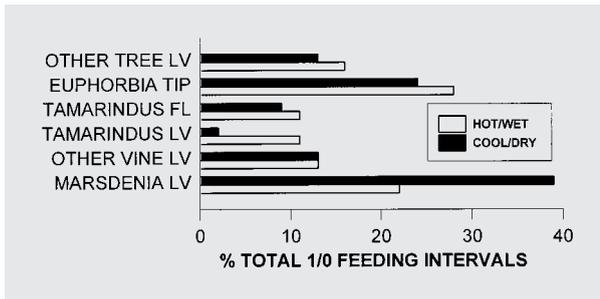


Fig. 2. Percent of total 1/0 feeding records (see text) devoted to each food type in each season. FL=Flowers; LV=leaves; see text for explanation of *Euphorbia* 'tip'.

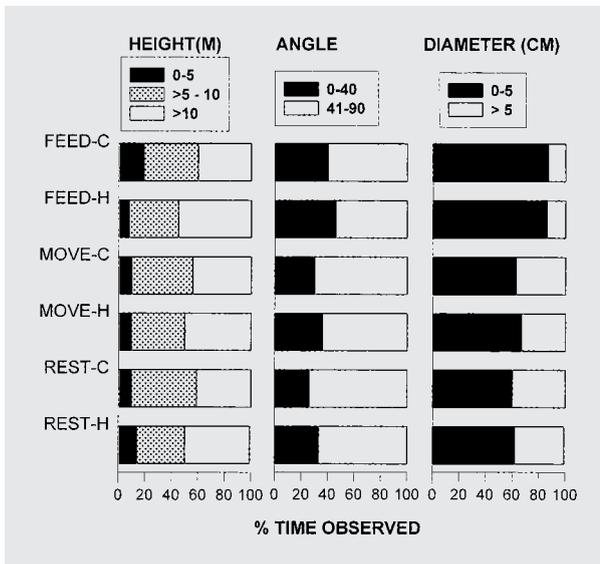


Fig. 3. Percent of activity scan samples in each substrate category, for each activity state and season. C=Cool, dry season; H=warm, wet season; Move=travel.

patterns. In this case (fig. 3), the data are simply the aggregated percents of all observations (across all Ss) in each season for each combination of behavior and substrate use category, and are presented for descriptive purposes only. For simplicity, fewer category intervals are used for each substrate variable than in table 1 and the rare behavior category of OTHER is omitted. In the case of substrate height, there is little difference between behavior categories in the distribution of heights used. During the cool/dry season, slightly less time was spent at the highest level across all behavior categories. For substrate angle, FEED occurred slightly more at more horizontal angles than did TRAVEL or REST. All behavior categories showed a slight increase in time at steeper angles during the cool season. Support diameters showed the largest disparity of use patterns across behavior categories. Small diameter supports were used more to FEED than to TRAVEL or REST. Within each behavioral category, no seasonal differences were apparent.

Discussion

To summarize, the diet of *Lepilemur* at Beza Mahafaly Special Reserve was almost entirely of leaves from two tree species and one vine species. Neither the foods chosen nor dietary diversity changed markedly from the warm, wet season to the cool, dry season. Animals spent the majority of time resting. Feeding time did not change between seasons. During the cold season, resting was more frequent and moving was less frequent than in the warm season. It must be remembered that these 'seasons' did not include data for the end of the dry season, during which time mature leaves would have been at their lowest availability but buds and new leaves would be available [14]. In general, *Lepilemur* sits on what it eats and eats what it sits on.

No major shift in substrate use was found between seasons, despite the shift in activities and the association of differing activities with different 'typical' positional repertoires. Substrate heights between 5 and 15 m, diameters less than 5 cm, and more vertical supports were used most. Feeding occurred more on small diameter and more horizontal supports, while travelling and resting occurred more on somewhat larger, more vertical supports.

Diet

The apparent lack of seasonality of foods used at this site contrast with reports from Berenty where *Lepilemur* was studied in a *Didiereacea* forest. There *Lepilemur* ate flowers when *Alluaudia* leaves were less available. However, opinions differ as to whether food is actually limited at that time [3, 4, 7]. *Lepilemur* at Beza did consume *Tamarindus* flowers, but only 10–12% of the time. Fruit eating at this study site and Berenty was rare, so, at least for *Lepilemur leucopus*, it does not seem that fruit is a 'substantial part' of the diet (contra [15]). Fruit may be more important for other *Lepilemur* species elsewhere [6, 16, 17], but more quantitative data are needed to clarify this claim. The diet of *Lepilemur* at both Beza and Berenty is considerably less diverse than that of either species of the other small-bodied primate folivore, *Avahi* [15,18], or of a larger folivorous lemur, *Propithecus verreauxi verreauxi* [19].

It was not possible to test if the foods eaten changed in quality between the seasons, though in general the quality of *Lepilemur* foods was similar to that reported for the genus elsewhere [8, 20]. It would be interesting to know if leaf quality (though not quantity) might increase during the dry season as some leaves fall and more sunlight is available to the remaining plants carrying leaves. Ganzhorn [21] found that in more open, low-intensity logged forests, where sunlight was more available, leaves had higher protein and sugar concentrations than leaves in unlogged forests, but similar fiber concentrations.

If the quality of food is always low, does this require caecotrophy? Caecotrophy was never *indisputably* seen in the animals at Beza (as distinct from anogenital grooming, Nash [pers. obs.]). Russell [7] has questioned the energetic need and the evidence from behavior and digestive tract morphology for this pattern. In addition, it has more recently been found that some small mammals have considerable ability to capture energy through hindgut fermentation [22] (to which the gut of *Lepilemur*, with its huge caecum, appears to be adapted). This, too, would suggest that caecotrophy might not be required. Definitive work on this issue would probably require captive studies, and, unfortunately, *Lepilemur* have survived very poorly in captivity [23]. Captive studies would also be complicated by the fact that energy balance might not require feces

ingestion and the possibility that, as in other captive primates, coprophagy might develop as an 'abnormal behavior'.

Activity Budgets, Possible Thermoregulatory Costs, and Digestion Limitations

As is true with other folivorous primates, *Lepilemur* is quite inactive [24–26] (table 2). Its activity budget may, in particular, be compared to other small bodied nocturnal primates. *Aotus* comes the closest in size. It spends most of its time active (feeding and moving) with only about 22% of its time resting [27]. The small- (*Galago moholi*, 200 g) and large- (*Otolemur crassicaudatus*, 1,800 g) bodied galagos of South Africa are both species which also must cope with a cold winter [28]. During the winter, the larger species rests about as much as *Lepilemur* did at Beza in the cool season, but this galago rests less than *Lepilemur* in the summer. The smaller galago species rests less than *Lepilemur* in the cool season. Both galagos show a negative relationship between resting and feeding time, but in different seasonal patterns (table 2). Both species probably eat a higher quality diet (gums and insects) than *Lepilemur*, but the exact nature of the quality of gum is unclear [29].

It is hypothesized that *Lepilemur* may be seasonally affected by cold-stress (as opposed to the seasonal heat-stress that may affect diurnal and/or more tropical species) [30, 31]. At Beza, during the day, animals were often seen resting in sunny spots (though near a possible retreat into a tree hole or tangle of branches and vines). They might huddle with another adult during the day, but not all did so. During the night, none of the resting time reported here involved a social huddle. This contrasts with *Avahi* (in the eastern rain forest), which apparently huddled for a substantial portion of its night-time resting, though precise figures are not reported [18].

In addition, *Lepilemur* is very hypometabolic [32], even more so than other lemurs [9, 32, 33]. *Lepilemur* fits at least three of the four hypothesized causes of hypometabolism reviewed by Kurland and Pearson [34]: it may have to cope with thermoregulatory problems in a seasonally arid environment, it is a folivore, and it has a diet 'deviant' in quality from that expected for its body size. At Beza, *Lepilemur* mated during the early part of the cool, dry season, and gave birth during November and December, the period when temperatures were increasing, rainfall usually began, and supplies of leaves were increasing [14]. Thus it would be gestating during the time of maximal cold stress and lowest leaf availability. Some female mammals may raise their metabolic rate during gestation and lactation [31, 35]. This would further increase energy costs. Unfortunately, the only female observed did not have an infant with her during the period of observation, though she was observed to mate on 8 June (during the cool season). However, the study ended prior to the end of the dry season. Young et al. [33] noted that *Lepilemur* did not appear to have the high rate of maternal prenatal investment in reproduction that characterized most other lemurs, though the necessary data on gestation length and neonate body weights for *Lepilemur* are very limited. If *Lepilemur* is on an especially tight energy budget in the cool season (see below), such an increased maternal investment rate during that season might not be possible.

Across other nonhuman primates (table 2), what energy budget trade-offs seem most common? While admittedly a crude estimate, and the data in table 2 are not meant to be exhaustive, there is no correlation across these species in feeding and travel time (Kendall tau=0.135, n=32, p=0.117; *Lepilemur*, galago data, and *C. polykomos* data omitted due to seasonal shifts). In contrast, both feed and travel time are

Table 2. Activity budgets in various folivorous and non-folivorous nonhuman primates¹

Species – season or site	Activities				References
	feed	travel	rest	other	
<i>'Folivores' (by diet and/or gut characteristics)</i>					
<i>Lepilemur leucopus</i> – cool, dry season	31	10	54	5	this study
<i>Lepilemur leucopus</i> – warm, wet season	35	15	44	6	this study
<i>Avahi laniger laniger</i>	22	13	60	5	[18]
<i>Propithecus verreauxi</i> – N, wet/dry seasons	37/30	wet > dry	50/62		[19]
<i>Propithecus verreauxi</i> – S, wet/dry seasons	33/24	wet > dry	57/70		[19]
<i>Procolobus badius</i> Gombe	25	8	54	13	[37]
<i>Procolobus badius</i> Kibale	45	9	38	8	[37]
<i>Colobus guereza</i>	20	6	63	11	[37]
<i>Colobus satanus</i>	23	4	60	13	[37]
<i>Colobus polykomos</i> (ranges across seasons)	27–38	8–16	43–62	1–4	[41]
<i>Presbytis entellus</i>	26	13	42	19	[40]
<i>Presbytis aygula</i>	29	5	63	3	[37]
<i>Presbytis thomasi</i>	32	8	60		[37]
<i>Presbytis pileata</i>	35	18	40	7	[37]
<i>Alouatta seniculus</i>	6	13	78	3	[56]
<i>Alouatta fusca</i> Montes Carlos	11	17	72		[39]
<i>Alouatta fusca</i> Santa Genebra	18	13	64	5	[42]
<i>Alouatta palliata</i>	16	10	66	8	[38]
<i>Brachyteles arachnoides</i> Montes Carlos	28	10	61	1	[39]
<i>Brachyteles arachnoides</i> Barreiro Rico	19	29	49	3	[55]
<i>Gorilla gorilla</i>	55	7	34	4	[36]
<i>'Nonfolivores'</i>					
<i>Galago moholi</i> ² – cool season	43	18	38	1	[28]
<i>Galago moholi</i> – warm season	26	28	44	2	[28]
<i>Otolemur crassicaudatis</i> ² – cool season	20	16	54	10	[28]
<i>Otolemur crassicaudatis</i> – warm season	38	23	35	4	[28]
<i>Lemur catta</i> Berenty	31	13	39	17	[24]
<i>Lemur catta</i> Antserananomby	25	19	41	15	[24]
<i>Lemur fulvus rufus</i> Antserananomby	26	5	57	12	[24]
<i>Lemur fulvus rufus</i> Tongobato	17	20	50	13	[24]
<i>Cercopithecus mitis</i>	36	27	29	8	[45]
<i>Macaca silenus</i>	28	42	25	5	[43]
<i>Aotus trivirgatus</i>	54	21	22	13	[27]
<i>Saimiri sciureus</i>	61	27	11	1	[56]
<i>Saguinus imperator</i>	51	21	25	3	[56]
<i>Saguinus fuscicollis</i>	32	20	44	4	[56]
<i>Lagothrix lagotricha</i>	26	39	30	5	[56]
<i>Cacajao calvus</i>	36	35	29		[56]
<i>Cebus apella</i>	66	21	12	1	[56]
<i>Cebus albifrons</i>	61	21	18		[56]
<i>Ateles belzebuth</i>	15	22	63		[56]
<i>Ateles geoffroyi</i>	28	11	51	7	[56]

¹ Within the diet classes, species are sorted by major adaptive radiation and then approximate body size. The list is not meant to be exhaustive. Examples particularly targeted folivores and similar sized nonfolivores from the same major primate radiations. To the extent possible given definitions in original sources, 'rest' includes self-grooming and 'other' includes social behavior, including social grooming (though some sources incorporated all grooming into one category). In some cases, 'other' was determined by subtraction of sum of other three from 100%. Some of the figures have been estimated from graphs. Original sources should be consulted.

² Taxonomic designations of galagos have been updated based on Nash et al. [58].

negatively correlated with resting, more strongly so for feeding (feed: $\tau = -0.672$, rest: $\tau = -0.393$, $p < 0.001$ in both cases). Thus, across a variety of primates of different sizes and diets, all three activities appear to be available for a trade-off.

Intraspecifically, various patterns of activity budget trade-offs have been reported, but none seems to follow the pattern reported here for *Lepilemur* (no change in feeding time, while rest and move are traded off). Trade-offs have been documented for seasonal changes in activity budgets, and less commonly, across different habitats. Some species appear to vary their activity budget little across seasons (*Gorilla*, *Presbytis pileata*, *Alouatta palliata*, *Brachyteles*) [36–39]. However, *Brachyteles* spent more time both resting and feeding, and less time travelling, in a habitat where food quality (more leaves, less fruit) was low [39]. Gorillas also showed an inverse correlation of feeding time and resting time, and fed for more time in areas where food was less abundant or of lower quality [36]. In other species, there is a negative correlation of resting and feeding time, with little change in travel time, and usually more feeding time when eating lower quality foods (*P. entellus*, *C. polykomos*, *Alouatta fusca*, *M. silenus*) [40–43]. Some show complex seasonal variations in time budgeted to moving, feeding and resting which may vary between age-sex classes, possibly in relation to a complex mix of nutritional and thermoregulatory stresses (*Propithecus verreauxi*, South African galagos and samango monkeys, *Varecia* [19, 28, 44, 45]).

If *Lepilemur* does, indeed, represent a relatively unique pattern among nonhuman primates of not shifting its feeding time while it trades off moving and resting time, this might suggest that it is minimizing energy expenditure but not changing its diet. It is possible that in the cold period it moves as little as possible while eating as much as possible at all times. This could be so if digestive tract limitations in gut capacity, ability to gain net energy from fermentation of leaves, and gut transit time set an upper limit on *Lepilemur* feeding time [46]. Using assumptions about the average amount of metabolizable energy in leaves [22, 46, 47], of metabolic rate based on Schmid and Ganzhorn's recent work [32], and models of digestive strategies for small folivores [22, 46], *Lepilemur* might be predicted to have to consume 20–50% of its body weight in fresh leaves per day. This may not be attainable. Could it be that *Lepilemur* is eating as much as it can, at all seasons, so that the only way it might conserve energy is to rest more, since it is constrained in its ability to acquire more energy? This hypothesis would be supported if it could be shown that diet quality (vs. quantity) was no different between the seasons, but this would require quantified observations at a site with better visibility conditions. Since the structure of the hindgut may allow for selective retention of solutes and finer particles, while larger particles of dietary fiber are more rapidly excreted [46], information on gut transit time of these two fractions of gut contents, while on natural diets, would also be of interest.

Substrate Use

The patterns of substrate use of *Lepilemur* at Beza are similar to those reported elsewhere in confirming the species' vertical clinging habit [6, 8, 9]. Hladik et al. [6] report similar heights and diameters were used by *Lepilemur* at Marosalaza. Warren and Crompton [48] provide detailed quantified data on locomotor patterns for *Lepilemur* at Ampijoroa. They also show that more vertical, very small diameter substrates are most used. Since their data did not cover postural (versus locomotor) behavior (e.g. during rest and feeding) and are reported as proportions of displacements, direct comparisons to the figures reported here are not possible. However, the overall con-

clusions of that study and this are the same. Dagosto [49] also reports that several diurnal lemurs showed a lack of seasonal shifts in positional behavior, in spite of (1) seasonal shifts in activity budgets, and (2) an association of each activity type with different 'typical' positional patterns. The lack of seasonal changes in heights of substrates used contrasts with seasonal variation in feeding height used by South African galagos [28]. This was apparently due to shifts in gum feeding sites. The data presented here provide for comparisons with the substrate use patterns of other nocturnal primates [6, 28, 50, 51] and other prosimians [49]. Quantification of heights used is of interest in interpreting locomotor patterns, but also may be important to other biological differences between species. For example, the ratio of stable carbon isotopes in the hair of *Lepilemur* and two species of sympatric galagos from Kenya reflect the position in the canopy each species most commonly used [52, 53].

Conservation Implications

Milton [54] suggested that animals using a very low quality diet might be particularly vulnerable to occasional mass-starvation if their food crop failed [55]. This area of Madagascar has occasional, relatively unpredictable, periods of drought which may last several years. If future work confirms that *Lepilemur* lives on a very tight energy budget, without much ability to increase the quantity or quality of foods used during the season when it minimizes energy expenditures, it might be at a higher conservation risk than its relatively high population densities indicate. Most *Lepilemur* species are currently listed as 'rare' or 'vulnerable' [17]. They might be more 'vulnerable' than we currently think.

Acknowledgements

This study was supported by the Wenner Gren Foundation, the National Geographic Society and donations of supplies from Nails Pro and 3M Company. It was carried out under an approved animal research protocol reviewed by Arizona State University's Institutional Animal Care and Use Committee. I thank the Government of Madagascar, M. Berthe Rakotsamimana, Ministry of Higher Education, and P. Rakotomanga, School of Agronomy, University of Antananarivo for permission to work at Beza Mahafaly Special Reserve and R. Sussman and A. Richard for their help and enthusiasm for this work at Beza. P. Wright, B. Andriamihaja and S. O'Connor provided invaluable logistic help. For help and companionship in field: R. Randriambololona, T. Bertrand, L. Gould, J. Ratsimbaza, and the entire staff at Beza, especially Enafa, for his expertise with a blow-dart. M. Nash provided the design and installation of solar powering system, as well as infinite support and patience. The organizers of the International Conference on the Biology and Conservation of Prosimians, held at the Chester Zoo provided a superb collegial experience. Helpful comments on the manuscript were made by W. Miller, K. Weisenseel and L. McGeehan.

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