

Sex and seasonal differences in diet and nutrient intake in Verreaux's sifakas (*Propithecus verreauxi*)

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Fluctuations in food availability are a major challenge faced by primates living in seasonal climates. Variation in food availability can be especially challenging for females, because of the high energetic costs of reproduction. Therefore, females must adapt the particular demands of the different reproductive stages to the seasonal availability of resources. Madagascar has a highly seasonal climate, where food availability can be extremely variable. We investigated the seasonal changes in diet composition, nutrient and energy intake of female and male sifakas (*Propithecus verreauxi*) in a dry deciduous forest in western Madagascar. We examined how females adjust their diet to different reproductive stages. Seasonality affected the diet of both sexes; particularly in the dry season (Apr–Oct) with low availability of food items, especially fruits, males and females had a reduced nutrient and energy intake compared to the wet season (Nov–Mar) with higher food and fruit availability. The comparison of the diet between sexes in different reproductive stages showed that during the late stage of lactation (Nov–Jan) females had higher food intake, and as a result they had a higher intake of macronutrients (crude protein, fat and non-structured carbohydrates (TNC)) and energy than males. These differences were not present during the pregnancy of females, with both sexes having similar intake of macronutrients and energy during that stage. The increase in the intake of macronutrients observed for females during late lactation could be related to the higher energetic demands of this stage of reproduction. Thus, the observed pattern in the diet indicates that sifaka females are following a capital breeding strategy, whereby females potentially store enough nutrients to cope with the reproduction costs in periods of low food availability.

KEYWORDS

capital breeder, food quality, primates, reproduction, seasonality

1 | INTRODUCTION

Fluctuations in food availability are a major challenge faced by primates living in seasonal climates. The variance in availability of food can have different impact for males and females, due to differences in energy requirements between sexes (reviewed in Key & Ross, 1999). Reproduction is highly demanding for females (National Research Council, 2003). Therefore, it is expected that reproductive females are more affected by changes in food availability than males and non-reproductive females (Hemingway, 1999; McCabe & Fedigan, 2007; Oftedal, 1985). For instance, to assure adequate nutrition, pregnant females can spend more time feeding than non-pregnant ones

(Boinski, 1988; Hemingway, 1999; Lee, 1984), select higher quality diets (McCabe & Fedigan, 2007) or ingest larger amounts of food (Hemingway, 1999; Rothman, Dierenfeld, Hintz, & Pell, 2008). Moreover, in green monkeys (*Chlorocebus sabaues*), lactating females adopted an energy conservation strategy during periods of food scarcity, in which they increased the time resting and avoided excessive activity in competition with others over food (Gittleman & Thompson, 1988; Harrison, 1983).

In many mammalian species, including primates, males are typically larger than females and have to cope with high costs of body maintenance (Ralls, 1976; reviewed in Key & Ross, 1999). However, in some species there is little sexual dimorphism in size,

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including the majority of Lemuriformes (Jolly, 1984; Kappeler, 1990, 1991). Interestingly, the absence of sexual dimorphism in size may be energetically advantageous to males, since they are exempt from costly maintenance of a larger body size (Richard, 1992), while females still cope with the costs of reproduction (Jolly, 1984). Additionally, in lemurs, females are typically dominant to males and have priority of access to food (Dunham, 2008; Jolly, 1984; Kappeler, 1990; Richard & Nicoll, 1987). Since lemurs occur in Madagascar with a highly seasonal climate (Fleagle, 1999; Wright, 1999), females can ensure through social dominance to access enough resources for their survival and reproduction (Jolly, 1984; Richard & Nicoll, 1987; Wright, 1999).

With respect to the timing of reproductive stages with the availability of resources, animals can adopt different reproductive strategies to adapt the energy requirements of reproduction to the environmental conditions. In that sense animals can be classified as *income or capital breeders* (Drent & Daan, 1980; Stearns, 1989, 1992). *Income breeders* synchronize the most demanding period of their reproduction with the period when availability of food is high, while *capital breeders* rely on nutrients stored previously to pay for the costs of their reproduction.

Sifakas are among the largest diurnal lemurs in Madagascar. They include large amounts of leaves in their diets (Richard, 1978), and rely on anatomical adaptations such as high molar crests, enlarged stomach, and elongated cecum and colon (Hill, 1953) to digest a fibrous diet. The highly seasonal climate of Madagascar, particularly in the dry deciduous forests where the majority of trees lose their leaves during the dry season (Sorg & Rohner, 1996), raises important questions on how animals adapt their diet to the fluctuation of food availability among seasons.

Despite the fact that sifakas are seasonal breeders with a short mating season (Brockman, Whitten, Richard, & Schneider, 1998; Mass, Heistermann, & Kappeler, 2009), adult females cope with the demands of reproduction year round, spending 6 months being pregnant and another 6 months lactating (Jolly, 1984; Kappeler & Fichtel, 2012). The lack of male parental care and the fact that infants are born during the peak of the dry season, when food availability is low (Lewis & Kappeler, 2005a; Richard & Nicoll, 1987) contributes to the high reproductive costs for sifaka females (Jolly, 1984).

The reproductive strategy adopted by sifaka females, being classified as capital or income breeders, however, is still debated. According to Richard, Dewar, Schwartz, and Ratsirarson (2000) sifakas are capital breeders, with females storing energy during the wet season to cope with the scarcity of food and the expenses of reproduction over the dry season. In contrast, Lewis and Kappeler (2005a) classified sifakas as "classic breeders." This classification is very similar to the definition of income breeding, where females synchronize the most demanding portion of their reproduction (mid/late lactation) with the period of highest availability of food.

Several studies investigated the impact of seasonality on the diet and nutrient intake in sifakas (Hemingway, 1999; Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2014; Lewis & Kappeler, 2005a, 2005b; Norscia, Carrai, & Borgognini-Tarli, 2006; Richard et al., 2000), showing that they had lower intake of food and macronutrients during the dry season. However, detailed information on sex

differences in the diet and nutrient intake across reproductive seasons is still missing.

To build on this past research, we investigated the effect of seasonality, sex, and female reproductive stages in diet patterns of a population of Verreaux's sifakas (*Propithecus verreauxi*) in a dry deciduous forest in western Madagascar. We examined the following aspects of diet of sifakas between seasons, sexes and reproductive stages: (1) the diet composition in terms of the importance of food items in the diet (fruits, leaves, and flowers); (2) the intake of macronutrients and energy. We first investigated the general impact of seasonality to the diet of both sexes. Second, we compared the diet of males and females across different reproductive stages. And finally, we explored the concepts of "capital" and "income" breeders, discussing them according to the characteristics of diet adopted by females in different reproductive stages. This comparison will contribute to our comprehension on important traits of Lemuriformes, such as female dominance and lack of sexual dimorphism, that have been related to the high costs of reproduction of females in a seasonal environment.

2 | METHODS

2.1 | Study site and behavioral observations

The study was conducted in the forest concession of Kirindy/CNFEREF, a dry-deciduous forest in western Madagascar (44°39'E, 20°03'S) (Kappeler & Fichtel, 2012). The climate in this region is characterized by a long dry season from April to early November, and a short wet season between mid-November and the end of March (Sorg & Rohner, 1996).

We observed the behavior of 23 habituated adults (9 females and 14 males), of eight neighboring groups of Verreaux's sifakas from March 2012 to April 2013. However, given that not all 23 individuals were present in all seasons (due to dispersal or death), in the present study we used data only from focal individuals that were present in all seasons ($N = 18$, nine females and nine males) for a better comparison of diet between sexes and seasons.

Two observers conducted simultaneous observations of the adults in two different groups. All groups were followed every month, and each focal individual was observed continuously for 1 hr using the focal animal sampling (Altmann, 1974). We recorded the beginning and end of each defined behavioral state such as resting, locomotion, feeding, and social. Information on feeding behavior was collected in more detail as presented next. Each observer followed one group for 3 hr (three focals) in the morning from 7:30 (± 30 min) to 10:30 (± 30 min) and a different group for 3 hr (three focals) in the afternoon from 14:00 (± 30 min) to 17:00 (± 30 min), thereby focal individuals from four different groups were observed per day. We followed this particular protocol including hourly observations instead of full day focal observations because the present study was part of a project that aimed to investigate other questions apart of feeding ecology, and for those questions hourly observations were more suitable. Observations of focal individuals and groups followed a rotation system that

alternates the orders of observation to achieve full statistical days for all individuals. Sifakas were habituated and individually marked with combinations of colored nylon collars and pendants or color-coded radio collars, respectively (Kappeler & Fichtel, 2012). Group size ranged from three to eight individuals, with one adult female and one to three adult males per group, with the exception of one group where two adult females were present during the study. We recorded 1,046 hr of observation, with an average of 59 hr (± 3) for each focal.

In order to investigate sex differences in the diet, we compared the diet of males and females across different reproductive stages of females. We categorized the reproductive stages of females into pregnancy and lactation according to earlier studies (Kappeler & Fichtel 2012). Because the different stages of lactation and pregnancy have different energy requirements, we split the categories of gestation and lactation in a more detailed classification, as follows: early pregnancy (February to April), late pregnancy (May to July), early lactation (August to October), and late lactation (November to January). The period of pregnancy was determined retrospectively after each infant was born. Because gestation is known to be about 6 months in length (Jolly, 1984), the total gestation period can be determined in retrospect once the infant is born. Since the estrus in sifaka females is synchronized (Mass et al., 2009), all females give birth around the same time (within a month). We used nursing behavior as the criterion to classify a female in the lactation category. Because all groups are monitored on a daily basis as part of the long term data collection, the exact birthday of each infant was known. During the period of this study the first infant was born on 20 June 2012 and the last infant was born on 21 July 2012. In the subsequent year (based on information from the long term data collection) the first infant was born on 20 June 2013 and the last one on 23 July 2013. The sample size used for the comparison between reproductive stages among males and females was nine adult males and seven females. One female did not give birth in 2012 and in 2013, and another female lost the infant shortly after giving birth in 2012.

2.2 | Feeding behavior

Feeding bouts started when a focal individual inserted food in its mouth and ended when it stopped feeding for at least 30 s. For each feeding bout, we recorded the food type (young or mature leaves, unripe or ripe fruits, open flowers or flower bud, barks, and seeds), the tree species, and the location of the tree with a GPS (Garmin® GPS 60CSx, Garmin, Schaffhausen, Switzerland). Given the high diversity in the diet of sifakas we were not able to collect samples of all foods they fed on. For that reason, we only collected samples from “important food resources” (IFR), defined as food items of the same species consumed by a focal individual consecutively for more than 5 min. For feeding bouts on IFR we also estimated the feeding rates (intake of food per minute) specific for each food (combination of item and species). In the case of small food items one bite often meant one item ingested. For larger items, we counted the bites necessary to ingest the whole item, and then we converted this number to the number of items ingested in a certain period of time. Intake rates were calculated as follows: whenever we processed a sample we weighed a single food item from that sample, for example, one single young leaf from species

X. Afterwards, we multiplied the weight of this one food item by the total number of items ingested per minute, obtaining the intake in grams per minute. Therefore, if the focal animal had an intake of 10 leaves per minute, fed for 5 min on this particular food, and supposing that each leaf weight 0.05 g, then this animal had a total intake of 2.5 g. All calculations were based on dry weight.

The intake rates (bites per minute) were observed by FK, and we used the averages for each item-species to complete the dataset of the field assistant. FK recorded 651 feeding rates and the intake of all possible combinations of item-species included in the diet of sifakas was rated at least once. For foods consumed more often, few intakes were recorded and averaged afterwards. We used the same averages for males and females because there was no sex difference in the feeding rates (GLMM $\chi^2 = 0.74$, $df = 1$, $P = 0.38$).

The collection of samples was performed on the same day or within a maximum of 3 days after the feeding was recorded, and whenever possible, from the same tree from which sifakas were feeding. All IFR were sampled regardless if the same species had been already sampled (since foods can be intra-specifically variable in nutritional content (Chapman, Chapman, Rode, Hauck, & Mcdowell, 2003)), resulting in 1,143 plant samples that were used for nutritional analyses (see below). When nutritional and intake information for certain foods were not available, we followed the method used by Irwin, Raharison, Raubenheimer, Chapman, and Rothman (2014), using the average of all samples from the same species and food item to replace missing values.

The availability of food was based on monitoring monthly phenology of 690 trees from 166 species distributed in 47 families. Five trees were randomly selected (whenever possible) based on a list of species available in Kirindy Forest. This list was produced on a pilot study conducted by FK when two methods of diversity were implemented and more than 25,000 trees distributed within the home range of the eight groups of sifakas were identified on the species level by a local field assistant. We used a semi-quantitative method (Fournier, 1974) in which the availability for each food item was scored ranging from 0 to 4, where 0 was the complete absence of the item and 4 represented its maximum abundance (100%). We calculated the average of the scores from all trees for each item per month to infer its availability. To investigate if sifakas selected their diet based on the availability of items, we performed a Spearman correlation between the importance of items in the diet (based on time spent feeding) per month and its availability (based on the scores of abundance of food items).

2.3 | Processing samples and chemical analyses

The samples were processed, weighed, and prepared for drying by placing them in paper bags and storing them in containers filled with dried ECO silica (non-toxic, 1.3 mm pearls with color indicator Roth®, Karlsruhe, Germany) where they stayed until they were completely dried (i.e., water content did not change). The containers were inspected at least twice a day to control for possible mold. The silica gel was oven dried and replaced on a daily basis. Before drying, fruit pulp was sliced into small pieces, and seeds (in the case sifakas ate the seeds) were dried separately from the pulp of the fruits to optimize drying.

After samples were dried, they were ground in an analytical mill (IKA, A11) through a 1 mm screen, and stored in plastic tubes. The samples were analyzed for neutral detergent fiber (hereafter, NDF) (NDF-ANKOM fiber analyzer), nitrogen (Kjeldahl), ash (combustion), and fat (ether extract) (Donati, Baldi, Morelli, Ganzhorn, & Borgognini-Tarli, 2009; Naumann & Bassler, 1976; Van Soest, Robertson, & Lewis, 1991; Voigt et al., 2004) following standard chemical procedures. A comparison of methods is provided by Ortmann, Bradley, Stolter, and Ganzhorn, (2006) and Rothman, Chapman, and Soest (2011).

Due to the large number of samples for analysis, we applied near infrared spectroscopy (NIRS) (Foley et al., 1998; Rothman, Chapman, Hansen, Cherney, & Pell, 2009; Stolter, Julkunen-Tiitto, & Ganzhorn, 2006) in the Department of Zoology of the University of Hamburg (Germany). NIRS models were developed with the plant samples collected for the present study and with the Quant two-method using partial least squares (PLS) regression with the software Opus NT Version 2.02 (Bruker GmbH, Germany). We used cross-validation (jack-knifing, internal validation) and test-set-validation (external validation) to test the accuracy of the developed NIRS models (Table 1). Standard NIRS procedures use the same data for generating the NIRS models and to test them. Though these procedures are used routinely, they can result in erroneous estimates when applied to samples that had not been used in model development (Stolter et al., 2006). We therefore applied the NIRS models to another test set of samples that had not been used for model development (independent test set validation; following Stolter et al. (2006)). The original NIRS model was only used when the concentrations predicted by the NIRS model deviated less than 10% from the results obtained by wet chemical analyses of the independent test set (Stolter et al., 2006). Since the NIRS models were unreliable for fat, all 255 fruit samples were analyzed for fat using ether extraction. Though nitrogen can be predicted reliably with NIRS models, 346 samples of fruits and flowers were analyzed for total nitrogen with the Kjeldahl method as the data were needed for other purposes. NIRS model performance is listed in Table 1.

We estimated crude protein as nitrogen *6.25. Total non-structural carbohydrates (TNC) were calculated following the formula:

$$\text{TNC} = 100 - (\text{fat} + \text{crude protein} + \text{fiber} + \text{ash}).$$

This measure of TNC has flaws as the errors of each analysis accumulate in the calculation (Rothman, Chapman, & Soest, 2011), but is

nevertheless an estimation of the nonstructural and most digestible carbohydrates in a food item. The calculations of energy from TNC, fiber, protein, and fat were based on the conventional conversion values of 4 kcal per gram protein, 4 kcal per gram of TNC, and 9 kcal per gram of fat (National Research Council, 2003). A specific value for digestibility of fiber is currently not available for *Verreaux's sifakas*. Therefore, the digestibility coefficient for fiber used in this study was 40% of 3 kcal, and it was based on a study that investigated digestibility in two species of *Propithecus* (*P. coquereli* and *P. tattersalli*) in captivity (Campbell, Eisemann, Glander, & Crissey, 1999). In the case of fiber, we used a conversion factor of 1.2 kcal per gram, instead of 4 kcal, since we subtracted 1 kcal which is lost to the anaerobic microbes processing the fermentable fractions, plus the coefficient of digestibility for fiber (40%) (Campbell et al., 1999; Conklin & Wrangham, 1994). Leaves were not analyzed for "fat" because ether extracts from leaves are very low. Therefore, only fruits were analyzed for fat contents. In the case of leaves, we set the concentrations for "fat" = 0 in energy calculations. We calculated the nutrient concentration per food sifakas fed on based on the percentage of dry matter. All analyses of nutrient intake were based on grams per hour of time spent feeding.

2.4 | Statistical analysis

For the statistical analyses, we calculated the weighted averages for the nutritional content of food seen eaten by each focal in each hour of observation. Despite the fact that we counted on a balanced data set, we divided the total nutritional content consumed from each focal in each season and reproductive stage by the total hours of observation of each focal individual in each period. We included in the analyses only focal individuals that were present in all seasons ($N = 18$ individuals, nine males and nine females). Linear Mixed Models [LMM, Baayen, 2008] in R (R, version 3.1.2; R Core Team, 2014), from the package lmer4 (Bates, Maechler, & Bolker, 2012) were applied to investigate the influence of season on energy and macronutrient intake. Seasons were the predictors, and food intake, intake of macronutrients (TNC, crude protein, NDF, fat, measured in grams) and the intake of energy (measured in calories) were our response factors. Since the availability of food in Kirindy Forest drops gradually (Lewis & Kappeler, 2005a; Norscia et al., 2006) we divided the wet and dry seasons into: early dry season (April to July), late dry season (August to

TABLE 1 Model performance of NIRS-models used to estimate concentrations of nitrogen, NDF and ash; sample size in brackets

Plant part	Component	Validation ^a	R ²	RMSEP/RMSECV ^b
Fruits	NDF (19)	Cross	99.35	1.140
Flowers	NDF (13)	Cross	95.41	1.600
Mature leaves	Nitrogen (57)	Test-set	96.15	0.144
	NDF (34)	Cross	80.29	3.440
Young leaves	Nitrogen (57)	Test-set	96.15	0.144
	NDF (34)	Cross	90.32	2.800
All parts	Ash (89)	Test-set	89.79	0.941

^aCross, cross validation; test-set, test-set validation.

^bRMSEP: root of the mean square error of the prediction based on the test-set validation; RMSECV: root of the mean square error of the prediction of cross validation [Stolter et al., 2006].

October), early wet season (November to December), and late wet season (January to March) to investigate seasonal patterns in more detail. The analyses were done separately for each macronutrient; therefore each LMM had the intake from a particular macronutrient, for instance crude protein, as a response variable, and season as the explanatory factor. Squared root and log transformations were applied to variables that were not normally distributed in order to achieve normality. Figures are representing the original data without transformation, which were used only for the statistical models. All models were controlled for focal and group identity by integrating them as random factors (individual ID nested in group ID). For the LMMs, *P* values were obtained with the R-package lmerTest (Kuznetsova, Brockhoff, & Bojesen Christensen, 2013). We checked all the relevant assumptions (multicollinearity, and existence of influential cases) for each linear mixed model, and we verified the significance of the full model (including the predictors and controlled factors) to the null model (only with the controlled factors) using ANOVA.

Non-parametric tests (Friedman and Wilcoxon Signed Rank Test) were applied for the comparison between sexes and seasons on time spent feeding on different food items: flowers (FL), fruits (FR), young leaves (YL), and mature leaves (ML). In order to correct for multiple testing, we reduced the value of *P* from 0.05 to 0.008 (0.05/6 different tests) using the method “Bonferroni” in the “*P*-adjust” function from the package “Stats” (version 3.1.0) in R.

With respect to sex differences in diet across reproductive stages (*N* = 7 females) we used LMM to compare food intake, energy and macronutrient intake between males and females in different reproductive stages of females. This comparison was relevant due to the lack of sexual size dimorphism in sifakas, and was done to confirm that differences in diet between the sexes were due to the high demands of reproduction for females, rather than to the increase of food availability in the forest. All statistical analyses were performed in R.

3 | RESULTS

3.1 | Seasonal differences

Sifakas in Kirindy spent 47% of their time feeding. Their diet was composed of 118 species from 44 plant families. During the wet season, sifakas spent 42% of their time feeding from 88 species, while during the dry season they spent 48% of their time feeding and included 99 species.

The time spent feeding on different food items differed between seasons for all food categories (Friedman tests: fruits: $\chi^2 = 92.25$, *df* = 4, *P* < 0.001; flowers: $\chi^2 = 71$, *df* = 4, *P* < 0.001; mature leaves: $\chi^2 = 154.84$, *df* = 4, *P* < 0.001; young leaves: $\chi^2 = 67.73$, *df* = 4, *P* < 0.001). Sifakas spent more time feeding on fruits during the late wet season; on flowers in the transition between late dry and early wet seasons; on mature leaves during the early dry season, and more time feeding on young leaves during the early wet season (Supplementary Table S1A). The proportion of fruits included in the diet of sifakas was correlated with the availability of this item ($R^2 = 0.52$, *df* = 10, *F* = 13.06, *P* = 0.005, Figure 1). However, they did not select their diet based on the availability of young and mature leaves, and flowers.

There was no difference in food intake (amount of food eaten) between the dry and the wet season (Supplementary Table S1B). However, sifakas had a higher intake of macronutrients during the wet season, in particular during the late wet season (Jan–Mar). They had a higher intake of TNC ($\chi^2 = 13.87$, *df* = 3, *P* < 0.001), crude protein ($\chi^2 = 28.08$, *df* = 3, *P* < 0.001), NDF ($\chi^2 = 24.58$, *df* = 3, *P* < 0.001), fat ($\chi^2 = 152.3$, *df* = 3, *P* < 0.001), and energy ($\chi^2 = 62.99$, *df* = 3, *P* < 0.001) compared to the other season stages (Figure 2). Results of Linear Mixed Models are available in supplementary material (TNC: Supplementary Table S1C; crude protein: Table S1D; NDF: Table S1E; fat: Table S1F; and energy: Table S1G).

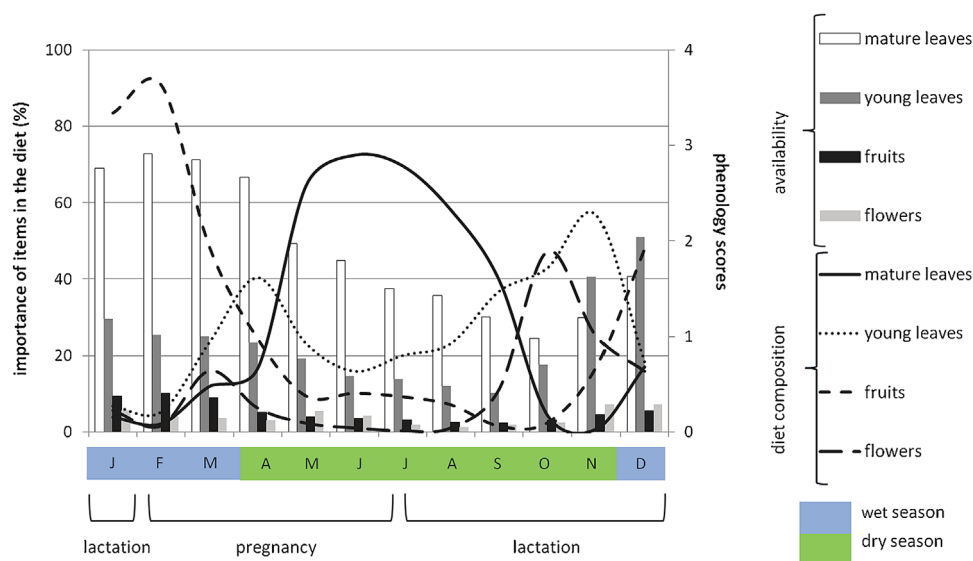


FIGURE 1 Diet composition and food availability across seasons. Lines indicate the percentage of items in the diet. The bars indicate the monthly availability of food items in the forest, based on the phenology

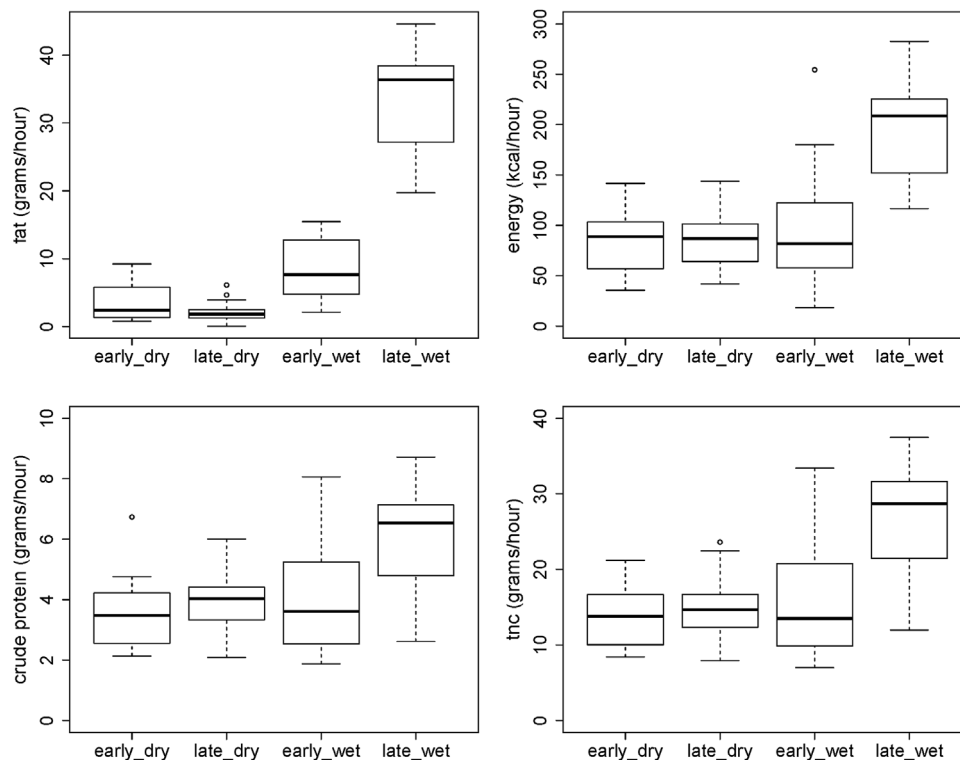


FIGURE 2 Intake of macronutrients (grams/hour) and energy (cal/hour) during season stages. The intake of all macronutrients and energy was high during the late wet season in comparison to the other stages (LMM, $P < 0.001$, tables with model parameters are available in SM)

3.2 | Sex differences

In terms of food items, females spent more time feeding on young leaves ($V = 53$, $P = 0.002$), mature leaves ($V = 48$, $P = 0.04$), and fruits ($V = 54$, $P = 0.003$) than males. There was no sex difference in the time spent feeding on flowers ($V = 40$, $P = 0.23$) (Figure 3).

Across reproductive stages, females had a higher intake of food than males during the late stage of lactation (Nov–Jan) ($\chi^2 = 11.68$, $df = 1$, $P < 0.001$, Supplementary Table S1H). Females also had a higher intake of macronutrients during the late stage of lactation than males with a higher intake of TNC ($\chi^2 = 8.38$, $df = 1$, $P = 0.003$, Supplementary Table S1J), crude protein ($\chi^2 = 8.19$, $df = 1$, $P = 0.004$, Supplementary Table S1K), NDF ($\chi^2 = 6.47$, $df = 1$, $P = 0.01$, Supplementary Table S1L), fat ($\chi^2 = 8.35$, $df = 1$, $P = 0.004$, Supplementary Table S1M), and energy ($\chi^2 = 4.73$, $df = 1$, $P = 0.03$, Supplementary Table S1N) (Figure 4). There was no sex difference in intake of macronutrients and energy within the other reproductive stages.

4 | DISCUSSION

Our study shows that sex and seasonality influenced feeding patterns of Verreaux's sifakas. The dry season was indeed a period in which the availability of food dropped drastically, and both males and females had lower intake of nutrients in comparison to the wet season. Sifakas consumed fruits in relation to their availability, but did not do so for other plant parts. The comparison of dietary patterns between sexes across reproductive stages showed that females had higher intake of

macronutrients and energy than males, but this pattern was present only during the late stage of lactation and not during pregnancy. Our results on seasonal patterns of diet agree with Norscia et al. (2006) who worked on the same population of Verreaux's sifakas in Kirindy Forest. The authors reported the negative impact of the dry season on the intake of macronutrients. Sifakas were also highly selective in their diet, giving priority to high quality foods (here defined as high protein/low fiber content) regardless of the general availability of food in the forest.

One possible explanation for the sex differences in nutrient intake can be related to different requirements for body maintenance (Key & Ross, 1999). However, that is not the case for sifakas since there is no sex dimorphism in size (Kappeler, 1991), or any other physical or physiological difference between males and females, other than reproduction that could justify differences in energy and nutrient intake. Therefore, we suggest that the sex differences in diet observed in our study are due to the high costs of reproduction for females.

Reproduction is indeed a highly demanding period for mammals, particularly the lactation period for females (Coelho, 1974; reviewed in Gittleman & Thompson, 1988). For example, in white-faced capuchins (*Cebus capucinus*), lactating females consumed more food than cycling or pregnant females, suggesting that lactation is the most costly period of reproduction (McCabe & Fedigan, 2007). The same pattern has been observed in howler monkeys (*Alouatta palliata*), in which reproductive females had higher intake of energy than non-reproductive ones (Serio-Silva, Hernández-Salazar, & Rico-Gray, 1999). In the case of lemurs, reproduction has been suggested to be even more costly for females than in other primates because of the

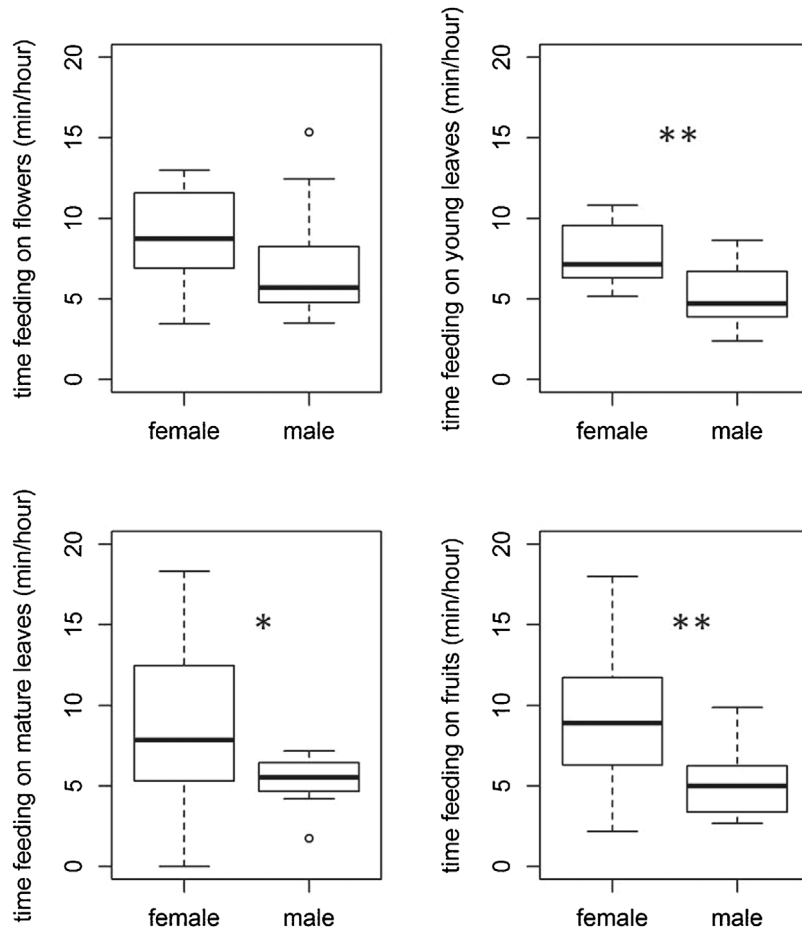


FIGURE 3 Time spent feeding (min/hour of feeding time) on fruits, flowers, young leaves, and mature leaves between females and males (Wilcoxon-signed paired test, significance levels * $P < 0.05$, ** $P < 0.01$)

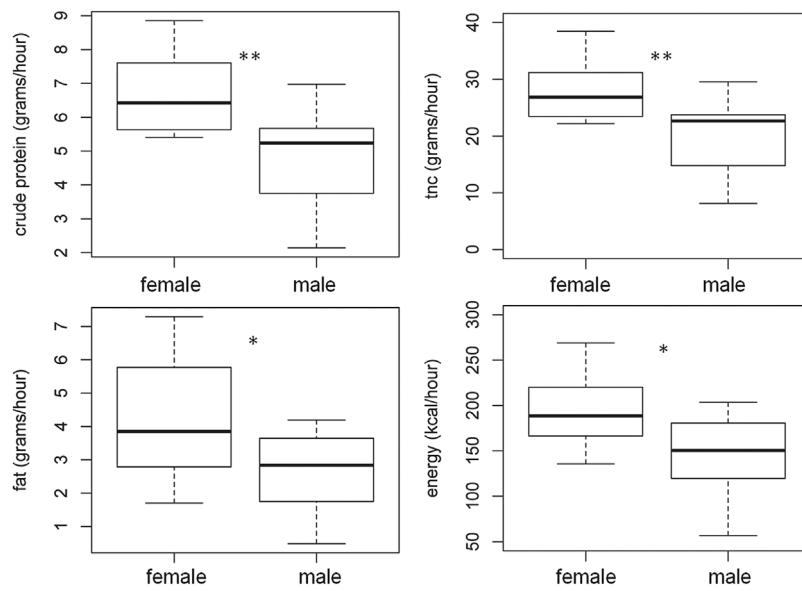


FIGURE 4 Sex differences in the intake of macronutrients (grams/hour) during the late stage of lactation (LMM, Significance levels * $P < 0.05$, ** $P < 0.01$, tables with model parameters are available in SM)

highly seasonal climate of Madagascar (reviewed in Wright, 1999), altricial infants and low basal metabolic rates (Jolly, 1984).

Reproductive stages require different amounts of energy from females. It has been suggested that mid/late lactation is the most demanding stage for female mammals (Coelho, 1974; Payne & Wheeler, 1968). Since the availability of foods with easily digestible carbohydrates such as fruits is concentrated in a short period of the year in Madagascar (Janson & Verdolin, 2005; Wright, 1999), sifakas have to strategically adjust the reproductive stages, in particular the most demanding ones, across fluctuations in food availability (Richard et al., 2000; Wright, 1999).

In that regard females may synchronize the most demanding period of their reproduction, mid/late lactation, to the period of highest availability of food, following the income breeding strategy. Alternatively, females can store energy from the periods of high food availability in order to pay for the costs of reproduction in periods of low food availability, following then the capital breeding strategy. It has been debated if sifakas are following a capital or an income breeding strategy, and there is no consensus on this aspect up to this date (Janson & Verdolin, 2005; Lewis & Kappeler, 2005a, 2005b; Richard et al., 2000; Van Schaik & Brockman, 2005; Wright, 1999). Reproductive females in our study indeed increased their food intake during the most demanding period of reproduction (late lactation). However, the period of late lactation was not synchronized with the period of highest availability of food. In addition, by the time of the peak of abundance of food (late wet season), infants were already weaned (total length of lactation period was around 5 months, based on our observations, and unpublished data from C. Fichtel).

Although we did not include measurements of body mass in our study as an indicator of storing energy, previous studies already showed that both male and female sifakas lose weight during the dry season and gain weight during the wet season (Lewis & Kappeler, 2005a; Richard et al., 2000). This pattern of seasonal oscillation in body mass is in fact more accentuated in females (Meyers & Wright, 1993; Richard et al., 2000, 2002). Richard, Dewar, Schwartz, and Ratsirason (2002) suggest that the higher oscillation of body mass in females is due to the necessity of storing nutrients from the wet season to pay for the costs of reproduction. Females that have a better body condition (higher body mass) around the mating season had higher chances of giving birth, and were more successful in caring for their infant (Lewis & Kappeler, 2005a; Richard et al., 2000). Our findings indeed show that females had a higher intake of TNC than males during the late lactation. Carbohydrates can be stored as glycogen or fat for later use (National Research Council, 2003).

In our study, females synchronized the timing of weaning their infants with the period of high availability of food. This seems to be an adaptive strategy for two reasons: first from the perspective of the infants that will have plenty of high quality food to explore and to get prepared for the harsh dry season; second from the perspective of females that can concentrate all their energy in recovering the body condition and storing enough nutrients for their next reproduction (Janson & Verdolin, 2005; Richard et al., 2000). Additionally, females in our study gave birth during the peak of the dry season and were dealing with at least half of the lactation period while the availability of

food in the forest was still low, probably relying on reserves. The increase in food intake, which resulted in higher intake of energy and macronutrients, observed during the late lactation probably indicates that the amount of nutrients stored by female sifakas during the abundant season is probably not enough to pay for all the costs of reproduction, as seen in classical capital breeders. Therefore, our results are in accordance with Richard et al. (2000) and indicate that sifakas are capital breeders.

In conclusion, our study showed that despite the fact that seasonality affected the diet of both sexes, reproductive females managed to have a higher intake of food than males. Since we can exclude different costs of body maintenance between sexes, we suggest that the high costs of reproduction drive the patterns of the diet of females in this species. As suggested, it is likely that one of the mechanisms used by female sifakas to ensure their access to a better diet is their priority to access food resources through social dominance over males (Jolly, 1966). In addition, the capacity for storing nutrients and the synchronization of reproductive stages, including the period weaning infants, to the seasonal fluctuations of food, also contribute to the improvement of their diet after scarce periods and thereby to their reproductive success. The storage capacity has been also described for red-tailed sportive lemurs (*Lepilemur ruficaudatus*), another folivorous lemur species inhabiting the same forest (Ganzhorn, 2002; but see also Dröscher, Rothman, Ganzhorn, & Kappeler, 2016 for *Lepilemur leucopus*). Likewise, storage capacity is one prerequisite for hibernation in gray mouse lemurs (*Microcebus murinus*) and fat-tailed dwarf lemurs (*Cheirogaleus medius*, Dausmann, 2014; Schmid, 2000). Thus, this might be a basic trait of lemur biology that requires reconsideration of the importance of lean and rich seasons for lemur evolution. Hence, factors such as social organization, reproductive strategy, and storage capacity are supporting the successful persistence of sifakas in extreme seasonal environments.

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