The Influence of Seasonal Availability of Young Leaves on Dietary Niche Separation in Two Ecologically Similar Folivorous Lemurs

Marco Campera

Michela Balestri

Fiona Besnard

Megan Phelps

Faniry Rakotoarimanana

Vincent Nijman

K.A.I. Nekaris

Jörg U. Ganzhorn

Giuseppe Donati

Abstract

Socio-ecological models indicate that diet influences the degree of inter- and intraspecific feeding competition, and consequently group size, ranging patterns, social behaviour, and activity patterns of primates [Wrangham, 1980; Isbell, 1991; Janson and Goldsmith, 1995]. In particular, larger groups are expected to deplete food patches quickly and to compensate the smaller intake per patch by having larger daily ranges and increased travel costs [Janson and Goldsmith, 1995]. It is assumed that folivorous primates, especially in forest habitats, experience limited feeding competition due to the low quality, high abundance, and even distribution of leaves [Wrangham, 1980; Isbell, 1991; Sterck et al., 1997]. For this reason, in socio-ecological models, folivorous primates are expected to be less constrained than frugivorous species to increase group size, resulting in lower predation risk and cohesive groups with relatively egalitarian social relationships [Wrangham, 1980; Isbell, 1991]. Evidence supporting this hypothesis originates from studies that found no relationship between group size and day range or travel cost in folivorous primates [e.g., Isbell, 1991; Janson and Goldsmith, 1995; Korstjens et al., 2002; Robbins et al., 2007].

Keywords

Introduction

In contrast to traditional models, some folivorous primates live in small groups even when they are expected to experience limited feeding competition; this inconsistency has been named the folivore paradox [Steenbeek and van Schaik, 2001]. It has been hypothesised that some folivorous primates experience scramble competition since their food resources vary in quality, availability, and spatial distribution [Snaith and Chapman, 2007]. For example, the food intake of the Ugandan red colobus (*Piliocolobus tephrosceles*) decreases over time despite the increase in daily distance travelled to find food, suggesting that some folivorous primates deplete food patches [Snaith and Chapman, 2005, 2008]. Also, several species of folivorous primates respond to the decrease in food availability by increasing daily distances travelled, number of patches visited per day, percentage of time spent resting, and/or dietary diversity (eastern lowland gorilla *Gorilla beringei* [Ganas and Robbins, 2005]; eastern black-and-white colobus *Colobus guereza* [Harris et al., 2010]; Guatemalan black howler *Alouatta pigra* and Tana River red colobus *Procolobus rufomitratus* [Reyna-Hurtado et al., 2018]). This response to food availability indicates that folivores select leaves with higher quality and have different strategies to deal with decreased availability of high-quality leaves.

Based on the optimal foraging theory, primates may respond to the reduction of food availability and distribution by either minimising their time spent foraging to reach a fixed energy threshold that depends on food availability (time-minimising strategy) or spending as much time as possible foraging to maximise their energy intake (resource-maximising strategy) [Schoener, 1971; Hixon, 1982]. When resource availability is low, resource maximisers spend more time foraging, forage

3

on more feeding trees, and spend less time resting than energy minimisers [Schoener, 1971; Hixon and Carpenter, 1988]. Resource maximisers are thus expected to have similar feeding patterns between seasons of abundance of food resources and lean periods, while time minimisers spend less time foraging and more time resting in lean periods [Schoener, 1971; Nagy-Reis and Setz, 2017].

The optimal foraging theory can be applied to most primate species, but additional complementary models may help to explain feeding behaviours [Garber, 1987]. The diet breadth model, for example, predicts that when preferred food items (i.e., high-quality food item) become scarce and the available food items have a much lower ratio of energy intake to time, dietary diversity increases [MacArthur and Pianka, 1966; Hemingway and Bynum, 2005]. In some cases, the nutrient-balancing strategy (i.e., selecting food items to balance the daily nutrient intake) may better explain dietary patterns than energy-maximising or time-minimising strategies [Felton et al., 2009; Dröscher et al., 2016]. In particular, protein balance has repeatedly been reported to have a central role in the dietary choices of folivorous primates, although other studies reported no selection on proteins (see Ganzhorn et al. [2017] for a detailed review).

The extent to which folivorous primates are influenced by variation of food quality, distribution, and abundance varies between species [Snaith and Chapman, 2007]. Some folivores select high-quality young leaves that are patchily distributed and vary in nutritional quality and availability [Glander, 1982; Harris, 2006]. Even mature leaves, which are expected to be ubiquitous and evenly distributed, may vary vastly in their nutritional quality, and they need to be selected by folivorous primates carefully [Koenig et al., 1998; Koenig, 2000]. Though with some methodological flaws [Wallis et al., 2012], the protein-to-fibre ratio has been considered as a proxy of

leaf quality for primates, considering the importance of protein balance [Oates et al., 1990; Ganzhorn, 1992; Chapman and Chapman, 2002]. Given the negative effect of condensed tannins and polyphenols (e.g., reduce protein availability), leaves with low levels of such secondary compounds should be preferred, although there is evidence that condensed tannins can also have positive effects (e.g., medicinal) [Carrai et al., 2003; Mueller-Harvey, 2006]. Young leaves are considered high-quality and patchily distributed resources for folivores as they usually have higher protein and lower acid detergent fibre contents and secondary compounds than mature leaves [Norscia et al., 2012; Ganzhorn et al., 2017]. More recently, however, Isbell (2012) has reported an alternative hypothesis to patch depletion to explain the need for more patches. She suggested funnelling (i.e., physical constraints that reduce group size when travel routes are narrow and food items are sparse) as an alternative hypothesis to explain the relationship between group size and day range or travel cost in some species. She suggests that for some species, individuals in larger groups will leave the patch and move to next patches more quickly than those in smaller groups because they will be physically pushed forward by succeeding animals. The question of how folivores are constrained by food abundance, quality, and availability is thus open to debate and needs further evidence from other species.

The sympatric lemur genera *Avahi* (Indriidae) and *Lepilemur* (Lepilemuridae) are good models to understand whether food availability constrains folivores since they are both nocturnal, folivorous, and have a comparable body mass [Thalmann, 2001]. The body mass of these two lemur genera is relatively small (ranging from 560 to 1,210 g [Razafindratsima et al., 2018]), which is considered at the lower end for folivory in primates [Kay, 1984; Lehman, 2007], although many small rodents

have smaller body sizes [Foley and Cork, 1992; Verde Arregoitia and D'Elía, 2021], and this limitation might not be supported. Thus, they should be more constrained and compete more compared to other folivores. Previous studies highlighted feeding competition and mechanisms of niche separation between western woolly lemur *Avahi occidentalis* and Milne-Edwards' sportive lemur *Lepilemur edwardsi* in the deciduous forest of Ampijoroa, where both genera occur at high density [Ganzhorn, 1993; Warren and Crompton, 1997; Thalmann, 2001].

We aim to investigate whether the southern woolly lemur, *Avahi meridionalis*, and the Madame Fleurette's sportive lemur, *Lepilemur fleuretae*, in the Ampasy area of the Tsitongambarika Protected Area showed a dietary niche separation and how they were influenced by seasonality of young leaves. The Tsitongambarika lowland moist forest hosts a high density of both *A. meridionalis* and *L. fleuretae* [Campera et al., 2020]. We previously found that the two species separate their times of activity with *A. meridionalis* having more crepuscular activity and *L. fleuretae* having more activity in the central hours of the night [Campera et al., 2019a]. The quality of leaves is also expected to be lower in moist forests than in deciduous forests since leaves in moist forests live longer, have lower nitrogen concentrations, and accumulate secondary compounds over time [Hemingway, 1998; Reich, 2001]. It is thus possible that folivores in moist forests are more constrained by secondary compounds. The two folivores in the Tsitongambarika forest might be influenced by seasonal variations as the forest is located in the southernmost part of Madagascar and is exposed to important photoperiodic variation (from 10.6 to 13.7 h) for a tropical/subtropical rain forest [Campera, 2018]. We expect limited niche separation and no major influence of seasonal variations on the diet and energy expenditure of the two species based on the traditional socio-ecological models [Wrangham, 1980;

Isbell, 1991, 2012; Sterck et al., 1997], or vice versa a large dietary niche separation and significant seasonal variations on the diet and energy expenditure of the two species if they are limited by food availability [Snaith and Chapman, 2005, 2007, 2008; Harris et al., 2010]. We tested these alternative hypotheses by investigating the influence of seasonality on dietary niche separation and breadth, nutritional content of food items, and daily distance travelled (proxy of energy expenditure [Hixon, 1982]) in the two species.

Methods

Study Site

We conducted the study at the Ampasy research station (S 24°34'58'', E 47°09'01''), located in a valley around 3 km^2 in the northernmost portion of the Tsitongambarika Protected Area. The Tsitongambarika forest represents one of the last large expanses of lowland rain forest in Madagascar [Campera et al., 2020]. The annual rainfall during the study period was 2,382 mm, and the average monthly temperature was 21.9°C (range: 18.4–25.0°C); see Campera [2018] and Campera et al. [2019b] for a detailed description of the study area.

Phenological Data Collection

We recorded phenological data via four 500-m trails twice a month from July 2015 to June 2016 (Fig. 1). We tagged adult trees with a diameter at breast height (DBH) larger than 10 cm within 5 m each side of four trails [Chapman et al., 1994; Bollen and Donati, 2005], covering a total area of 2 ha. Since the number of trees along the trails varied between species, we considered up to 5 trees per species randomly selected with a minimum distance of 100 m between individual trees. In

total, we tagged 769 trees corresponding to 200 different species. Seven trees died during the sampling period and were excluded from the analysis. We considered the following phenological phases: leaf flushing (presence or absence of leaf buds or young leaves), flowering (presence or absence of flower buds or open flowers), and ripe fruiting (presence or absence of ripe or fallen fruits). We thus used a binary scoring system for the phenological phases. Tree identification was made in the field using vernacular names obtained from the local guide Mara Berge and matched to the plant list compiled by botanists from Asity Madagascar [A. Ravoahangy, unpubl. report]. We collected herbarium specimens when the vernacular name was not present in the list (63 tree species). Scientific names of these specimens were identified by botanists from the Faculty of Sciences of the University of Antananarivo. Six of these species remained unidentified, and we used vernacular names.

We established 33 plots of 10 × 100 m to estimate density and mean size of the tree species present in the phenological trails. We sampled adult trees with a minimum DBH of 10 cm [Chapman et al., 1994]. Plots were at a minimum distance of 200 m apart to minimise spatial autocorrelation. A total of 165 species out of 200 (82.5%) was present both in the plots and in the phenological trails. For the species not present in the vegetation plots, we estimated the density and DBH based only on the phenological trails. In the case of plants only present in phenological trails, we considered the sum of the total area covered by the plots (3.3 ha) and the area covered by the phenological trails and not overlapping with the plots (1.1 ha) as the total area to calculate the tree density.

Behavioural Data Collection

We collected data on 5 adult individuals of *A. meridionalis* (4 females and 1 male) and 5 adult individuals of *L. fleuretae* (3 females and 2 males). We collected 148.2 h of behavioural data on *A. meridionalis* and 140.4 h on *L. fleuretae* from August 2015 to July 2016 via continuous focal sampling [Altmann, 1974]. During the period of young leaves' scarcity (March-August; Fig. 2), we collected 83.4 h on *A. meridionalis* and 72.3 h on *L. fleuretae*, while in the period rich in young leaves (September-February), we collected 64.8 h on *A. meridionalis* and 68.1 h on *L. fleuretae*. We followed one individual per night. To ensure systematic observations, we equipped the individuals with radiocollars (RI-2D, Holohil System Ltd., 11 g, approx. 1% of animals' body weight). The darting was conducted by an expert team of the Madagascar Biodiversity Partnership that anaesthetised the animals via a dose of 15 mL of Telazol 100 mg/mL (tiletamine HCl and zolazepam HCl; Zoetis Inc.) using a CO_2 air rifle for remote injection [Balestri, 2018; Campera, 2018]. There were no injuries as a consequence of the captures.

We recorded lemur locations every hour via a handheld GPS (Garmin 60CSx). Since direct observations were often impossible in the study area, we mainly recorded lemur locations via the triangulation method [Gese, 2001] from July 2015 to June 2016. With this method, we were able to collect data on multiple individuals each night as the trails used encompassed the home ranges of multiple individuals. Firstly, we flagged the forest trails every 25 m and mapped each flag. To have an accurate fix and to reduce the error in collecting locations via triangulation, we recorded 10 GPS points with an error <6 m for each flag and averaged them. We limited our records to triangulation angles between 30 and 150° [Gese, 2001], and we collected them from dusk to dawn to gather independent data. We plotted bearings using LOAS 4.0 (Ecological Software Solutions) to determine the locations.

9

We collected a total of 822 fixes for *A. meridionalis* (430 during the lean period, 392 during the period of abundance) and 734 fixes for *L. fleuretae* (374 during the lean period, 360 during the period of abundance). We extracted the daily path lengths for each individual with home range tools (HRT 2.0 [Rodgers and Kie, 2011]) for ArcMap 10.2.2 (ESRI, Redlands, CA, USA).

Analysis of the Nutritional Content

During behavioural observations, we collected continuous data on feeding tree species and food categories consumed (mature leaves, young leaves, fruits, flowers and insects). We considered spring buds and leaf shoots as young leaves [Grueter et al., 2009], and used a binocular for the identification of food items when necessary. We analysed the nutritional content of each food item consumed (i.e., the combination of food categories and tree species, e.g., the flower and the young leaves of *Humbertia madagascariensis* are two separate food items). To determine the nutrient content, we collected food samples from the feeding trees when possible. Most individuals fed frequently above 15 m, so most of the food samples were collected the following day on accessible trees of the same species. We air-dried samples under the sun until completely dry and sealed them in plastic bags. We conducted biochemical analyses on dried food samples at the Department of Animal Ecology and Conservation of the University of Hamburg. Nitrogen content was measured by the Kjeldahl method. We obtained neutral and acid detergent fibre via the "Ankom fibre analyser" [van Soest, 1994]. We calculated sugar content as the equivalent of galactose after hydrolysation of 50% methanol extract. We measured condensed tannins as equivalents of quebracho tannin [Oates et al., 1977], and we determined polyphenols following Folin-Ciocalteu [Stolter et al., 2009]. We

determined fat content by extraction using petroleum ether, followed by evaporation of the solvent. A detailed review of the procedures and their biological relevance is provided by Ortmann et al. [2006]. We analysed alkaloids qualitatively via triple assays with Mayer's, Dragendorf's, and Wagner's reagents [Cromwell, 1956], and we considered a sample to contain alkaloids when at least one of the reagents showed a positive reaction.

Data Analysis

We calculated the food availability index (FAI) as the product of stem density (trees/ha) and the phenological score for each species (modified from Guo et al. [2007]). To obtain the phenological score, we calculated the proportion of trees with young leaves, flowers, or ripe fruits for each species and multiplied by the mean DBH for that species. We did not estimate a score for the quantity of leaves, flowers, and ripe fruits since these measures were unreliable in the study area due to the low visibility of canopy and emergent trees. Also, the number and weight of fruits on trees were very variable between species, thus adding unreliability for a fine-grained quantitative score. For this reason, we preferred to include the mean DBH for each species in the formula as a proxy of tree productivity [Chapman et al., 1994]. The density of trees varied from 0.22 to 60.61 ind./ha (mean: 4.74 ± SE 0.65 ind./ha) and the mean DBH varied from 1.06 to 5.19 cm (mean: 1.87 ± SE 0.04 cm). Thus, DBH could substitute the phenological score in the formula to calculate FAI since also the phenological score usually varies between 1 and 5 [e.g., Fashing, 2001]. We calculated the highest possible FAI, called total FAI, by adding the maximum FAI for all the species (online suppl. material; for all online suppl. material, see www.karger.com/doi/10.1159/000517297). We calculated a monthly percentage for

each phenological phase with the following formula: Σ monthly FAIi/total FAI × 100, where the monthly FAIi is the monthly FAI for the species i considering the 200 tree species.

To determine the diet of the two lemur species, we calculated the proportion of time spent feeding (in seconds) on each food item over the total amount of time spent feeding in the two periods (lean and rich, based on the availability of young leaves). We obtained the total proportion of each food category in the diet during each period. We then calculated the dietary overlap between the two species in the two periods via the Pianka index of dietary overlap [Pianka, 1973]. Pianka's index (O) varies between 0 (total separation) and 1 (total overlap). We also determined the dietary breadth during the two periods via the standardised Levin's index (B$_{sta}$) applied to the proportions of food items consumed. The standardised Levin's index ranges from 0 (minimal niche breadth) to 1 (maximal niche breadth) [Levins, 1968].

To investigate whether there was a difference in the selection of food items between periods and species based on their nutritional content and availability, we ran Spearman correlations with the proportion of time spent feeding on a food item as dependent variable and the availability and nutritional content of food items as independent variables. We corrected the p value (i.e., q value) with a Benjamini-Yekutieli correction to avoid a type I error in multiple hypotheses testing and considered the q value <0.05 for significance [Benjamini and Yekutieli, 2001]. To investigate whether feeding and resting time were different between seasons, we ran generalised linear mixed models via the "glmmPQL" command in the package "MASS" with season (rich/lean) as a fixed factor and individual as a random effect. We fitted the dependent variables in the previous models to a quasibinomial family since the values were proportions with overdispersion [Zuur et al., 2009]. We ran

12

general linear mixed models via the "lmer" command in the package "lme4" to evaluate differences in daily distance travelled (monthly average per animal) with season (rich/lean) as fixed factor and individual as random effect. We used R version 3.5.1.

Results

Phenological Patterns

The lowland rain forest of Ampasy exhibited a seasonal pattern for the three phenological phases (Fig. 2). The peak of leaf flushing occurred between October and January for most of the species (60.5–75.5% of the total FAI), while the period of low leaf flushing lasted from March to August (less than 30% of the total FAI). The peak of flowering occurred in November-December for most of the species (59.2–62.9% of the total FAI), while the period of low flowering lasted from February to September (7.6–10.7% of the total FAI) with a small increase in May (14.4% of the total FAI). The peak of ripe fruiting occurred from December to February (44.2–58.0% of the total FAI) with the highest percentage in January. The period of low ripe fruiting lasted from April to October (5.1–12.0% of the total FAI).

Diet and Daily Distances Travelled

We recorded 19 food items during the lean period and 15 during the rich period for *L. fleuretae*, while 25 food items during the lean period and 32 during the rich period were observed for *A. meridionalis*. The diet of *A. meridionalis* was exclusively folivorous, with a higher consumption of young leaves during the rich period. Conversely, *L. fleuretae* was almost exclusively folivorous during the lean period, while it consumed also flowers (42.3%) and fruits (13.5%) during the rich

period, with an additional 0.2% of its time spent eating insects. The two lemur species showed a moderate dietary overlap during the lean period (37%) and very limited overlap during the rich period (6%). The dietary breadth in *A. meridionalis* was larger during the rich period, while *L. fleuretae* did not change its dietary breadth over the year (Table 1). The food items consumed during the lean and rich periods by the two species were not significantly different in nutritional content (Table 2). The time spent feeding on food items was not influenced by the availability and nutritional content of food items in both species, apart from a selection of leaves based on high nitrogen and low polyphenols by *A. meridionalis* during the rich period (Table 3). Only one food item consumed by both species (the young leaves of *Sarcostemma viminale*) contained alkaloids.

Avahi meridionalis fed more (β = –0.63 ± SE 0.24, *p* = 0.014; random effect covariance: estimate = 0.01 ± SE 0.01, *p* = 0.302) and rested less (β = 0.50 ± SE 0.22, *p* = 0.048; random effect covariance: estimate = 0.01 ± SE 0.02, *p* = 0.525) during the period of food abundance than during the lean period. *Lepilemur fleuretae* did not change feeding (β = –0.43 ± SE 0.30, *p* = 0.160; random effect covariance: estimate = 0.01 ± SE 0.02, *p* = 0.544) and resting (β = 0.17 ± SE 0.30, *p* = 0.574; random effect covariance: estimate = 0.01 ± SE 0.02, *p* = 0.688) over the year. The daily distances travelled by *A. meridionalis* were longer during the season of food abundance than the lean season (β = –7.35 ± SE 2.87, *p* = 0.012; random effect covariance: estimate = 37.16 ± SE 30.29, *p* = 0.220), while for *L. fleuretae* there was no statistical difference (β = –5.17 ± SE 4.61, *p* = 0.265; random effect covariance: estimate = 158.52 ± SE 128.44, *p* = 0.217).

Discussion

We found that *A. meridionalis* and *L. fleuretae* at Ampasy showed little dietary overlap, especially during the period of food abundance, and used strategies to face lean periods. These observations suggest that the strategies of these two folivorous species are shaped by food availability in a similar way to frugivorous primates [Snaith and Chapman, 2005, 2007, 2008; Harris et al., 2010]. However, overall the two species did not select their food items based on food availability or nutritional content, and only *A. meridionalis* selected leaves high in nitrogen and low in polyphenols during the period of abundance. This finding is partially in accordance with Chapman and Chapman [2002], who found no avoidance of secondary compounds in the western red colobus *Procolobus badius*. Other studies on Indriidae, however, found a clear selection of leaves based on their nutritional content: *A. occidentalis* [Thalmann, 2001]; indri *Indri indri* [Powzyk and Mowry, 2003]; Verreaux's sifaka *Propithecus verreauxi* [Norscia et al., 2006], summarised in Ganzhorn et al. [2017]. A possible explanation for this pattern is that food availability of nutritious food items is particularly high at Ampasy. The selection of high-quality food is, in fact, required only when the food items in the environment have average protein concentrations below the required needs [Ganzhorn et al., 2017]. It would be important, in future studies, to control for the nutritional content of non-food items to check for the hypothesis that food items are particularly nutritious at Ampasy. This hypothesis is still partially supported by the fact that the nutritional contents of food items fed on by the two species at Ampasy are rich in nitrogen and low in secondary compounds and alkaloids when compared to the items consumed by *A. meridionalis* in the littoral forest of Sainte Luce that is located around 30 km south of Ampasy

[Norscia et al., 2012]. There, items eaten contained only an average of 0.9% nitrogen (vs. approx. 1.6% at Ampasy), which should be at the lower end of primate nitrogen requirements [Oftedal, 1991].

Common strategies used by primates to face lean periods include increasing time spent foraging [Garber, 1993], reducing their activity to conserve energy [Oates, 1987], increasing dietary breadth [Nagy-Reis and Setz, 2017], switching their diet by including different food items [McConkey et al., 2002], and relying on fall-back species [Terborgh, 1983; Brockman and van Schaik, 2005; Hemingway and Bynum, 2005]. Our data indicate that the primary diet of *A. meridionalis* and *L. fleuretae* converges or diverges over the year, with young leaves as preferred food items during the period of abundance for the former and a combination of young leaves, flowers, and ripe fruits for the latter. The dietary overlap between the two species at Ampasy was slightly higher than between *A. occidentalis* and *L. edwardsi* in the deciduous forest during the lean period (0.37 vs. 0.33), while it was lower during the period of abundance (0.06 vs. 0.14) [Thalmann, 2001]. These values represent in general a low dietary overlap between *Avahi* and *Lepilemur*, which is similar to what was found in other sympatric folivores like colobines (Mentawai langur *Presbytis potenziani* and pig-tailed langur *Simias concolor* – 0.32 [Hadi et al., 2012]). During the lean period, the diets of the two lemurs converge, and they seem to shift to the same fall-back food (i.e., mature leaves) when the preferred food is not available [Markham et al., 2013]. Furthermore, *A. meridionalis* reduces its activity to conserve energy, while *L. fleuretae* switches its diet between periods while still maintaining a similar energy expenditure.

The lower feeding time, the higher resting time, and the shorter daily distances travelled by *A. meridionalis* during the lean period as compared to the

period of food abundance provide evidence of a time-minimising strategy [Hixon, 1982; Hemingway and Bynum, 2005; Nagy-Reis and Setz, 2017]. *Avahi* spp. have an expensive locomotion as vertical clingers and leapers [Warren and Crompton, 1998] and this, coupled with the low-energy strictly folivorous diet, may explain why this genus relies heavily on energy-minimising strategies [Warren and Crompton, 1998; Norscia et al., 2012]. Conversely, *Lepilemur* spp., despite being also vertical leapers, usually have a less expensive locomotion than *Avahi* spp. since they climb more [Warren and Crompton, 1998]. We must note, however, that it is difficult to discern the importance of young leaf availability from the effect of low temperatures and thermoregulatory costs as periods of low food availability were coincident with periods of low temperatures in the study area [Donati et al., 2011; Campera, 2018]. Contrary to *A. meridionalis*, the highly folivorous guerezas *Colobus guereza* showed a resource-maximising strategy with an increase in daily distances travelled, time spent feeding, number of feeding patches visited, and dietary breadth during the period of scarcity of the preferred food items [Harris et al., 2009]. A similar resource-maximising strategy was found in *C. angolensis*, mainly linked to high-quality specialist diet and a clumped distribution of their main food items [Arseneau-Robar et al., 2021]. This difference might be explained by the fact that *C. angolensis* and *C. guereza* are highly specialised (they mainly rely on a few food items when available, thus needing to travel longer distances when these food items are scarce), while *A. meridionalis* at Ampasy is more of a generalist folivore since it forages on a wide range of plant species. The generalist *Alouatta palliata*, however, travelled longer distances to reach preferred food items despite having other food sources nearby [Hopkins, 2016]. A time-minimising strategy may be due to the usually low metabolism of lemurs [Wright, 1999] and the fact that an energy maximiser strategy

may increase predation risk, thus becoming disadvantageous in a cryptic species [Kie, 1999].

The diet of *L. fleuretae* can be described as generalist as it was rich in flowers and fruits when compared to the diet of other more folivorous *Lepilemur* spp. (0.4–14.5% [Nash, 1998; Thalmann, 2001; Dröscher and Kappeler, 2014; Seiler et al., 2014; Dinsmore et al., 2016]). We have to note that sportive lemurs have usually a more generalist diet than woolly lemurs also in other habitats in Madagascar [Warren and Crompton, 1997; Thalmann, 2001]. This might be because *Avahi* spp., living in pairs, win the competition for high-quality leaves against the solitary *Lepilemur* spp., so sportive lemurs are pushed towards a more generalist diet. In addition, *L. fleuretae* can be more generalist than other sportive lemurs, and it appears to be mainly solitary as we never recorded focal animals sleeping together with pair mates, contrary to other sportive lemurs (e.g., *L. edwardsi* and *L. ruficaudatus* [Kappeler, 2014]). It would be interesting to compare the diet with other populations of *L. fleuretae* not in sympatry with *A. meridionalis*. The difference in diet might also indicate that *L. fleuretae* at Ampasy had a higher energy expenditure than other sportive lemurs. This interpretation was indirectly confirmed by the distances travelled at night, which were longer in *L. fleuretae* (approx. 660 m) than in the other species of the same genus for which these data are available: *L. edwardsi* (approx. 350 m [Warren and Crompton, 1997], red-tailed sportive lemur *L. ruficaudatus* (approx. 400 m [Ganzhorn et al., 2004]), Sahamalaza sportive lemur *L. sahamalaza* (approx. 260 m [Mandl et al., 2018]). Flowers and fruits usually have a clumped distribution [Isbell, 2012], which might have contributed to the longer distances travelled per night, especially considering that *L. fleuretae* at Ampasy was highly selective on flowers and ripe fruits (i.e., *Syzygium* sp. and *Rothmannia* sp. were the

preferred trees for ripe fruits, and *Albizia* sp. and *H. madagascariensis* were the preferred trees for flowers).

In conclusion, we highlighted the influence of food availability and interspecific competition on the behavioural ecology of the strictly folivorous *A. meridionalis* and the moderately folivorous *L. fleuretae*. There was, however, no evident selection based on the nutritional content of food items, apart from *A. meridionalis* during the rich period. This pattern may be the consequence of a particularly high number of plant species that are highly nutritious at Ampasy. In addition, the time-minimising strategy found in *A. meridionalis* might be the consequence of thermoregulatory strategies and not necessarily related to a strong influence of food limitations. It is unclear why, however, *L. fleuretae* did not show a time-minimising strategy as other *Lepilemur* spp. (e.g., *L. leucopus* [Bethge et al., 2017]; *L. sahamalaza* [Mandl et al., 2018]). This genus has received relatively little attention in moist forests, so we cannot exclude that the pattern we observed is not uncommon in this habitat. What is clear from both species, is that: (i) when available, young leaves are the prevalent food item of their diet; (ii) there is a strong niche separation between the two species, and this brought differences in diet (*L. fleuretae* consume more flowers and fruits than other *Lepilemur* spp. in other sites) and time of activity (*A. meridionalis* has a considerable proportion of activity during the day [Campera et al., 2019a]). We suggest that the availability of young leaves is important in shaping several aspects of the ecology of sympatric folivorous species, and it is important to consider the fluctuation of this resource to interpret the feeding strategy of these species and their niche boundaries.

Acknowledgements

Statement of Ethics

We obtained permission for the field research from the Ministry of Environment and Forests of Madagascar (53/16/MEEMF/SG/DGF/DAPT/SCBT.Re; 54/16/MEEMF/SG/DGF/DAPT/SCBT.Re). All procedures performed in studies involving animals were in accordance with the ethical standards of Oxford Brookes University following the "Guidelines on the observation, handling and care of animals in field research."

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

Funding Sources

Author Contributions

M.C., M.B., and G.D. conceived and designed the research. M.C., M.B., F.B., and M.P. conducted the research. M.C., M.B., J.G., and G.D. analysed and interpreted the data. F.R., V.N., and K.A.I.N. contributed to the interpretation of the data. M.C., M.B., and G.D. led the writing of the manuscript. F.B., M.P., F.R., V.N., K.A.I.N., and J.G. revised the paper critically for important intellectual content. All authors gave final approval for publication.

References

Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.

Arseneau-Robar TJM, Changasi AH, Turner E, Teichroeb JA (2021). Diet and activity budget in *Colobus angolensis ruwenzorii* at Nabugabo, Uganda: are they energy maximizers? *Folia Primatologica* 92: 35–48.

Balestri M (2018). *Ecology and Conservation of the Southern Woolly Lemur (*Avahi meridionalis*) in the Tsitongambarika Protected Area, South-Eastern Madagascar*. PhD dissertation, Oxford Brookes University.

Benjamini Y, Yekutieli D (2001). The control of the false discovery rate in multiple testing under dependency. *Annals of Statistics* 29: 1165–1188.

Bethge J, Wist B, Stalenberg E, Dausmann K (2017). Seasonal adaptations in energy budgeting in the primate *Lepilemur leucopus*. *Journal of Comparative Physiology B* 187: 827–834.

Bollen A, Donati G (2005). Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica* 37: 32–43.

Brockman DK, van Schaik CP (2005). *Primate Seasonality: Studies of Living and Extinct Human and Non-Human Primates.* Cambridge, Cambridge University Press.

Campera M (2018). *Ecological Flexibility and Conservation of Fleurette's Sportive Lemur,* Lepilemur fleuretae*, in the Lowland Rainforest of Ampasy, Tsitongambarika Protected Area*. PhD dissertation, Oxford Brookes University.

Campera M, Balestri M, Chimienti M, Nijman V, Nekaris A, Donati G (2019a). Temporal niche separation between the two ecologically similar nocturnal primates *Avahi meridionalis* and *Lepilemur fleuretae*. *Behavioural Ecology and Sociobiology* 73: 55.

Campera M, Phelps M, Besnard F, Balestri M, Eppley TM, Nijman V, et al (2019b). Does forest management and researchers' presence reduce hunting and forest exploitation by local communities in Tsitongambarika, south-east Madagascar? *Oryx* 53: 677–686.

Campera M, Santini L, Balestri M, Nekaris KAI, Donati G (2020). Elevation gradients of lemur abundance emphasise the importance of Madagascar's lowland rainforest for the conservation of endemic taxa. *Mammal Review* 50: 25–37.

Carrai V, Borgognini-Tarli SM, Huffman MA, Bardi M (2003). Increase in tannin

consumption by sifaka (*Propithecus verreauxi verreauxi*) females during the

birth season: a case for self-medication in prosimians? *Primates* 44: 61–66.

Chapman CA, Chapman LJ (2002). Foraging challenges of red colobus monkeys:

influence of nutrients and secondary compounds. *Comparative Biochemistry

& Physiology Part A Physiology* 133: 861–875.

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR (2004).

Predicting folivorous primate abundance: validation of a nutritional model.

American Journal of Primatology 62: 55–69.

Chapman CA, Wrangham R, Chapman LJ (1994). Indices of habitat-wide fruit

abundance in tropical forest. *Biotropica* 26: 160–171.

Crockett CM, Janson CH (2000). Infanticide in red howlers: female group size, group

composition, and a possible link to folivory. In *Infanticide by Males and Its

Implications* (van Schaik CP, Janson CH, eds.), pp 75–98. Cambridge,

Cambridge University Press.

Cromwell BT (1956). The separation, micro–estimation and distribution of the

alkaloids of hemlock (*Conium maculatum*). *Biochemical Journal* 64: 259–266.

Dinsmore M, Louis EE Jr, Randriamahazoamanana D, Hachim A, Zoanarivelo JR,

Strier KB (2016). Variation in habitat and behavior of the northern sportive

lemur (*Lepilemur septentrionalis*) at Montagne des Français, Madagascar.

Primate Conservation 30: 73–88.

Donati G, Ricci E, Baldi N, Morelli V, Borgognini-Tarli SM (2011). Behavioral

thermoregulation in a gregarious lemur, *Eulemur collaris*: effects of climatic

and dietary-related factors. *American Journal of Physical Anthropology* 144:

355–364.

Dröscher I, Kappeler PM (2014). Competition for food in a solitarily foraging folivorous primate (*Lepilemur leucopus*)? *American Journal of Primatology* 76: 842–854.

Dröscher I, Rothman JM, Ganzhorn JU, Kappeler PM (2016). Nutritional consequences of folivory in a small-bodied lemur (*Lepilemur leucopus*): effects of season and reproduction on nutrient balancing. *American Journal of Physical Anthropology* 160: 197–207.

Fashing PJ (2001). Feeding ecology of guerezas in the Kakamega forest, Kenya: the importance of Moraceae fruit in their diet. *International Journal of Primatology* 22: 579–609.

Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Lindenmayer DB (2009). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology* 20: 685–690.

Foley WJ, Cork SJ (1992). Use of fibrous diet by small herbivores: how far can the rules be "bent"? *Trends in Ecology and Evolution* 7: 159–162.

Ganas J, Robbins MM (2005). Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: a test of the ecological constraints model. *Behavioral Ecology and Sociobiology* 58: 277–288.

Ganzhorn JU (1992). Leaf chemistry and the biomass of folivorous primates in tropical forests. *Oecologia* 91: 540–547.

Ganzhorn JU (1993). Flexibility and constraints of *Lepilemur* ecology. In *Lemur Social Systems and Their Ecological Basis* (Kappeler PM, Ganzhorn JU, eds.), pp 153–165. New York, Plenum Press.

Ganzhorn JU, Arrigo-Nelson SJ, Carrai V, Chalise MK, Donati G, Droescher I, Eppley TM, Irwin MT, Koch F, Koenig A, Kowalewski MM, Mowry CB, Patel ER, Pichon C, Ralison J, Reisdorff C, Simmen B, Stalenberg E, Starrs D, Terboven J, Wright PC, Foley WJ (2017). The importance of protein in leaf selection of folivorous primates. *American Journal of Primatology* 79: 1–13.

Ganzhorn JU, Pietsch T, Fietz J, Gross S, Schmied J, Steiner N (2004). Selection of food and ranging behaviour in a sexually monomorphic folivorous lemur: *Lepilemur ruficaudatus*. *Journal of Zoology* 263: 393–399.

Garber PA (1987). Foraging strategies among living primates. *Annual Review of Anthropology* 16: 339–364.

Garber PA (1993). Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability. *International Journal of Primatology* 14: 145–166.

Gese EM (2001). Monitoring of terrestrial carnivore populations. In *Carnivore Conservation* (Gittleman JL, Funk SM, Macdonald DW, Wayne RK, eds.), pp 372–396. Cambridge, Cambridge University Press.

Glander KE (1982). The impact of plant secondary compounds on primate feeding behavior. *Yearbook of Physical Anthropology* 25: 1–18.

Grueter CC, Li D, Ren B, Wei F, Xiang Z, van Schaik CP (2009). Fallback foods of temperate-living primates: a case study on snub-nosed monkeys. *American Journal of Primatology* 140: 700–715.

Guo S, Li B, Watanabe K (2007). Diet and activity budget of *Rhinopithecus roxellana* in the Qinling Mountains, China. *Primates* 48: 268–276.

Hadi S, Ziegler T, Waltert M, Syamsuri F, Mühlenberg M, Hodges JK (2012). Habitat use and trophic niche overlap of two sympatric colobines, *Presbytis potenziani*

and *Simias concolor*, on Siberut Island, Indonesia. *International Journal of Primatology* 33: 218–232.

Harris TR (2006). Evidence for between group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). *Behavioral Ecology and Sociobiology* 61: 317–329.

Harris TR, Caillaud D, Chapman CA, Vigilant L (2009). Neither genetic nor observational data alone are sufficient for understanding sexbiased dispersal in a social-group-living species. *Molecular Ecology* 18: 1777–1790.

Harris TR, Chapman CA, Monfort SL (2010). Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. *Behavioral Ecology* 21: 46–56.

Hemingway CA (1998). Selectivity and variability in the diet of Milne-Edwards' sifaka (*Propithecus diadema edwardsi*): implications for folivory and seed-eating. *International Journal of Primatology* 19: 355–377.

Hemingway CA, Bynum N (2005). The influence of seasonality on primate diet and ranging. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-Human Primates* (Brockman DK, van Schaik CP, eds.), pp 57–104. Cambridge, Cambridge University Press.

Hixon MA (1982). Energy maximizers and time minimizers: Theory and reality. *The American Naturalist* 119: 596–599.

Hixon MA, Carpenter FL (1988). Distinguishing energy maximizers from time minimizers: a comparative study of two hummingbird species. *American Zoologist* 28: 913–925.

Hopkins ME (2016). Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. *Animal Cognition* 19: 387–403.

Isbell LA (1991). Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. *Behavioural Ecology* 2: 143–155.

Isbell LA (2012). Re-evaluating the ecological constraints model with red colobus monkeys (*Procolobus rufomitratus tephrosceles*). *Behaviour* 149: 493–529.

Janson CH, Goldsmith ML (1995). Predicting group size in primates: foraging costs and predation risks. *Behavioural Ecology* 6: 326–336.

Kappeler PM (2014). Lemur behaviour informs the evolution of social monogamy. *Trends in Ecology & Evolution* 29: 591–593.

Kay RF (1984). On the use of anatomical features to infer foraging behavior in extinct primates. In *Adaptation for Foraging in Non-Human Primates* (Rodman RS, Cant JGH, eds.), pp 21–53. New York, Columbia University Press.

Kie JG (1999). Optimal foraging and risk of predation: Effects on behavior and social structure in ungulates. *Journal of Mammology* 80: 1114–1129.

Koenig A (2000). Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology* 48: 93–109.

Koenig A, Beise J, Chalise MK, Ganzhorn JU (1998). When females should contest for food – testing hypotheses about resource density, distribution, size and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology* 42: 225–237.

Korstjens AH, Sterck EHM, Noe R (2002). How adaptive or phylogenetically inert is primate social behaviour? A test with two sympatric colobines. *Behaviour* 139: 203–225.

Lehman SM (2007). Ecological and phylogenetic correlates to body size in the

Indriidae. *International Journal of Primatology* 28: 183–210.

Levins R (1968). *Evolution in Changing Environments. Monographs in Population

Biology Volume 2.* Princeton, Princeton University Press.

MacArthur RH, Pianka ER (1966). On the optimal use of a patchy environment.

American Naturalist 100: 603–609.

Mandl I, Holderied M, Schwitzer C (2018). The effects of climate seasonality on

behavior and sleeping site choice in Sahamalaza sportive lemurs, *Lepilemur

sahamalaza*. *International Journal of Primatology* 39: 1039–1067.

Markham AC, Guttal V, Alberts SC, Altmann J (2013). When good neighbors don't

need fences: temporal landscape partitioning among baboon social groups.

Behavioral Ecology and Sociobiology 67: 875–884.

McConkey KM, Aldy F, Chivers DJ (2002). Selection of fruit by gibbons (*Hylobates

muelleri × agilis*) in the rain forests of Central Borneo. *International Journal of

Primatology* 23: 123–145.

Mueller-Harvey I (2006). Unravelling the conundrum of tannins in animal nutrition

and health. *Journal of the Science of Food and Agriculture* 86: 2010–2037.

Nagy-Reis MB, Setz EZF (2017). Foraging strategies of black-fronted titi monkeys

(*Callicebus nigrifrons*) in relation to food availability in a seasonal tropical

forest. *Primates* 58: 149–158.

Nash LT (1998). Vertical clingers and sleepers: seasonal influences on the activities

and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve,

Madagascar. *Folia Primatologica* 69: 204–217.

Norscia I, Ramanamanjato JB, Ganzhorn JU (2012). Feeding patterns and dietary profile of nocturnal southern woolly lemurs (*Avahi meridionalis*) in Southeast Madagascar. *International Journal of Primatology* 33: 150–167.

Oates JF (1987). Food distribution and foraging behavior. In *Primate Societies* (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds.), pp 197–209. Chicago, University of Chicago Press.

Oates JF, Swain T, Zantovska J (1977). Secondary compounds and food selection by colobus monkeys. *Biochemical Systematics and Ecology* 5: 317–321.

Oates JF, Whitesides GH, Davies AG, Waterman PG, Green SM, Dasilva GL, et al (1990). Determinants of variation in tropical forest primate biomass: new evidence from West Africa. *Ecology* 71: 328–343.

Oftedal OT (1991). The nutritional consequences of foraging in primates: The relationship of nutrient intake to nutrient requirements. *Philosophical Transactions of the Royal Society B: Biological Sciences* 334: 161–170.

Ortmann S, Bradley BJ, Stolter C, Ganzhorn JU (2006). Estimating the quality and composition of wild animal diets: a critical survey of methods. In *Feeding Ecology in Apes and Other Primates. Ecological, Physical and Behavioural Aspects* (Hohmann G, Robbins MM, Boesch C, eds.), pp. 397–420. Cambridge, Cambridge University Press.

Pianka ER (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53–74.

Powzyk JA, Mowry CB (2003). Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *International Journal of Primatology* 24: 1143–1162.

Razafindratsima OH, Yacoby Y, Park DS (2018). MADA: Malagasy animal trait data archive. *Ecology* 99: 990.

Reich PB (2001). Body size, geometry, longevity and metabolism: do plant leaves behave like animal bodies? *Trends in Ecology and Evolution* 16: 674–680.

Reyna-Hurtado R, Teichroeb JA, Bonnell TR, Hernández-Sarabia RU, Vickers SM, Serio-Silva JC, et al (2018). Primates adjust movement strategies due to changing food availability. *Behavioral Ecology* 29: 368–376.

Robbins MM, Robbins AM, Gerald-Steklis N, Steklis HD (2007). Socioecological influences on the reproductive success of female mountain gorillas (*Gorilla beringei beringei*). *Behavioral Ecology and Sociobiology* 61: 919–931.

Rodgers AR, Kie JG (2011). HRT: home range tools for ArcGIS®, version 1.1, 10.8.2011.

Schoener TW (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369–404.

Seiler M, Holderied M, Schwitzer C (2014). Habitat selection and use in the Critically Endangered Sahamalaza sportive lemur *Lepilemur sahamalazensis* in altered habitat. *Endangered Species Research* 24: 273–286.

Snaith TV, Chapman CA (2005). Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus. *Behavioral Ecology and Sociobiology* 59: 185–190.

Snaith TV, Chapman CA (2007). Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evolutionary Anthropology* 16: 94–106.

Snaith TV, Chapman CA (2008). Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. *Behavioral Ecology* 19: 1289–1296.

Steenbeek R, van Schaik CP (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and Sociobiology* 49: 100–110.

Sterck EHM, Watts DP, van Schaik CP (1997). The evolution of female social relationships in nonhuman primates. *Behavioural Ecology and Sociobiology* 41: 291–309.

Stolter C, Niemela P, Ball JP, Julkunen-Tiitto R, Vanhatalo A, Danell K, Varvikko T, Ganzhorn JU (2009). Comparison of plant secondary metabolites and digestibility of three different boreal coniferous trees. *Basic and Applied Ecology* 10: 19–26.

Terborgh J (1983). *Five New World Primates: A Study in Comparative Ecology.* Princeton, Princeton University Press.

Thalmann U (2001). Food resources in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. *International Journal of Primatology* 22: 287–324.

van Soest PJ (1994). *Nutritional Ecology of the Ruminants.* Ithaca, Cornell University Press.

Verde Arregoitia LD, D'Elía G (2021). Classifying rodent diets for comparative research. *Mammal Review* 51: 51–65.

Wallis IR, Edwards MJ, Windley H, Krockenberger AK, Felton A, Quenzer M, et al (2012). Food for folivores: nutritional explanations linking diets to population density. *Oecologia* 169: 281–291.

Warren RD, Crompton RH (1997). A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar. *Journal of Zoology* 243: 397–415.

Warren RD, Crompton RH (1998). Diet, body size and the energy costs of locomotion in saltatory primates. *Folia Primatologica* 69: 86–100.

Wrangham RW (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262–300.

Wright PC (1999). Lemur traits and Madagascar ecology: coping with an island environment. *American Journal of Physical Anthropology* 110: 31–72.

Zuur AF, Leno EN, Walker NJ, Saveliev AA, Smith GM (2009). *Mixed Effects Models and Extensions in Ecology with R.* New York, Springer.

Table 1. Seasonal variation in diet, feeding time, and daily distances travelled (DDT) of *Avahi meridionalis* and *Lepilemur fleuretae* at Ampasy (South-East Madagascar) based on 289 h of continuous observation between July 2015 and June 2016

	Avahi meridionalis		*Lepilemur fleuretae*	
	lean	rich	lean	rich
Dietary breadth	0.36	0.47	0.42	0.42
Mature leaves, %	68.5	35.8	73.3	13.5
Young leaves, %	31.5	64.2	21.0	30.4
Flowers and fruits, %	0.0	0.0	5.7	55.9
Feeding time (mean ± SE), %	22.1±4.2	31.8±4.8	24.4±5.2	33.6±5.0
Resting time (mean ± SE), %	71.6±5.6	60.8±5.9	58.8±5.8	54.4±5.6
DDT (mean ± SE), m	540.0±38.2	628.2±42.3	623.8±77.0	685.9±81.6

The lean period is between March and August, while the rich period is between September and February. Values for feeding and resting time, and DDT are estimated means from general or generalised linear mixed models.

33

Table 2. Chemical composition (units per 100 g of dry matter) of food items consumed by *Avahi meridionalis* and by *Lepilemur fleuretae* at Ampasy (South-East Madagascar) between July 2015 and June 2016 during the lean (March-August) and the rich (September-February) periods

	Nitrogen	NDF	ADF	Sugar	Condensed tannins	Polyphenols	Lipids
Avahi meridionalis							
Lean (*n* = 27)	1.59±0.55	51.24±11.02	35.86±11.84	5.45±3.60	1.02±1.03	2.25±1.66	2.80±1.93
Rich (*n* = 23)	1.51±0.66	47.08±12.04	33.64±10.04	6.86±5.45	1.09±.06	2.88±2.47	2.60±2.40
t	0.46	1.28	0.71	1.09	0.25	1.08	0.33
Lepilemur fleuretae							
Lean (*n* = 17)	1.56±0.59	49.90±12.30	36.27±11.29	6.57±3.87	1.45±1.20	3.24±2.47	3.07±2.33
Rich (*n* = 12)	1.45±0.71	45.29±15.40	34.23±13.62	5.88±3.82	0.80±0.87	2.41±1.98	2.43±1.90
t	0.45	0.90	0.44	0.47	1.59	0.96	0.79

Values are means and standard deviations. NDF, neutral detergent fibre; ADF, acid detergent fibre. *t* values are based on *t* tests for samples with equal or unequal variance; none of the comparisons is significant.

Table 3. Spearman correlations between concentrations of chemical components and the time spent feeding by *Avahi meridionalis* and by *Lepilemur fleuretae* at Ampasy (South-East Madagascar) between July 2015 and June 2016 during the lean (March-August) and the rich (September-February) periods

	FAI	Nitrogen	NDF	ADF	Sugar	Condensed tannins	Polyphenols	Lipids
Avahi meridionalis								
Lean (*n* = 27)	0.09	0.01	−0.02	0.41	−0.25	−0.32	−0.18	0.02
Rich (*n* = 23)	0.03	0.60*	0.44	0.50	−0.51	−0.51	−0.60*	−0.14
Lepilemur fleuretae								
Lean (*n* = 17)	0.28	−0.22	−0.16	−0.03	0.18	0.01	0.03	0.17
Rich (*n* = 12)	0.02	−0.05	−0.08	−0.03	0.08	0.18	0.01	−0.59

FAI, food availability index; NDF, neutral detergent fibre; ADF, acid detergent fibre. * Significant based on *q* value (after Benjamini-Yekutieli correction) <0.05.
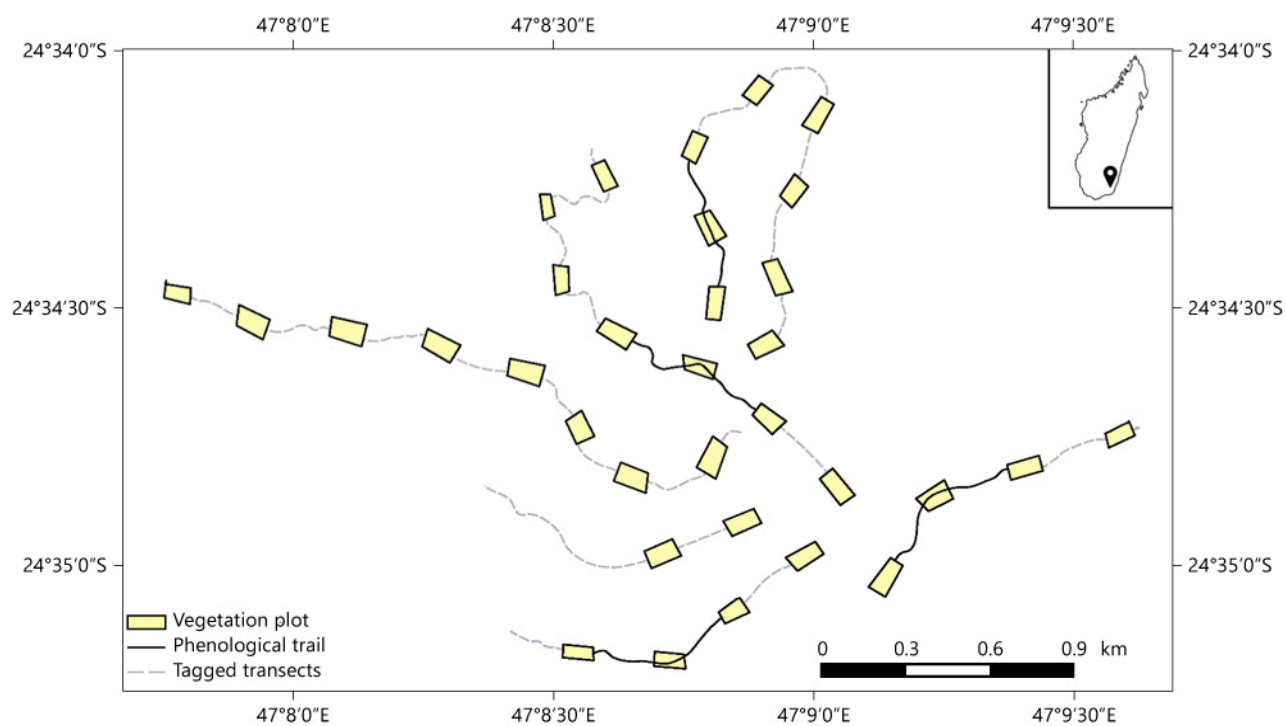
Fig. 1. Location of the Ampasy valley in relation to Madagascar. The map indicates the position of the four transects used for the collection of phenological data and the 33 plots used for the collection of vegetation data.
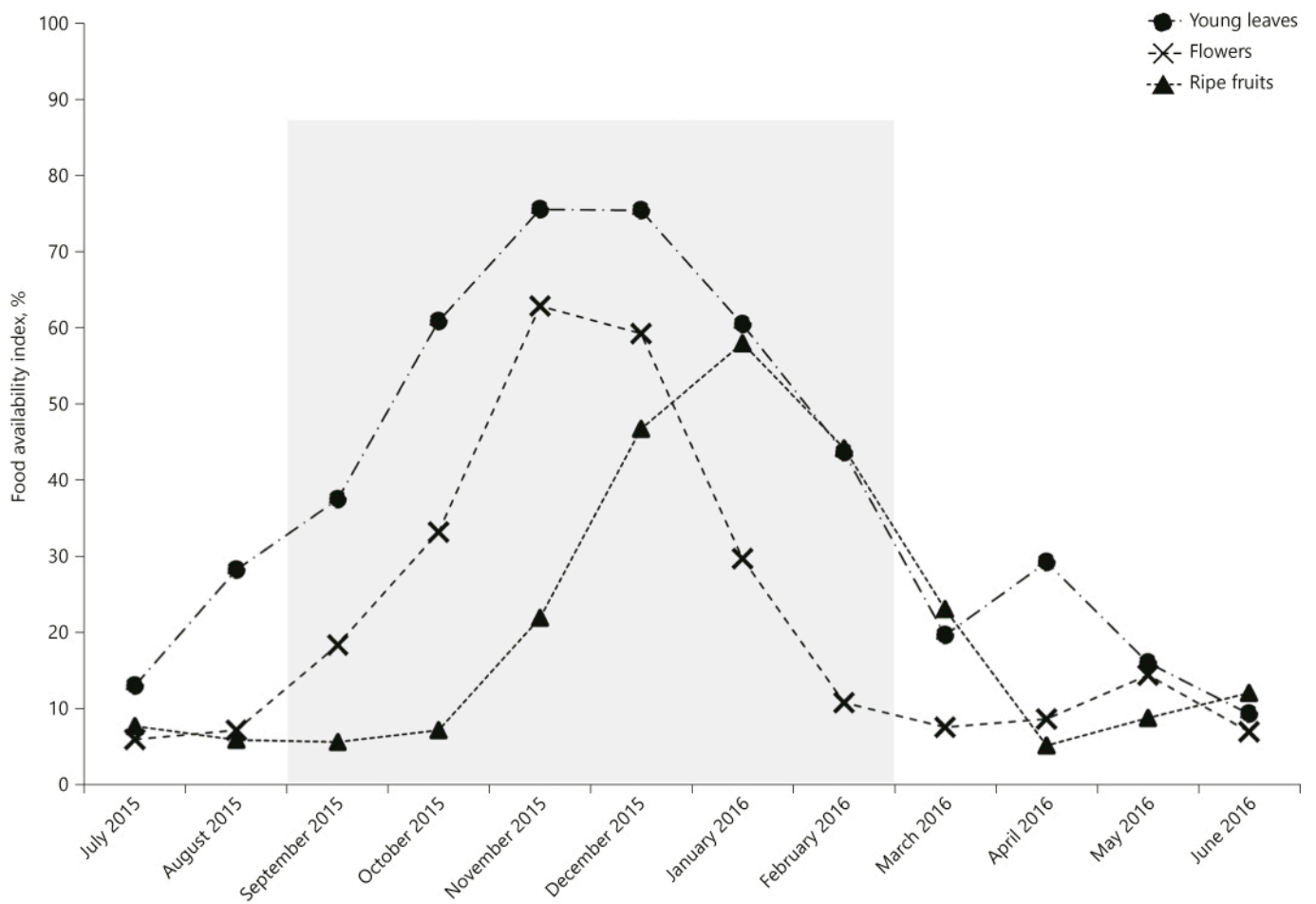
Fig. 2. Phenological profiles obtained via food availability index (FAI) at Ampasy, South-East Madagascar. Data are monthly percentages over the total FAI. The FAI for each species is the product of stem density (trees/ha), mean diameter at breast height, and proportion of trees in the phenological phase. The grey background indicates the period rich in young leaves.