

Nutritional Correlates of the “Lean Season”: Effects of Seasonality and Frugivory on the Nutritional Ecology of Diademed Sifakas

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ABSTRACT Primate field studies often identify “lean seasons,” when preferred foods are scarce, and lower-quality, abundant foods (fallback foods) are consumed. Here, we quantify the nutritional implications of these terms for two diademed sifaka groups (*Propithecus diadema*) in Madagascar, using detailed feeding observations and chemical analyses of foods. In particular, we sought to understand 1) how macronutrient and energy intakes vary seasonally, including whether these intakes respond in similar or divergent ways; 2) how the amount of food ingested varies seasonally (including whether changes in amount eaten may compensate for altered food quality); and 3) correlations between these variables and the degree of frugivory. In the lean season, sifakas shifted to non-fruit foods (leaves and flowers), which tended to be high in protein while low in other macronutrients and energy, but the average composition of the

most used foods in each season was similar. They also showed dramatic decreases in feeding time, food ingested, and consequently, daily intake of macronutrients and energy. The degree of frugivory in the daily diet was a strong positive predictor of feeding time, amount ingested and all macronutrient and energy intakes, though season had an independent effect. These results suggest that factors restricting how much food can be eaten (e.g., handling time, availability, or intrinsic characteristics like fiber and plant secondary metabolites) can be more important than the nutritional composition of foods themselves in determining nutritional outcomes—a finding with relevance for understanding seasonal changes in behavior, life history strategies, competitive regimes, and conservation planning. *Am J Phys Anthropol* 153:78–91, 2014. © 2013 Wiley Periodicals, Inc.

Temporal and spatial variation in nutrient availability affects animal populations in a variety of ways. For example, it is linked to local density of populations or guilds (Ganzhorn, 1992; Chapman et al., 2002), individual spacing patterns (Ganzhorn, 2002), mortality patterns (Gogarten et al., 2012), ranging, including seasonal migrations (Overdorff, 1993; Gates et al., 2001; Moore et al., 2010), and body condition and growth (Koenig et al., 1997; Post et al., 1999; Ganzhorn, 2002; Randriambinina et al., 2003). Although many primate studies have investigated seasonal variation in diet composition (Hemingway and Bynum, 2005), less is known about seasonality in the availability and intake of nutrients. The existence of a “lean season” is often inferred based on indirect evidence, such as reduction in body mass or condition (Ganzhorn, 2002), switching to foods that are assumed to be “fallback foods” (Lambert et al., 2004; Marshall and Wrangham, 2007), or reduction in energy expenditure, including ranging (Hemingway and Bynum, 2005). However, relatively few studies have defined how the “lean season” differs in terms of nutrient intake (Bee-son, 1989; Altmann, 1998; Conklin-Brittain et al., 2006; Rothman et al., 2008; Felton et al., 2009; Norconk et al., 2009; Gould et al., 2011; Vogel et al., 2012).

Although mounting evidence corroborates the assumption that primate habitats offer reduced resource availability and/or quality in the lean season (Brockman and van Schaik, 2005), reductions in macronutrient intakes do not necessarily follow. Some primates may compensate for reduced food quality by ingesting more food, if their digestive system and/or ranging constraints allow. These differences can be hard to detect through comparisons of feeding time, since time spent feeding is often a poor proxy for mass ingested (Schülke et al., 2006). Other primates may switch to resources of similar

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nutrient density for which consumption is somehow limited (e.g., by availability), causing declines in realized intakes. Additionally, when dietary macronutrient intakes do change, the macronutrients are unlikely to vary in parallel; for example, since many primates increase folivory in the lean season, and young leaves tend to have higher protein than other foods, protein intake may increase, while carbohydrate and fat intake decreases (Curtis, 2004; Rothman et al., 2006; Felton et al., 2009). Thus, changes in diet should be considered along two axes, which are not necessarily dependent, and are both linked to nutritional consequences: changes in food quality, and changes in the quantity of food ingested.

Many lean season foods are classified as “fallback foods” (Marshall and Wrangham, 2007), or foods for which use is negatively correlated with the availability of preferred foods; these foods are assumed to be of poor nutritional quality and high abundance. The distinction between preferred and important is critical: importance refers simply to the quantitative representation of a food in the diet, regardless of its nutritional quality, while preference is a measure of active selection and therefore more likely linked to food quality. Fallback foods are not preferred (though this can change in disturbed habitat; Sauter and Cuzzo, 2009), but can be important in the sense that they contribute a large proportion of the diet, at least seasonally. Though these definitions have proved useful in categorizing foods (including different types of fallback foods), they are primarily based on quantifying foraging effort in relation to availability. The next step is to examine the nutritional properties of fallback foods (Doran-Sheehy et al., 2009; Vogel et al., 2012), and how they interact with food availability to influence the nutritional composition of primate diets.

Studies characterizing these seasonal nutritional shifts may be especially important in Madagascar because of its strongly seasonal climate and supra-annual variation in food availability (Wright, 1999; Dewar and Richard, 2007), factors thought to have contributed to certain “puzzling” and “idiosyncratic” behavioral and physiological traits of lemurs (Kappeler and Schaffler, 2008). However, since few studies have provided direct comparisons with other continents (Wright, 1999; Ganzhorn et al., 2009), testing these assertions will require better characterizations of lemurs’ nutritional landscapes.

We investigated daily macronutrient and energy intakes in two diademed sifaka groups across an annual cycle. Although sifaka diets have been quantified at several sites (Richard, 1978; Powzyk and Mowry, 2003; Irwin, 2006b; Norscia et al., 2006; Irwin, 2008b; Yamashita, 2008), and some of these studies have quantified food nutritional composition, our study is the first to document daily intakes; even less is known about nutritional ecology of other Indriids (Faulkner and Lehman, 2006). In this study, we 1) contrast nutrient intake between lean and abundant seasons, and 2) examine how frugivory, food quality, and overall food intake interact to determine these nutritional outcomes. First, we examine seasonal variation in time spent feeding, the amount of food ingested, and the degree of frugivory. Second, we quantify seasonal differences in the daily intake of individual macronutrients and energy, predicting lower levels in the lean season. Third, we compare foods used in lean and abundant seasons with respect to macronutrient and energy content, predicting lower lev-

els in the lean season. Finally, we examine the effects of the degree of frugivory in daily diets on these foraging and intake variables, to assess whether seasonality can explain some of the remaining variance in nutrient intakes once the effect of frugivory is accounted for.

METHODS

Study site and subjects

Tsinjoarivo Forest is a mid-altitude forest located in central-eastern Madagascar. Diademed sifakas (*Propithecus diadema*) in this area have been studied since 2002 (Irwin, 2008a,b; Irwin et al., 2010). Here we report on data from two groups (CONT1 and CONT2) observed from June 2006 to July 2007 in continuous, relatively undisturbed habitat at Vatateza (19°43.250S, 47°51.410E; 1,396 m); the groups’ home ranges are 72 and 79 ha respectively, contain interior and edge habitat and are contiguous. CONT1 contained one adult male, one adult female, and three juveniles; CONT2 contained two adult males (one natal), one adult female, and one juvenile. The diet was quantified by Irwin (2008b): 53% of feeding time was devoted to young leaves, 31 to fruit/seed and 15 to flowers.

Observational data

We collected data in 12 data collection periods, each comprising 11–21 days of observation. For analysis, these periods were categorized into five seasons: 1 (16 June–2 August 2006), 2 (29 October–17 December 2006), 3 (2 February–3 April 2007), 4 (27 April–26 May 2007), and 5 (18 June–9 July 2007). Within each period and season, the groups were sampled roughly evenly. Seasons 1, 4, and 5 represent lower than average temperature and rainfall (average $T = 11\text{--}16^\circ\text{C}$, monthly rainfall 68–119 mm), while seasons 2 and 3 have higher than average temperature and rainfall (average $T = 17\text{--}18^\circ\text{C}$, monthly rainfall 188–578 mm; Irwin unpublished data, 2003–2007); detailed descriptions of seasons are provided in Irwin (2006a; 2008b). Herein, we refer to seasons 1, 4, and 5 as the lean season and seasons 2–3 as the abundant season. Sifakas give birth in June or July (Seasons 1 and 5), lactate until roughly January (Seasons 1–3), mate in December (roughly between seasons 2 and 3), and gestate between December and June/July (seasons 3–4). The CONT2 adult female lactated during the first half of the study, but was not gestating during the second half; the CONT1 adult female lactated during the first half and gestated during the second half.

Data were collected on all adults and animals ≥ 2 years old at the beginning of the study (2-year-olds are roughly 70% adult body mass) during all-day focal-animal follows, led by MTI and/or local research assistants. Body mass data were available for most animals from captures within 2 years of this study. When observers returned to groups on subsequent days animals were almost always found in the same sleeping sites, suggesting that they did not feed at night. For each feeding bout, we recorded start and stop time, plant part (BD: flower bud; FL: flower; URF: unripe fruit without seed; RF: ripe fruit without seed; URFSD: unripe fruit with seed; RFSD: ripe fruit with seed; SD: seed; YL: young leaves; ML: mature leaves; PT: petiole; GALL: gall), and species consumed. Bouts were stopped when a pause in feeding (defined as ingestion, chewing and/or swallowing) exceeded 10 s. Soil feeding bouts were recorded but

not included in analyses (0.3% of feeding time). Our sample includes 197 focal-animal days (CONT1: 106; CONT2: 91), 2389 h (CONT1: 1234 h; CONT2: 1064 h; average 12.1 h/day), 9,309 feeding bouts (CONT1: 4495; CONT2: 4814), and 528 h of feeding time (CONT1: 261 h; CONT2: 267 h) across nine animals (CONT1: 5; CONT2: 4). Animals were well-habituated and were rarely out of sight during a focal (0.2% of 5-min instantaneous records).

Whenever observation conditions were favorable, we recorded intake rates in one of two ways. For rapidly consumed items, such as young leaves or flowers, we sampled 1-min intervals within feeding bouts, recording the number of units consumed. For items that took longer to consume (e.g., larger fruits and seeds), we recorded the start and stop time for each item, or a subset of items, within the feeding bout. We amassed 9,002 intake records totaling 157 h. The intake unit was always a pre-defined single unit (fruit, seed, leaf, etc.), with two exceptions. First, flowers of *Bakerella* species were “cropped” (one mouthful included multiple items), so we used an estimated conversion factor (two flowers/bite) based on close observation to estimate how many units were ingested in a feeding bout. Second, for one larger fruit (*Salacia madagascariensis*) the sifakas consumed seeds; therefore, we recorded intake rates in terms of fruits but used a correction factor (two seeds per fruit) to estimate number of seeds ingested.

Sample collection and chemical analyses

Concurrent with the observation we collected 134 food samples representing 58 plant species and 87 distinct foods (species–plant part combination). Plant parts sampled were flower buds, flowers, fruit without seed (when seeds were spit or dropped), fruit with seed, seed, young leaves, and distal growing shoots. We did not distinguish mature and immature seeds as this was logistically difficult in the field; sifakas tended to eat from full-sized fruit verging on ripeness so likely consumed a mix of mature and immature seeds. If possible, samples were collected from plants actually fed on; failing that we selected nearby conspecific plants as similar as possible to those used (in terms of size and phenological state). Samples were processed in the same way as by sifakas (referring to part selection and maturation stage). Samples were dried in trays inside a tent pitched in direct sun (samples were not in sunlight). We placed desiccant on trays and sliced items finely to accelerate drying. Samples were weighed (to 0.01 g) as soon as possible after collection (wet weight) and daily during drying. After weight stabilized, samples were placed in Ziploc bags with additional desiccant and stored in the dark. After export, samples were ground in a Wiley Mill through a 1-mm screen at McGill University. Although incidental animal consumption is likely (e.g., insects within fruit or seeds), deliberate animal consumption was never observed.

Nutritional analyses followed Rothman et al. (2012). At Cornell University’s Animal Nutrition Laboratory, total nitrogen was estimated using a Leco FP-528 combustion analyzer and crude protein (CP) was calculated by multiplying N by 6.25 (Licitra et al., 1996; AOCC method 990.03). Ash was determined by burning the sample at 550°C. At Dairy One Forage Laboratory (Ithaca, NY), three further analyses were performed. Acid detergent-indigestible protein (ADICP) was esti-

mated following Rothman et al. (2008); we estimated available protein (AP) as CP–ADICP. Fat content was estimated using ether extract; for leaves, we subtracted 1% from the result as an estimate to account for the presence of related non-nutritive compounds, such as waxes, detected by this assay (Rothman et al., 2012). All fruits, seeds and flowers were assayed but only a subsample ($n = 10$) of leaf samples were analyzed as leaves typically have low fat content. Water soluble carbohydrates (WSC) were extracted with boiling water and estimated using the phenol–sulfuric acid assay with sucrose as a standard (Dubois et al., 1956). Finally, at McGill University’s Primate Health Lab, all three fiber fractions (neutral detergent fiber, acid detergent fiber, and lignin) were measured by sequential analysis using an A200 Fiber Analyzer (ANKOM, Macedon, NY). NDF was estimated using α -amylase but without sodium sulfite. High-fat samples (>10% fat by dry matter) were extracted using acetone before fiber analysis. The dry matter coefficient for each sample was calculated on the day of analysis whereby a subsample was dried at 105°C for 24 h to remove moisture; all nutrient contents and individual intakes are reported on a dry matter basis.

Nutrient intake calculations

We estimated “Total Non-structural Carbohydrates” (TNC) for each food as:

$$TNC = 100 - (\text{Fat} + (\text{CP} - \text{ADICP}) + \text{Ash} + \text{NDF})$$

The method of estimating TNC should be regarded as a crude estimate for two main reasons. First, it does not account for the subtraction of vitamins, plant secondary metabolites, and other minor amounts of non-carbohydrate substances. Second, a measure by subtraction means that any errors associated with the analysis of each portion will accumulate (Rothman et al., 2012). Despite these drawbacks, we used this measure because we felt it more completely estimated all of the soluble fiber, starch and sugars in a sample. The WSC measurement is also imperfect, as it contains only soluble sugars, and is a spectrophotometric assay whereby an external standard (sucrose) is used to estimate the quantity of unknown sugar solutions. We thus present both WSC and TNC.

We estimated energy content of foods (kJ/g), through summing the physiological fuel values of their components (National Research Council, 2003), as follows:

$$E = (\text{AP} \times 16.736) + (\text{TNC} \times 16.736) + (\text{Fat} \times 37.656) \\ + (\text{Dig}_{\text{cell}} \times (\text{ADF} - \text{Lignin}) \times 12.552) \\ + (\text{Dig}_{\text{hc}} \times (\text{NDF} - \text{ADF}) \times 12.552)$$

where E = energy content (kJ/g); $\text{Dig}_{\text{cell}} = 0.3911$, and $\text{Dig}_{\text{hc}} = 0.5197$. Fiber digestibilities were not available for this population, so we substituted average values for two congeners (*P. coquereli* and *P. tattersalli*) in captivity (using data from Campbell et al., 1999). This experimental diet consisted of 85% Mazuri biscuits and 15% *Rhus copallina* browse; we assumed Mazuri biscuits were 1.65% lignin as dry matter (L. Koutsos, personal Communication, 1.5% lignin as fed, assuming 90% dry matter), and *R. copallina* was 6.1% lignin (Campbell et al., 2001). Assuming 0% digestibility of lignin, we calculated

cellulose digestibility as (observed ADF digestibility) \times [(ADF)/(ADF - lignin)], and hemicellulose digestibility as [(observed NDF digestibility \times NDF) - (calculated cellulose digestibility) \times (ADF - lignin)]/(NDF - ADF). Captive primate diets are not necessarily similar to wild diets, but no digestibility estimates for our genus in the wild are available. In addition, digestibility may vary intraspecifically as well as interspecifically (Power and Oftedal, 1996). Rather than assume no fiber digestion, or complete digestion, we use these digestibility estimates from captive primates to provide an estimate as in other reports (Conklin-Brittain et al., 2006).

Following Altmann (1998), we used the following formula to calculate daily nutrient intakes for focal animals:

$$DI_y = \sum_{i=1}^B D_i \times R_x \times M_x \times C_x \times Q_{x,y}$$

where DI_y = daily intake of y (expressed in grams for nutrients, kJ for energy), B = number of feeding bouts, D_i = duration of feeding bout i (s), R_x = average intake rate (units/s) for food x (plant part/species combination), M_x = mass per intake unit (g/unit dry matter) for food x , C_x = intake conversion factor for food x (for *Bakerella* flowers and *Salacia madagascariensis* seeds), and $Q_{x,y}$ = nutrient concentration or energy density of macronutrient y in food x (percent of dry matter for nutrients, kJ/g for energy).

Because of the high dietary diversity observed, we were unable to sample all foods; we made an effort to preferentially sample those foods most important to overall diet. When nutritional information for a certain food was unavailable, we substituted data from other samples representing the same plant part and stage. If congeners had been sampled, these values were used; when no congeners were in the diet, we used the average for all species for that plant part/stage. In total, nutritional data were available for those foods representing 76% of feeding time. The coverage in seasons 1–5 for CONT1 was 85, 48, 93, 86, and 80%; coverage for CONT2 was 86, 54, 81, 79, and 83%, respectively.

Statistical analysis

We used Kruskal–Wallis tests to examine differences among plant parts in macronutrients and energy because of small sample size for some food categories, and Dunn's post-hoc tests for pairwise comparisons ($\alpha = 0.05$). We compared frugivory and macronutrient intakes with repeated-measures ANOVA, using data collection period as a within-subjects factor and group as a between-subjects factor. Because two individuals were not sampled in periods 3 and 4, we excluded these periods for ANOVAs; two immature individuals that left natal groups during the study were also excluded. Energy and nutrient intakes were scaled to metabolic body mass ($\text{mass}^{0.762}$); this may be higher than the true intraspecific allometric coefficient but has been suggested as a consistent scaling factor for field metabolic rates (Nagy, 1994). We compared the nutritional composition of important abundant and lean season foods (those contributing $>1\%$ of feeding time) using t -tests; Levene's test was used to ensure equality of variances. We examined the effect of fruit/seed consumption on foraging and intake variables with linear regression, using the proportion of daily dry matter intake derived from

fruit and seed as the independent variable; dependent variables were log-transformed as this improved model fitting. Finally, we examined the concurrent effects of season (lean vs. abundant) and frugivory on intakes using linear mixed models (because the two predictors are correlated) with season and frugivory as fixed effects and with individual as a subject (random) effect, and used loess regression curves to visualize relationships. All analyses used SPSS (v. 20.0).

RESULTS

Food nutritional composition and dietary profile

Average water and macronutrient compositions generally varied considerably among food types (Table 1). Young leaves were higher in protein concentration and lower in fat than reproductive parts. Within reproductive parts, seeds (which were digested, rather than passed) were exceptional in having the highest protein, carbohydrate, and fat, and the lowest fiber concentrations. Fiber was relatively invariant, with only one significant pairwise comparison (seeds lower than young leaves).

The dietary profiles of the two groups were broadly similar in terms of plant parts (Table 2). The abundant season diet was dominated by plant reproductive parts (fruit, fruit with seed, or seed), but the lean season saw a stronger contribution from young leaves and flower buds/flowers. However, the species composition of the diet showed considerable differences between groups, especially in the lean season.

Seasonality in foraging variables, intakes, and food content

Time spent feeding was low in the lean season (within-season average for all full focal animal days: CONT1: 2.2 h/day; CONT2: 2.4 h/day) and higher in the abundant season (CONT1: 2.7 h/day; CONT2: 3.5 h/day; Fig. 1). Sifakas also ate less than half as much food (dry matter ingested per day) in the lean season (CONT1: 185 g; CONT2: 216 g) compared to the abundant season (CONT1: 374 g; CONT2: 548 g; Fig. 1). Finally, the average proportion of food ingested (expressed as dry matter) derived from fruit, fruit + seed, and seed was lower in the lean season (CONT1: 41.6%; CONT2: 44.7%) than in the abundant season (CONT1: 70.3%; CONT2: 76.3%; Fig. 1). Repeated-measures ANOVA revealed a significant main effect of period and a significant period \times group interaction for all foraging and frugivory variables, and no effect of group (Table 3).

For all macronutrients, intakes (g/day) were lowest in the lean season and highest in the abundant season (Fig. 2). Lean season energy intakes (CONT1: 727 kJ/mass^{0.762}; CONT2: 683 kJ/mass^{0.762}) were less than half those in the abundant season (CONT1: 1547 kJ/mass^{0.762}; CONT2: 2058 kJ/mass^{0.762}), and macronutrients showed similar reductions. There was a significant effect of period and a significant period \times group interaction for all energy and macronutrient intakes, and a significant effect of group only for NDF (Table 3).

In contrast to intakes, macronutrient and energy content of important foods showed little variation between abundant and lean seasons (Table 4). Although there was a trend for lean season foods to be lower in available protein and fat, and higher in carbohydrates, t -tests comparing individual macronutrients between seasons

TABLE 1. Macronutrient and energy density of foods eaten by sifakas at Tsinjoarivo, Madagascar

Plant part	N	% H ₂ O	% CP	% AP	% WSC	%TNC	% FAT	% NDF	% ADF	% ADL	Energy (kJ/g)
All foods	77	74.3 ± 8.3	14.6 ± 8.8	9.3 ± 8.3	15.8 ± 13.5	39.7 ± 17.6	6.4 ± 8.3	42.3 ± 16.6	33.2 ± 15.9	21.2 ± 12.8	11.14 ± 3.18
Flower buds and flowers	8	74.1 ± 5.8 ^{a,b}	12.4 ± 7.0 ^{a,b}	6.1 ± 3.3 ^{a,b}	23.4 ± 19.6	46.3 ± 20.1	3.0 ± 1.7 ^{a,b}	41.2 ± 17.3 ^{a,b}	33.5 ± 15.1 ^b	24.2 ± 13.3 ^b	10.77 ± 2.90 ^{a,b}
Fruit without seed	5	86.9 ± 1.5 ^b	13.5 ± 7.5 ^{a,b}	5.7 ± 5.7 ^{a,b}	14.4 ± 8.4	39.3 ± 10.6	9.7 ± 12.1 ^{a,b}	39.4 ± 15.1 ^{a,b}	30.5 ± 14.6 ^{a,b}	17.1 ± 13.7 ^{a,b}	12.01 ± 3.21 ^{a,b}
Fruit with seed	19	76.6 ± 8.5 ^b	9.3 ± 4.0 ^a	5.4 ± 3.6 ^a	13.7 ± 9.6	36.0 ± 16.4	8.0 ± 8.4 ^a	46.5 ± 14.8 ^b	35.5 ± 14.5 ^b	20.6 ± 11.3 ^{a,b}	11.39 ± 2.96 ^{a,b}
Seed	8	62.5 ± 8.8 ^a	10.0 ± 7.2 ^{a,b}	7.1 ± 6.6 ^{a,b}	25.1 ± 22.3	57.6 ± 21.3	11.4 ± 13.0 ^{a,b}	22.1 ± 13.6 ^a	12.6 ± 9.1 ^a	6.7 ± 6.3 ^a	15.95 ± 3.88 ^a
Young leaves	37	74.4 ± 6.4 ^b	19.0 ± 9.5 ^b	12.8 ± 9.8 ^b	13.6 ± 11.4	36.9 ± 15.9	1.8 ± 1.8 ^b	45.1 ± 15.6 ^b	36.8 ± 15.3 ^b	24.6 ± 12.5 ^b	10.09 ± 2.37 ^b

Where significant differences among plant parts exist, shared superscripts within columns represent statistically indistinguishable pairs of plant parts. CP, crude protein; AP, available protein; WSC, water-soluble carbohydrates; TNC, total non-structural carbohydrates; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin. All percentage values represent percentage of dry matter (except % H₂O).

TABLE 2. Top contributors to sifaka diet by mass ingested (dry matter) across five seasons at Tsinjoarivo, Madagascar

Group	1 (June–August)	2 (October–December)	3 (January–March)	4 (April–May)	5 (June–July)
CONT1	SD, <i>Abrahamia cf. ditimena</i> (30.8%) SD, <i>Oncostemum</i> sp. (17.4%) YL, <i>Maesa lanceolata</i> (9.9%) YL, <i>Bakerella clavata</i> var. 1 (7.2%) URFSD/RFSD, <i>Solanum mauritianum</i> (6.8%)	SD, <i>Cryptocarya</i> sp. (47.1%) SD, * <i>Maintipototra</i> * (26.6%) SD, <i>Garcinia tsaratananensis</i> (4.8%) SD, <i>Syzygium</i> sp. 3 (3.7%) SD, <i>Syzygium</i> sp. 4 (2.7%)	SD, <i>Salacia madagascariensis</i> (48.7%) YL, <i>Garcinia</i> sp. (17.0%) SD, <i>Ocotea</i> sp. 1 (5.6%) YL, <i>Maesa lanceolata</i> (4.3%) URFSD, <i>Syzygium</i> sp. 2 (4.1%)	YL, <i>Garcinia</i> sp. (17.2%) YL, <i>Bakerella clavata</i> var. 1 (17.0%) SD, <i>Abrahamia cf. ditimena</i> (15.9%) YL, <i>Maesa lanceolata</i> (14.5%) YL, <i>Syzygium</i> sp. 1 (4.9%)	SD, <i>Abrahamia cf. ditimena</i> (32.0%) YL, <i>Maesa lanceolata</i> (15.9%) YL, <i>Bakerella clavata</i> var. 1 (9.1%) SD, <i>Pittosporum verticillatum</i> (7.0%) URFSD/RFSD, <i>Solanum mauritianum</i> (5.9%)
CONT2	SD, <i>Erythroxylum</i> sp. 1 (21.3%) YL, <i>Garcinia</i> sp. (19.3%) SD, <i>Chrysophyllum botvianum</i> (16.2%) YL, <i>Bakerella clavata</i> var. 1 (8.8%) SD, <i>Pittosporum verticillatum</i> (5.4%)	SD, <i>Cryptocarya</i> sp. (69.7%) SD, <i>Malleastrum</i> sp. (4.5%) YL, <i>Garcinia</i> sp. (4.2%) SD, <i>Syzygium</i> sp. 5 (4.0%) SD, <i>Syzygium</i> sp. 3 (3.4%)	SD, <i>Salacia madagascariensis</i> (43.4%) SD, <i>Dalbergia monticola</i> (30.6%) YL, <i>Garcinia</i> sp. (7.8%) URFSD, <i>Syzygium</i> sp. 2 (2.3%) URF/RF, <i>Drypetes madagascariensis</i> (2.2%)	SD, <i>Salacia madagascariensis</i> (51.7%) YL, <i>Garcinia</i> sp. (10.3%) YL, <i>Bakerella clavata</i> var. 1 (9.9%) YL, <i>Ocotea</i> sp. 4 (5.4%) SD, <i>Erythroxylum</i> sp. 1 (3.2%)	SD, <i>Salacia madagascariensis</i> (13.5%) YL, <i>Bakerella clavata</i> var. 1 (12.0%) YL, <i>Bakerella clavata</i> var. 2 (4.6%) URFSD, <i>Pittosporum verticillatum</i> (3.1%)

BD, flower bud;
FL, flower;
URF, unripe fruit;
RF, ripe fruit;
URFSD, unripe fruit with seed;
RFSD, ripe fruit with seed;
SD, seed;
YL, young leaf.

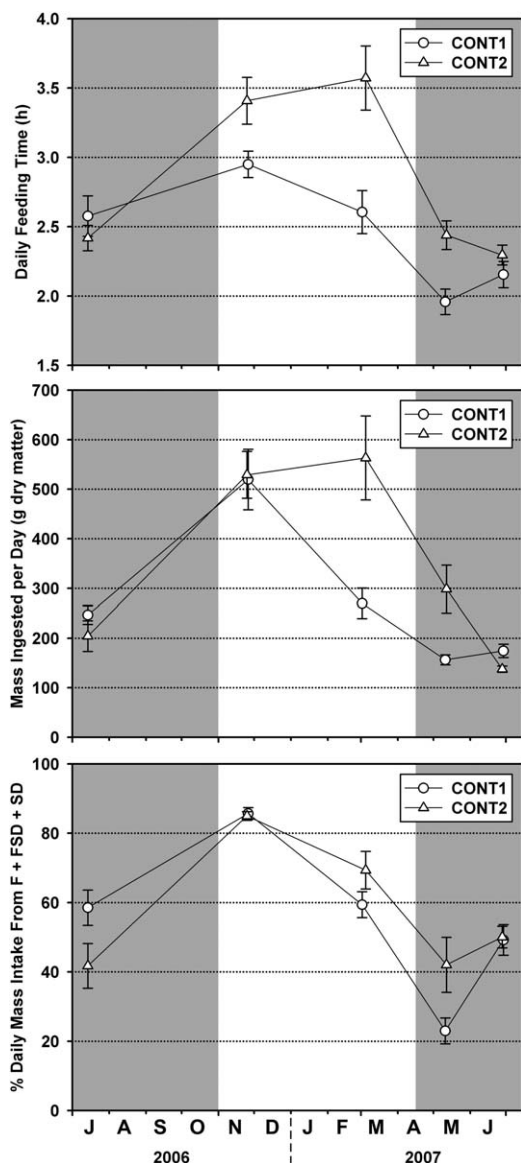


Fig. 1. Seasonal variation in sifaka daily feeding time, food ingested per day (dry matter), and proportion of diet derived from fruit and seeds at Tsinjoarivo, Madagascar. Vertical lines represent standard error; shaded areas represent lean season; seasons shown correspond to seasons 1–5 discussed in the text.

revealed no differences ($n = 8$ tests, $P > 0.18$). Energy concentrations were slightly, but not significantly, lower in lean season foods, being on average just 5% less ($P = 0.59$).

Concurrent effects of frugivory and season on intakes

In bivariate linear regressions, increasing frugivory (here defined broadly to include seeds) corresponded to increases in time spent feeding and dry matter ingested (Table 5). In terms of daily intake, there was a strong positive relationship between the degree of frugivory and the intake of energy and each macronutrient (Table 5). In most cases this relationship was curvilinear, with an accelerating effect of increased frugivory on intake variables (Fig. 3 for energy; other plots not shown). Loess regression curves reveal strong positive relationships between frugivory and intake. In linear mixed models concurrently examining the effects of both predictor variables (degree of frugivory and season), frugivory is a strongly significant predictor ($P < 0.001$; positive effect of frugivory on all intakes), while season (lean vs. abundant) was a significant factor predicting intakes for energy ($P = 0.015$; abundant season higher), as well as protein, fat, NDF and ADF ($P < 0.03$; abundant season higher in all cases), but not for TNC ($P = 0.5$), WSC ($P = 0.051$), or lignin ($P = 0.08$).

DISCUSSION

Characterizing the “lean season” and “fallback foods” for sifakas

For sifakas, the “lean season” is characterized by reduced feeding time, greatly reduced food intakes, lower fruit consumption as a proportion of dry mass ingested, and lower daily intakes of energy and all macronutrients. Despite the marked decrease in frugivory (from ~85% to ~25%), there were only modest seasonal differences in the macronutrient and energy density of foods consumed. This is consistent with several studies warning against inferring changes in nutritional composition of the diet from changes in plant parts consumed. This has been evidenced in mountain gorillas (*Gorilla beringei*) in different habitats and seasons (Rothman et al., 2007, 2008) and cercopithecines (Conklin-Brittain et al., 1998; Wrangham et al., 1998). Curtis (2004) reported a seasonal shift from leaves to nectar in the mostly frugivorous mongoose lemur (*Eulemur mongoz*), but no change in nutrient intakes; Yamashita (2008) suggested relatively stable nutrient availability across

TABLE 3. Repeated measures ANOVA results for foraging and intake variables using average intakes for sifaka individuals ($n = 7$) at Tsinjoarivo, Madagascar within data collection periods ($n = 10$)

Effects	Period	Group	Period × Group
Feeding time (s/day)	$F_{9,45} = 21.0 P < 0.001$	$F_{1,5} = 2.5 P = 0.2$	$F_{9,45} = 4.5 P = 0.022$
Intake (g/day dry matter)	$F_{9,45} = 58.4 P < 0.001$	$F_{1,5} = 5.9 P = 0.06$	$F_{9,45} = 17.1 P = 0.001$
Proportion of intake derived from fruit/seed	$F_{9,45} = 24.5 P < 0.001$	$F_{1,5} = 0.5 P = 0.5$	$F_{9,45} = 11.0 P = 0.001$
Energy (kJ/mass ^{0.762})	$F_{9,45} = 48.9 P < 0.001$	$F_{1,5} = 0.9 P = 0.4$	$F_{9,45} = 12.3 P = 0.001$
Available protein (g/mass ^{0.762})	$F_{9,45} = 58.3 P < 0.001$	$F_{1,5} = 1.0 P = 0.4$	$F_{9,45} = 11.5 P = 0.002$
TNC (g/mass ^{0.762})	$F_{9,45} = 42.5 P < 0.001$	$F_{1,5} = 0.7 P = 0.4$	$F_{9,45} = 13.6 P < 0.001$
WSC (g/mass ^{0.762})	$F_{9,45} = 39.2 P < 0.001$	$F_{1,5} = 0.2 P = 0.7$	$F_{9,45} = 18.1 P < 0.001$
Fat (g/mass ^{0.762})	$F_{9,45} = 54.2 P < 0.001$	$F_{1,5} = 0.2 P = 0.7$	$F_{9,45} = 6.4 P = 0.02$
NDF (g/mass ^{0.762})	$F_{9,45} = 69.2 P < 0.001$	$F_{1,5} = 6.7 P = 0.049$	$F_{9,45} = 18.2 P < 0.001$

P-values are Greenhouse–Geisser corrected values.

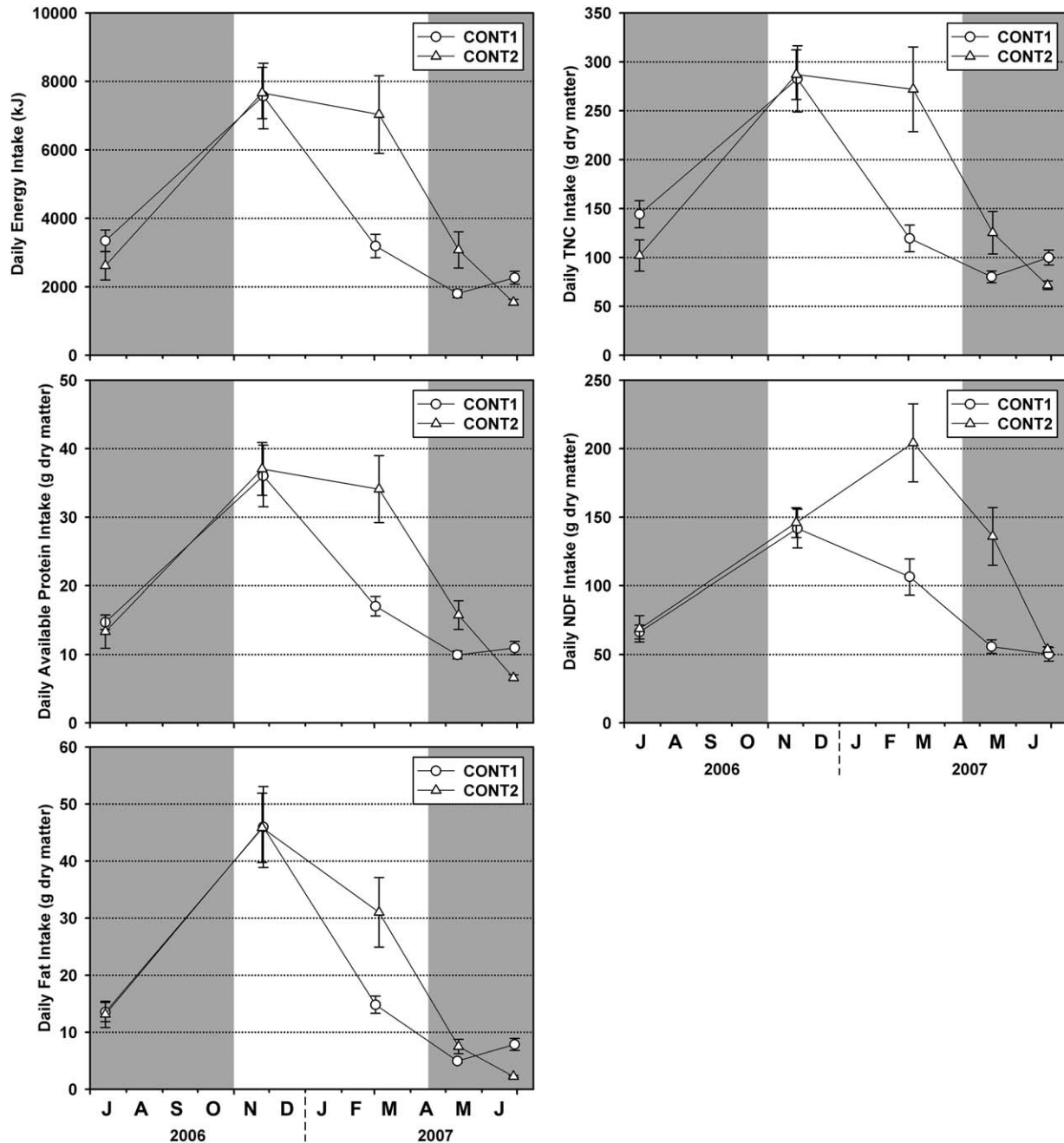


Fig. 2. Seasonal variation in daily energy and macronutrient intakes for sifakas at Tsinjoarivo, Madagascar. Vertical lines represent standard error; shaded areas represent lean season.

seasons in ring-tailed lemurs (*Lemur catta*) and Verreaux's sifakas (*Propithecus verreauxi*) but did not quantify intakes. This supports recent suggestions (Danish et al., 2006; Rothman et al., 2008) that earlier work may have overstated differences between food categories (e.g., fruit vs. leaves) in terms of macronutrient composition and effects on nutritional intakes at some sites, though certainly other key differences may exist (Janson and Chapman, 2000).

The fact that all macronutrient intakes show similarly large decreases in the lean season suggests a nutritionally compromised diet, but contrary to predictions this is not due to the nutrient composition of foods. In short,

the effects of reduced feeding time and mass ingested (from >500 g to <200 g) far outweigh any compositional changes in the diet. These results are consistent with seasonal differences in ring-tailed lemurs' protein and energy intake rates over 15-min samples (Gould et al., 2011), but in contrast to mountain gorillas at Bwindi, who exhibited no seasonal change in the daily amount of food ingested (Rothman et al., 2008). With the gorillas, seasonal energy intake differences were modest: adult females varied between 31,000 and 38,000 kJ/day (an 18% lean season reduction) and silverbacks varied only between 35,000 and 41,000 kJ/day (15% reduction). Sifakas at Tsinjoarivo averaged 7616 kJ/day at the height of

TABLE 4. Comparison of macronutrient and energy density of important sifaka foods at Tsinjoarivo, Madagascar in the abundant and lean season (those contributing >1% of feeding time)

Season	Abundant season	Lean season
N	24 (17 analyzed)	19 (16 analyzed)
Food types:	YL: 10, SD: 8, URFSD: 3, BD: 2, RF: 1	YL: 14, SD: 3, BD: 1, URFSD: 1
% CP	14.5 ± 6.4	12.4 ± 6.9
% AP	9.6 ± 6.7	7.4 ± 4.2
% Fat	6.9 ± 10.9 (n = 13)	2.4 ± 2.4 (n = 10)
% TNC	41.4 ± 11.9	47.9 ± 17.2
% WSC	18.5 ± 10.3	25.5 ± 18.4
% NDF:	40.0 ± 9.6	38.9 ± 15.4
% ADF	31.7 ± 10.5	31.5 ± 15.8
% ADL:	21.0 ± 9.0	20.3 ± 12.1
Energy (kJ/g)	11.60 ± 2.98	11.07 ± 2.61

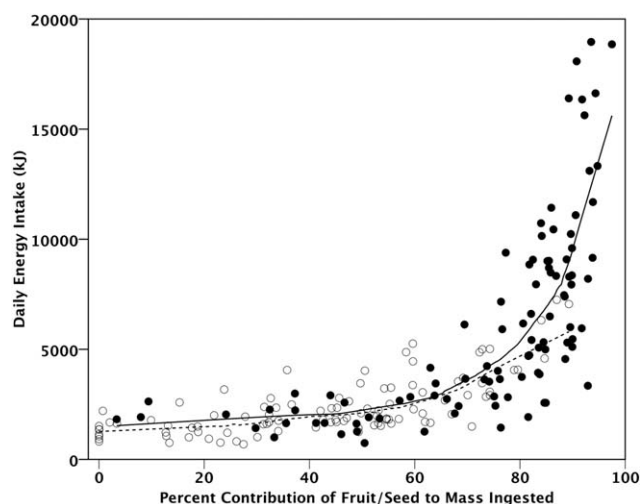


Fig. 3. Energy intakes increase with frugivory (percent contribution of fruits and seeds to mass ingested) for sifakas at Tsinjoarivo, Madagascar. Filled circles and solid line indicate abundant season; open circles and dashed line indicate lean season. Lines are loess regression curves (Epanechnikov kernels, using 50% of points to fit).

the rainy season (season 2) and 1945 kJ/day in the lean season (a 74% reduction). Conklin-Brittain et al. (2006) present energy intakes for chimpanzees (*Pan troglodytes*) at Kibale and orangutans (*Pongo pygmaeus*) at Gunung Palung: chimpanzees showed a moderate reduction from the highest to lowest month (46%), while the orangutans showed an extreme reduction (90%), consistent with their apparent catabolism of fat during extremely challenging food shortages (Vogel et al., 2012). It would be informative to know whether these differences are driven more by reduction in food intake or a change in the concentrations of nutrients in the diet.

The effects of frugivory and the nature of fruit resources

As the seasonal differences presented here may have been primarily driven by changes in the degree of frugivory, it is useful to decouple these two variables. The stronger effect of frugivory suggests that the variation in foraging strategy, diet composition and intakes might

TABLE 5. Results of linear regression exploring effects of “frugivory” (the proportion of daily diet derived from fruit and seeds, based on dry matter ingested) on daily sifaka feeding and foraging variables and daily energy and macronutrient intakes, at Tsinjoarivo, Madagascar

	CONT1 (n = 106)	CONT2 (n = 91)
<i>Feeding and foraging variables</i>		
Feeding time	+0.55/<0.001	+0.61/<0.001
Food ingested (dry matter)	+0.73/<0.001	+0.81/<0.001
<i>Daily nutrient intakes (g/day dry matter intake)</i>		
Energy	+0.77/<0.001	+0.82/<0.001
Available protein	+0.64/<0.001	+0.68/<0.001
Fat	+0.61/<0.001	+0.68/<0.001
TNC	+0.75/<0.001	+0.84/<0.001
WSC	+0.75/<0.001	+0.87/<0.001
NDF	+0.59/<0.001	+0.73/<0.001
ADF	+0.47/<0.001	+0.66/<0.001
ADL	+0.38/<0.001	+0.58/<0.001

All dependent variables log-transformed to improve fit. Each row shows dependent variable, and beta-coefficient (R) and P-value for each group.

best be understood as primarily being a response to fruit availability, an inference consistent with previous reports that sifakas consume fruits in relation to their abundance (Irwin, 2008b) and supported by variation among groups and years in the present dataset (Table 2). CONT1 had access to a rare, large tree species (*Abrahamia cf. ditimena*) that fruits in June–August, outside the main fruiting season. In contrast, CONT2’s home range has a greater abundance of *Salacia madagascariensis*, which fruits in the late rainy and early dry season (seasons 3–4), later than the typical fruiting peak (December–February). Finally, CONT2 heavily used a few large individuals of another lean-season-fruiting tree, *Syzygium* sp. 6, which was available in the 2007 lean season (season 5) but not the 2006 lean season (season 1). The relative paucity of *A. cf. ditimena* in CONT2’s home range and *S. madagascariensis* and *Syzygium* sp. 6 in CONT1’s home range is supported by both qualitative impressions and botanical transects (Irwin, unpublished data).

These divergences in fruit availability over small spatial and temporal scales likely result from the general rarity of lean-season-fruiting trees, and the tendency of trees to exhibit supra-annual fruiting frequency both in Madagascar (Wright et al., 2005) and elsewhere in the tropics (Chapman et al., 2005). These unpredictable differences in fruit availability may explain the tendency for CONT1 to have higher frugivory, and energy and macronutrient intakes, during seasons 1 and 5, while CONT2 has higher values in seasons 3 and 4. In other words, fruit resources may drive considerable and important variation in how “lean” the lean season is: this is exemplified by the divergence among groups in season 4.

Why do sifakas eat less when they need more?

Sifaka food intakes were lowest when all macronutrient intakes were lowest. If foods available in the lean season have lower nutrient concentrations, one might expect animals to eat more to compensate for this, but the opposite was seen. Three possibilities exist to explain this unexpected finding. First, it is possible that

handling time limits intakes, especially when lean season foods are small and/or require extensive pre-ingestive processing. However, while these foods (leaves and flowers) do have smaller unit size than fruit, no special processing is required, and feeding time decreases in the lean season (with average daily feeding time <4 h/day). Thus, handling time does not appear to limit sifakas. Second, food availability may limit lean season intakes. While it is hard to judge what constitutes acceptable food, certain predictions should hold if availability limits intakes, such as increased travel effort (Overdorff, 1993) and heightened intragroup feeding competition. For sifakas, the opposite is seen: daily path lengths (Irwin, 2008a) and intragroup aggression (Irwin, 2006a) both decrease in the lean season. Finally, intrinsic qualities of lean season foods could limit intakes and two strong possibilities present themselves. First, higher fiber content may necessitate slower gut passage, thereby limiting daily intakes, though little is known about the relative physical and chemical effects of fiber in this process (Clissold et al., 2009), or about how phenotypically plastic primate guts are. This is consistent with the fact that seeds (but not fruit, nor fruit with seed) had lower fiber content than foliage in this study. However, important lean and abundant season foods had nearly identical fiber concentrations (Table 4), leaving it hard to explain how fiber content alone could explain ~70% reductions in food intakes unless lean and abundant season fiber tend to act in different ways (Clissold et al., 2009). Second, deterrent and/or toxic plant secondary metabolites may limit lean season intakes, for example when further ingestion would exceed toxicity thresholds. This is consistent with the lean season increase in dietary diversity (Irwin, 2008b), because eating a range of foods containing different toxins can be a strategy to keep each below the toxic threshold (Marsh et al., 2006). Plant secondary metabolites have been documented in lemur foods (Yamashita, 2008) and a similar scenario has been observed in Australian marsupials, in which food intakes declined with the concentration of experimentally applied plant secondary metabolites (DeGabriel et al., 2009).

Though comparative data are patchy, it is interesting to note the emerging variation in behavioral responses to the lean season. Other lemurs exhibit a similar “energy conservation” response, including reduced travel (Overdorff, 1996; Vasey, 2006), though rufous lemurs (*Eulemur rufifrons*) expands its home range with lean season migrations. However, rufous and red-bellied lemurs (*E. rubriventer*) spent more time feeding in the lean season, opposite to the sifakas described here. Future research should examine whether these varied responses are linked to the factors limiting intakes of lean season foods.

Implications for ecology and conservation

Our results contribute to an extended definition of the fallback food concept. It has been suggested that “preferred foods tend to require relatively little manual or masticatory processing,” and “allow a fast intake of calories,” while fallback foods are “typically abundant – and easy to locate – but are hard to process, and therefore provide low rates of energy gain” (Marshall and Wrangham, 2007, p. 1223). Some of the sifakas’ important lean season foods (young leaves, *Bakerella* flowers) fit the definition of fallback foods in that their consump-

tion is negatively correlated with the availability of preferred foods (Irwin, 2008b), and they are abundant and easy to locate. They seem to present no additional challenge in terms of oral processing; in fact, feeding time is reduced in the lean season, suggesting this processing does not itself limit intakes. However, the greatly reduced food intake suggests greater post-ingestive processing challenges. Thus, though their nutritive composition is similar to abundant season foods, they provide lower daily energy and nutrient gain, due to the smaller amount of food ingested. The fallback food concept could thus be further refined (Sautther and Cuzzo, 2009) by other factors, including the specific characteristic by which they limit nutrient intakes (availability, quality, pre-ingestive challenges, post-ingestive challenges, etc.).

In terms of the nutritional consequences of seasonality, these results help contextualize lemur life history, including their extreme breeding seasonality (Wright, 1999; Janson and Verdolin, 2005), as part of an adaptive suite mitigating the effects of environmental seasonality and unpredictable resources (Wright, 1999; Dewar and Richard, 2007). Similar studies may also help explain some of the variation in primate life histories at finer taxonomic scales. Further research is needed to quantify seasonal variation across primate species, and to understand related behavioral and physiological adaptations, such as dietary shifts (Curtis, 2004), hibernation (Blanco and Rahalinarivo, 2010), seasonal mass change (Ganzhorn, 2002), fat storage (Vogel et al., 2012), and seasonally slowed or arrested growth (Castanet et al., 2004).

Ranging patterns are also thought to be influenced by the distribution of food resources (in combination with other factors), yet little is known about which food types, species, macronutrients, or seasons are most important in determining home range size and daily travel distances (Ganzhorn, 2002; Vasey, 2006). For Tsinjoarivo sifakas, decreased ranging in the lean season (Irwin, 2008a) suggests that lean season intakes are not limited by availability (indeed, the main fallback food, *Bakerella clavata*, is highly abundant; Irwin 2008b); instead, the rare, large trees that fruit in the rainy season may be driving home range size. Sifakas thus appear to match the prediction that preferred foods (fruits and seeds) primarily drive harvesting adaptations, such as efficient locomotion, and drive the optimal home range size (Irwin, 2008a), while fallback foods shape processing adaptations, such as teeth adapted to folivory, large guts for fermentation of fiber, and physiological strategies to neutralize the effects of plant secondary metabolites. In addition, the fact that dry forest sifakas exist at 50 times higher density than rainforest sifakas is still unexplained (Irwin, 2006b), and enigmatic, due to dry forests’ lower rainfall and prolonged dry season. van Schaik et al. (2005) suggest that this difference arises from the faster turnover, and resultant reduced chemical defense, of dry forests’ foliage; if true, this would suggest that fallback foods (leaves) were driving this difference.

Understanding competitive regimes among primate species and populations would also benefit from a deeper understanding of nutritional seasonality. Socioecology is built on the concept that animals compete for resources, with food considered “contestable” if it is high value, limited in availability, and spatially arranged such that it can be monopolized (Sterck et al., 1997; Shultz et al., 2011). Seasonal dietary shifts could change the balance between scramble and contest competition, adding to the complexity of classifying populations by the type of

competition they face. It thus becomes unclear when categorizing species which season is more important to consider. For Tsinjoarivo sifakas, competition over food is heightened in the fruiting season (since greater intakes are possible and the nearest alternative resource may be far away). While variation in lean season foods may actually have a greater impact on fitness, the low levels of competition for them may be explained if intakes are limited by factors other than their availability.

Finally, in terms of practical applications, understanding seasonal limitations on primate biomass will help guide conservation efforts. While simply “preserving habitat” is a logical first step in the absence of additional knowledge about its suitability, this ignores underlying variation in habitat characteristics and varying levels of degradation. Understanding how food chemistry limits primate densities, and in which season those limitations act, will afford greater success in preserving habitat suitability in the face of anthropogenic habitat change,

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APPENDIX A

TABLE A1. Nutrient and energy composition of 87 “foods” (=species-plant part combination) comprising the most important foods for *Tsinjoarivo sifakas* (*Propithecus diadema*) during 2006–2007

Scientific name	Vernacular name	Plant part	% H ₂ O	% CP	% AP	% WSC	% Fat ^a	% NDF	% ADF	% ADL	Energy (kJ/g)
Anacardaceae: <i>Abrahamia cf. ditimena</i>	Tsirimiramy	SD	56.4	3.1	2.5	64.3	4.3	5.4	1.4	0.8	16.71
Anacardaceae: <i>Abrahamia cf. ditimena</i>	Tsirimiramy	YL	78.4	13.0	7.0	22.1	na	45.1	42.1	31.6	9.78
Aphloiaceae: <i>Aphloia theiformis</i>	Fandramanana	SHOOT	74.1	16.0	na	na	na	26.4	20.6	10.9	na
Aphloiaceae: <i>Aphloia theiformis</i>	Fandramanana	YL	66.1	11.7	6.6	31.1	0.5	38.1	31.9	21.1	10.97
Apocynaceae: cf. <i>Plectanetia thoursii</i>	Vahimainty	YL	69.5	23.0	15.4	4.3	1.3	58.4	47.8	34.3	7.71
Apocynaceae: <i>Mascarenhasia arborescens</i>	Babona	BD	81.1	14.9	8.0	11.5	1.6	45.2	38.9	30.0	10.30
Apocynaceae: <i>Mascarenhasia arborescens</i>	Babona	FL	83.2	13.6	7.4	16.4	2.0	44.9	37.9	29.2	9.81
Araliaceae: <i>Polyscias</i> sp. 1	Vatsilana ravimboanjo	URFSD	73.3	10.1	6.3	9.3	8.2	41.6	34.2	19.6	12.35
Araliaceae: <i>Polyscias</i> sp. 2	Vatsilana ravimboanjobory	URFSD	78.1	8.9	7.4	4.9	1.6	46.9	35.1	14.3	10.46
Araliaceae: <i>Polyscias</i> sp. 3	Maniny	YL	78.3	25.3	17.6	7.7	na	38.1	27.0	17.1	11.36
Araliaceae: <i>Schefflera monophylla</i>	Manalo 2	YL	74.8	15.3	12.7	8.8	na	37.3	29.2	21.2	10.82
Araliaceae: <i>Schefflera staufferiana</i>	Vatsilana nify	YL	68.9	13.2	9.4	19.0	na	23.1	18.9	13.8	13.47
Araliaceae: <i>Schefflera vantsilana</i>	Vatsilambato	BD	67.2	9.9	7.7	41.2	1.3	21.6	14.6	7.4	13.32
Araliaceae: <i>Schefflera vantsilana</i>	Vatsilambato	URFSD/ RFSD	70.4	8.3	7.5	18.9	6.8	32.5	23.9	8.8	13.41
Araliaceae: <i>Schefflera vantsilana</i>	Vatsilambato	YL	64.2	14.2	10.2	18.1	na	23.5	17.1	11.4	13.53
Balanophoraceae: <i>Langsdorffia cf. malagascica</i>	Atoditany 1	FL	71.6	2.0	1.6	63.0	3.7	17.0	11.1	6.1	15.05
Balsaminaceae: <i>Impatiens</i> sp.	Benjy	YL	88.5	29.4	9.8	1.9	na	73.0	66.9	48.5	5.27
Celastraceae: <i>Salacia madagascariensis</i>	Vahivodiomy	FR	86.1	13.9	6.8	9.6	5.6	53.4	43.8	25.3	10.24
Celastraceae: <i>Salacia madagascariensis</i>	Vahivodiomy	SD	68.6	10.8	4.2	36.9	2.0	43.5	21.4	13.2	10.83
Clusiaceae indet.	Voamalambotaho	SD	65.9	5.7	5.2	7.7	4.6	14.0	6.7	2.4	15.54
Clusiaceae: <i>Garcinia</i> sp. 1	Voamalambotaholahy	RF	88.6	5.0	2.9	11.6	23.4	19.3	14.3	2.2	16.28
Clusiaceae: <i>Garcinia</i> sp. 1	Voamalambotaholahy	SD	65.9	3.2	2.5	7.2	21.6	4.3	2.6	0	20.49
Clusiaceae: <i>Garcinia</i> sp. 1	Voamalambotaholahy	YL	71.4	10.5	8.7	15.9	4.3	34.8	28.3	17.1	11.64

TABLE A1. Continued

Scientific name	Vernacular name	Plant part	% H ₂ O	% CP	% AP	% WSC	% Fat ^a	% NDF	% ADF	% ADL	Energy (kJ/g)
Clusiaceae: <i>Symphonia microphylla</i>	Kimba ditinina	YL	76.3	19.2	16.9	15.0	na	22.4	16.7	10.7	13.79
Clusiaceae: <i>Symphonia</i> sp. 1	Kimba tenany	YL	74.3	14.2	10.3	9.3	3.4	50.0	38.3	24.9	9.70
Cucurbitaceae: <i>Zehneria perrieri</i>	Soamalondona	SHOOT	89.4	35.3	na	na	na	28.7	18.6	7.6	na
Cucurbitaceae: <i>Zehneria perrieri</i>	Soamalondona	YL	87.7	30.3	28.9	15.6	na	29.6	18.7	8.9	11.95
Dennstaidtiaceae: cf. <i>Pteridium</i> sp.	Apanga	YL	82.7	27.7	21.4	4.0	0.9	46.0	31.5	17.0	9.47
Erythroxylaceae: <i>Erythroxylum</i> sp. 1	Taimboalavo BL	YL	73.7	20.2	12.7	19.8	na	36.6	29.8	21.7	11.30
Euphorbiaceae: <i>Macaranga macropoda</i>	Mokaranana	RFSFD	67.7	9.8	8.0	3.1	11.5	63.9	50.9	33.0	9.69
Fabaceae: <i>Albizia gummifera</i>	Volomborona	YL	80.0	58.9	56.2	4.2	na	36.1	22.5	14.1	11.81
Hamamelidaceae: cf. <i>Dicoryphe</i> sp.	Silaitra	YL	76.0	17.4	10.5	8.4	na	47.6	45.8	31.7	9.61
Lauraceae: <i>Cryptocarya</i> sp. 1	Tavolo	YL	72.1	22.1	13.5	3.9	na	48.6	39.8	30.3	9.50
Lauraceae: <i>Ocotea</i> sp. 1	Varongy ravinovy	SD	52.6	18.0	16.5	13.0	35.9	21.7	14.5	9.4	21.25
Lauraceae: <i>Ocotea</i> sp. 3	Varongy mavo	YL	76.2	22.3	5.3	1.8	na	84.6	71.6	60.1	4.12
Lauraceae: <i>Ocotea</i> sp. 4	Varongy ravimanga	YL	82.1	21.8	3.4	3.9	na	82.5	75.0	59.0	4.28
Loranthaceae: <i>Bakerella</i> cf. <i>clavata</i>	Manalo	URFSD/ RFSFD	77.4	4.3	0	3.8	33.3	35.5	27.9	15.6	17.18
Loranthaceae: <i>Bakerella clavata</i> var 1	Tongoalahy BL	BD	73.5	7.7	2.8	18.5	3.8	40.2	33.6	21.0	11.00
Loranthaceae: <i>Bakerella clavata</i> var 1	Tongoalahy BL	URFSD	73.1	5.1	0	4.3	25.3	46.6	38.7	26.9	13.96
Loranthaceae: <i>Bakerella clavata</i> var 1	Tongoalahy BL	YL	75.8	8.3	1.0	18.1	0	54.2	54.2	38.7	7.63
Loranthaceae: <i>Bakerella clavata</i> var 2	Tongoalahy SL	BD	73.4	10.6	4.7	24.5	6.3	33.9	28.9	18.6	12.54
Loranthaceae: <i>Bakerella clavata</i> var 2	Tongoalahy SL	URFSD	64.8	5.7	0.4	11.4	9.1	70.1	58.5	33.2	8.31
Loranthaceae: <i>Bakerella clavata</i> var 2	Tongoalahy SL	YL	71.7	9.2	3.8	26.5	na	41.3	32.0	17.1	11.05
Melastomataceae: <i>Medinilla humblotii</i>	Kalamasimbarika BL	URFSD	92.9	9.8	7.1	32.0	2.4	38.1	28.9	13.0	11.55
Melastomataceae: <i>Medinilla parvifolia</i>	Kalamasimbarika SL	URFSD	93.6	12.3	9.0	12.2	4.7	34.0	27.3	13.7	13.25
Meliaceae: <i>Turraea</i> sp.	Silaitra 2	YL	74.7	23.6	17.7	25.8	na	30.6	24.6	16.7	12.25
Monimiaceae: <i>Tambourissa</i> sp. 1	Tambonetra BL (Ambora)	FRSD	81.9	15.4	8.1	20.3	2.2	49.7	41.3	34.3	8.90
Monimiaceae: <i>Tambourissa</i> sp. 2	Tambonetra SL	URFSD	80.7	12.3	8.8	31.2	7.8	37.4	27.1	16.5	12.63
Myrsinaceae: <i>Embelia concinna</i>	Takaloparihy	YL	70.7	10.3	8.1	21.0	na	42.5	32.0	20.5	10.84
Myrsinaceae: <i>Oncostemum acuminatum</i>	Kalafambakaka	YL	75.6	14.2	3.4	11.3	na	44.9	41.2	25.9	9.51
Myrtaceae: indet	Rotramboa	SD	na	17.1	na	na	na	25.7	8.0	2.6	na
Myrtaceae: indet	Rotramboa	URF	na	23.4	na	na	na	44.7	25.7	12.3	na
Myrtaceae: <i>Syzygium</i> sp. 1	Rotra mena BL	YL	61.3	6.5	4.8	59.5	0.2	26.1	23.8	16.5	12.86
Myrtaceae: <i>Syzygium</i> sp. 2	Rotra mena SL	FRSD	76.4	6.3	2.6	22.9	2.0	35.8	28.0	17.2	11.80
Myrtaceae: <i>Syzygium</i> sp. 3	Rotra somikanakana	RFSFD	64.9	4.6	4.1	12.8	6.1	34.2	13.8	7.7	13.61
Myrtaceae: <i>Syzygium</i> sp. 5	Robary	URFSD	66.8	4.4	3.5	13.7	3.1	31.5	10.4	5.7	12.90
Myrtaceae: <i>Syzygium</i> sp. 5	Robary	YL	70.5	8.6	5.3	4.5	na	59.7	51.3	28.4	8.66
Myrtaceae: <i>Syzygium</i> sp. 6	Rotra somikanakana 2	SD	52.4	2.8	2.3	39.7	0.4	33.3	23.7	8.2	12.52
Phyllanthaceae: cf. <i>Wielandia mimosoides</i>	Fanjavala	URFSD	77.0	9.0	5.9	4.3	0.7	77.0	51.0	14.9	7.11
Pittosporaceae: <i>Pittosporum verticillatum</i>	Ambovitsika	YL	69.7	12.2	10.5	12.2	0.9	34.2	21.9	11.3	11.62
Primulaceae: <i>Maesa lanceolata</i>	Voarafy	YL	73.5	15.2	11.5	34.9	5.7	29.5	25.0	16.2	12.40
cf. Putranjivaceae: <i>Drypetes madagascariensis</i>	Ravitsakay	BD	75.9	26.4	12.0	4.1	1.4	68.4	52.4	39.1	6.01
cf. Putranjivaceae: <i>Drypetes madagascariensis</i>	Ravitsakay	RF	86.0	17.6	13.2	26.9	0.2	28.0	20.8	9.1	12.54
cf. Putranjivaceae: <i>Drypetes madagascariensis</i>	Ravitsakay	YL	73.1	30.6	27.5	8.3	na	35.5	19.5	11.6	11.67

TABLE A1. Continued

Scientific name	Vernacular name	Plant part	% H ₂ O	% CP	% AP	% WSC	% Fat ^a	% NDF	% ADF	% ADL	Energy (kJ/g)
Rutaceae: <i>Melicope madagascariensis</i>	Rebosa	YL	74.3	22.0	18.1	6.2	1.8	50.7	42.0	29.4	9.29
Sapindaceae: <i>Allophylus pinnatus</i>	Sakaihazo	RF	na	7.5	0.0	9.6	na	51.6	47.6	36.4	8.98
Sapindaceae: <i>Allophylus pinnatus</i>	Sakaihazo	URFSD	85.1	17.1	3.7	5.1	1.0	62.2	56.9	42.1	7.01
Sapindaceae: <i>Allophylus pinnatus</i>	Sakaihazo	YL	74.7	22.4	10.8	8.2	na	63.4	57.2	38.4	7.30
Sapindaceae: <i>Tina cf. isoneura</i>	Lanary elatrangidina	BD	67.3	14.2	4.8	8.3	3.8	58.5	50.9	42.0	8.10
Sapindaceae: <i>Tina cf. isoneura</i>	Lanary elatrangidina	SD	75.3	19.1	16.8	6.9	10.8	28.7	22.4	17.0	14.28
Sapindaceae: <i>Tina cf. isoneura</i>	Lanary elatrangidina	URFSD	77.3	4.8	0.7	15.7	13.5	31.7	24.8	11.8	15.19
Sapindaceae: <i>Tina cf. isoneura</i>	Lanary elatrangidina	YL	68.1	16.8	8.1	7.8	na	52.9	45.1	35.5	8.85
Smilacaceae: <i>Smilax anceps</i> var. <i>kraussiana</i>	Rohindambo	SHOOT	87.8	28.5	na	na	na	46.2	37.0	24.4	na
Smilacaceae: <i>Smilax anceps</i> var. <i>kraussiana</i>	Rohindambo	YL	83.4	20.7	15.7	4.5	na	54.3	43.5	26.9	8.78
Solanaceae: <i>Solanum mauritianum</i>	Seva	URFSD/ RFSD	69.4	14.5	12.6	28.7	7.9	45.8	35.5	20.3	11.02
Indet.	Fatsinakoho 2	RFSD	84.9	13.3	6.8	5.5	4.4	69.3	60.0	42.1	5.99
Indet.	Hazombato 2	YL	59.9	8.2	3.3	12.7	na	69.0	56.8	26.8	7.86
Indet.	Maintipototra	YL	74.8	19.8	15.7	4.0	na	31.6	25.5	18.0	12.05
Indet.	Vahiramy	SHOOT	88.5	25.4	na	na	na	52.4	39.3	18.9	na
Indet.	Vahiramy	YL	85.0	25.8	20.9	13.2	na	49.0	33.6	14.0	10.09
Indet.	Volomborona 2	YL	73.7	18.2	12.6	9.3	na	43.6	34.5	24.0	10.66