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Chapter 10

Intra- and Interannual Variation in the Fruit Diet of Wild Capuchins: Impact of Plant Phenology

Jeremy Hogan and Amanda D. Melin

Abstract Understanding primate diet plasticity and what causes foraging variation is crucial to understanding their ecology and evolution. Foraging choices are limited by food availability, and primate diets may shift within and between years. How primates respond to interannual variation and the extent of their dietary flexibility are poorly known. White-faced capuchins (*Cebus capucinus imitator*) have a diverse diet and are informative study subjects for investigating dietary shifts in response to environmental variation. We investigate the phenological characteristics of plant foods and calculate monthly fruit production and probability of fruiting for each dietary species and report on how capuchin foraging varies intra- and interannually. We compare the dietary importance of foods consumed over two 1 year-long sampling periods. Finally, we determine how food use changes seasonally by comparing biweekly diet variation. Most plant food species examined produce fruit seasonally, although two important species are aseasonal. The overall biomass of capuchin fruit foods varies considerably monthly and annually. During scan sampling, capuchins were observed to consume 90 different plant food species across 24 months of study. Almost half of these plant foods were only consumed during one of the two study years, but such foods accounted for only 10% of the plant diet. Within 2-week periods, capuchins were typically reliant on one or two plant foods (i.e., >50% of the diet for that period), but few plant foods were important for multiple periods. This study illustrates the importance of studying both food and foraging characteristics at different scales and demonstrates the necessity of long-term projects for interpreting foraging behaviour.

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10.1 Introduction

Foraging ecology has long been a focus of studies on wild animals because of the evolutionary implications that diet has for morphology, feeding patterns, social behaviour, and life history characteristics (Lambert and Rothman 2015). Primate diet choices often have important downstream implications for their foods as well. Many primate species positively impact plant reproductive success via seed dispersal (Chapman 1995; Gautier-Hion et al. 1985; Valenta et al. 2016), and some plant species may have evolved fruit characteristics specifically to attract primate consumers, likely through diffuse coevolution (Sussman 1991; Sussman et al. 2013). Importantly, food availability is rarely static, and very few primates will consume one food monotonously or even follow the same broad dietary patterns consistently (Altmann 2009; Marshall et al. 2009).

Intra-annual and spatial dietary variation is well documented throughout the primate order, and much of this variation is a product of seasonal fluctuation in resources (Brugiere et al. 2002; Campera et al. 2014; Marshall et al. 2014; Nagy-Reis and Setz 2016). Many animals attempt to maximize their fitness by timing their life history events to exploit predictable environmental variation (Fenner 1998; Snow and Whigham 1989). The factors that influence a plant's fruit, flower, and leaf production are highly variable and context-dependent, and the phenological patterns of strongly seasonal ecosystems are often driven by climatic events (Wright and van Schaik 1994). Phenological patterns are also scale-dependent: in many cases strikingly different patterns will be observed at the community, species, individual, and even branch levels (Boyle and Bronstein 2012). Furthermore, not all plant species respond in the same way to the same climatic conditions, and factors such as a taxon's evolutionary history and microsite differences within a habitat can have significant effects (Dahlgren et al. 2007). As data from long-term field projects become available, it is becoming apparent that interannual plant phenology patterns are inconsistent and often unpredictable (Chapman et al. 1999; Chapman et al., Chap. 17, this volume). Understanding the extent of fruit production variation at the habitat and species levels is important to fully understand what parameters shape primate food choice and is only possible after many years of continuous data collection.

One consequence of environmental variability and the plasticity of primate behaviour is that too often primate diets are broadly characterized from limited, short-term studies that do not capture the full extent of foraging variation and are likely not representative of longer time periods. For example, white-faced capuchin monkeys (*Cebus capucinus imitator*) are generally referred to as frugivore-insectivores, an accurate classification given that fruit and invertebrates combined comprise over 90% of the annual foraging budget (Bergstrom 2015; Bergstrom et al. 2018). However, such broad characterizations of diet choice risk masking important food choices over short timescales. For example, a multi-year comparison study of capuchin foraging behaviour revealed that flowers were important foods seasonally and that which flower species were important varied between years

(Hogan et al. 2016). Additionally, vertebrate prey can also be important to capuchins (Rose 1997). These results illustrate the value of collecting long-term data across different seasons to better understand foraging behaviour and dietary breadth. White-faced capuchins exhibit food preferences, selecting some foods more frequently than would be expected based solely on that item's abundance in the forest, and underselecting others (Leighton 1993; Melin et al. 2014). However, a plant food's abundance in the forest is subject to natural phenological variation and selectivity and preference may also vary over time. It is necessary, therefore, to explore food use patterns over variable lengths of time, under different phenological conditions, and at a finer scale (i.e., at the food-species level) than the broad food classes often employed. In this study, we aim to provide greater insight into the relationship between ecological variation and foraging flexibility in primate populations by examining phenological variation in capuchin fruit food trees in relation to detailed foraging records at two different timescales.

The specific purpose of our study is to determine the extent to which species-specific fruit production is predictable annually, and to investigate the dietary patterns of a population of wild white-faced capuchins at two different timescales (annually and between 2-week periods). White-faced capuchins are an appropriate study species for investigating dietary variation, as they are known to be omnivorous and highly plastic in their food choices (Fragaszy et al. 2004). Our primary research objectives are to assess (1) the extent of variation in fruit biomass and how predictable individual species' fruiting patterns are annually, (2) how diverse the capuchin diet is and which plant foods are consumed more frequently, and (3) to what extent the dietary importance of specific foods changes over time. To answer these questions, first we compared the monthly fruit production patterns of capuchin foods over a 9-year period to determine how consistent monthly fruit biomass production is, whether plants produced fruit in a predictable seasonal fashion, and to what extent individual conspecifics produced fruit seasonally. Second, we observed capuchin foraging behaviour over two study seasons and determined how diverse the capuchin diet was within each sampling period, which foods were important during both years, and which foods were uniquely consumed during just one sampling period. Finally, we analysed foraging data within smaller (2-week) timeframes to determine to what extent dietary patterns remain constant within a year.

10.2 Methods

10.2.1 Study Site

Data were collected in Sector Santa Rosa, Área de Conservación Guanacaste (hereafter referred to as Santa Rosa), located in the northwest corner of Guanacaste Province, Costa Rica. Santa Rosa's forests are mostly regenerating endangered tropical dry forest (DeGama-Blanchet and Fedigan 2006). Tropical dry forest is characterized by extreme seasonality of precipitation; in Santa Rosa, rainfall averages over 100 mm/month during the wet season (typically May–November), and almost no rainfall occurs during the dry season (December–April; see chapter by Campos 2018, in this volume, for detailed study of Santa Rosa's climate). Temperatures are relatively constant year-round, although the dry season is warmer and has a higher daily temperature range on average. During the dry season, up to 80% of the vegetation sheds leaves (Janzen 1988), resulting in little shade, and most water sources dry up (Campos and Fedigan 2009). Santa Rosa is home to three primate species: white-faced capuchins, mantled howler monkeys (*Alouatta palliata*), and black-handed spider monkeys (*Ateles geoffroyi*).

10.2.2 Phenological Data Collection

To investigate the fruit productivity patterns of capuchin foods, we analysed plant phenological data that has been collected consistently on important fruit foods since 2008. Within 3 days of the first of a month, researchers record the percentage of fruit coverage and maturity of selected food trees using a 0–4 scale (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%), resulting in two measurements monthly for each individual plant. Data have been collected from 38 species of capuchin plant foods continuously since 2008, with some species that were only included more recently being excluded from the present analysis. Whenever possible, eight individual representative plants per species are included in phenology data, although some species are underrepresented due to their rarity in the environment. In the case of tree death, a suitable replacement of the same species was added to the dataset as soon as possible. Interobserver reliability was established through a prolonged and rigorous training regime and was tested monthly by ensuring some trees were observed by several researchers.

10.2.3 Biomass Estimates

Capuchin plant food species are not uniformly distributed in Santa Rosa, nor are their fruit crops equal in size. To account for this, we calculated the estimated monthly fruit production (ripe fruit biomass index) for each species in our phenological sample. Plant species density and productivity estimates were obtained via transect sampling projects carried out in 2007–2010 and 2015–2017. Along 151 transects that were 100 m × 2 m (2007–2010) and 273 that were 100 m × 4 m (2015–2017), every individual tree of at least 0.5 cm in diameter and at least 1 m tall was identified to the species level, and its circumference at breast height (CBH) was recorded. In total 48,799 individual trees were identified in 9.06 ha of forest. Although figs are important capuchin foods, *Ficus* species are sufficiently rare in Santa Rosa that they were not captured in sampling transects. For these species, we calculated their biomass by all-occurrences sampling. We defined the sample area as the total area included within 25 m of capuchin group daily travel paths (791 ha; Campos et al. 2014), and we exhaustively searched for and recorded any *Ficus* trees ($n = 316$) in this zone from 2007 to 2014. Fruit productivity scales with tree size and can be estimated for animal-dispersed species from DBH measurements (Peters et al. 1988). For each species, we summed the estimated maximum productivity of every individual tree observed in a transect and divided this by the total transect area, providing an estimate of maximum fruit biomass density per species (kg/ha). This estimate represents an overestimate of fruit productivity that is only achieved if all individual conspecific trees were to fruit to their full potential simultaneously. Ripe fruit scores (i.e., fruit phenology score) were then calculated for each species from the phenology data by determining the average value of (coverage*maturity/4) for a species in a given month for each respective plant part. We then multiplied the species' maximum biomass estimate by its monthly fruit phenology score to calculate a monthly ripe fruit biomass index per species, which were summed to produce annual biomass estimates. To guard against overestimating productivity, we excluded individual transect trees if they were smaller than the smallest tree capuchins that have been observed foraging from during 2 years of behavioural follows (Melin et al. 2014). For biomass assessment, only species that were monitored in our phenology routes for all years were included in monthly and annual estimates. Finally, we also excluded wind-dispersed species because their fruit productivity is not well assessed via DBH (Peters et al. 1988). All calculations used for biomass estimates are contained within customized R scripts written by Fernando Campos and are publicly available at https://github.com/pace-primates/paceR.

10.2.4 Determining Seasonality of Fruiting Patterns

To determine how predictable fruiting patterns are for capuchin food species interannually, we used generalized linear mixed models with sinusoidal terms as predictor variables to determine whether fruit was produced significantly more often in a particular time period (season) yearly. This model system allows for analysis of a binomial dependent variable (i.e., fruit production) against a circular predictor variable (month of the year; Pewsey et al. 2013). Statistical analysis was conducted using R software and the lme4 package (Bates et al. 2015), and significance threshold was considered to be $P < 0.05$ for all analyses. We converted months to circular data by creating a numeric value for each month (e.g., January = 1, December = 12) and then converted these values to radians using the formula (month*2*pi/12). We calculated the number of representative trees producing fruit for each month and used cosinus of month in radian and sinus of month in radian as predictor variables to determine whether fruit production occurred in a predictable seasonal fashion. Models for each species were conducted separately. Since for each individual tree fruit production was a presence/absence observation, we used binomial distribution, and we included study year as a random effect. To test for model significance, we compared the results to null models that did not include the cosinus and sinus terms as predictors, using a chi-square test. Using the model coefficients, we then calculated and plotted predicted probability curves of fruit production per month for each species. These estimate the probability of fruit being produced for each species within any given month (i.e. the predicted proportion of phenology trees in fruit for that species).

10.2.5 Behavioural Data Collection

To determine the diversity of the capuchin plant food diet and to assess how the diet changes over time, we analysed data collected from four capuchin groups in 2007–2008 (LV, CP, EX, GN) and three groups in 2013–2014 (LV, AD, RM). In 2013, CP group fissioned to form groups AD and RM, therefore all three study groups observed in the second sampling period were directly comparable to those observed during the 2007–2008 season, and there is notable home range overlap amongst these groups (Bergstrom et al. 2017). Group sizes fluctuated during both study seasons due to births, deaths, and male transfer between groups (Table 10.1). The individuals living in these groups are well habituated and individually identifiable.

For this study, we analysed two sampling periods of data: 155 full days in 2007–2008 (Season 1) and 107 in 2013–2014 (Season 2). In 2007–2008 data were collected February–April 2007, September 2007–January 2008, and May–August 2008. In 2013–2014, data were collected between May–July 2013 and October 2013–March 2014. During both sampling periods, we followed study groups for 2–4 consecutive days per study "cycle", which was monthly in 2007–2008 and every 2 weeks in 2013–2014. Researchers followed the focal study group from sunrise to sunset (approximately 06:00–18:00 +/− 30 min) and conducted scan sampling every 30 min during this time. Data collection for scan samples lasted for up to 10 min, during which time field personnel attempted to locate and record the behaviour of every individual in the group. Only adults, subadults, and large juveniles were observed for scan sampling. If a monkey was foraging on plant or animal matter, researchers recorded the type of the food item, to the species and part level whenever possible for plant foraging. A total of 29,533 scan records were collected (14,591 of them in 2007–2008 and 14,942 in 2013–2014).

We aimed to determine how diverse the capuchin diet was, which foods were important, and how the diet varied interannually. We defined dietary diversity as the

Table 10.1 The range of the number of individuals living in each study group observed for this study. Groups AD and RM formed following fission of CP in early 2013

Group	2007–2008 population	2013–2014 population
LV	19–22	11–14
GN	27–35	Not observed
EX	8–12	Not observed
CP	20–25	N/A
AD	N/A	19–22
RM	N/A	18

number of plant food items included in the diet for a given study period. We measured the importance of food items as the proportion of scan samples during which at least one monkey was foraging on that food item; foods foraged on more frequently were considered more important. We calculated the total number of plant feeding records and the number of times a specific plant food item was consumed within a year, used these values to calculate the proportion of the overall plant foraging budget comprised of each food item, and ranked them in order of use. To assess interannual variation in food use, we compared the top 10 food items from each sampling period and determined how many foods were consistently used in both seasons and finally calculated how much of the diet consisted of the same foods in both seasons. Because the 2007–2008 data were collected over 12 months, we assumed a priori that the number of different food items observed during the first sampling period would be higher than those consumed over the course of the second field study. To account for this, we only used data from 2007 to 2008 that was collected within 2 weeks of the periods data were collected in 2013–2014.

To examine the variation in food use patterns across shorter timescales, and determine the extent to which foraging patterns in these short periods differ from annual and interannual patterns, we compared food use within 2-week study "cycles" from the 2013–2014 data. For each cycle, we determined the number of plant food items consumed and their relative importance within that cycle. We report the most important plant foods for each foraging cycle and compare these results to annual foraging results to investigate whether important foods remain important year-round or are only consumed within short timeframes (but in high quantities). To determine whether dietary diversity changes over time, we compare the number of plant foods consumed per cycle and compare this to the overall annual pattern.

10.3 Results

10.3.1 Inter- and Intra-Annual Variation in Available Fruit Biomass

The estimated biomass of capuchin fruit foods varied considerably across months and years (Fig. 10.1). The mean annual biomass of capuchin foods was 1179 kg/ha, meaning that if production were to be distributed equally throughout the year, we would expect approximately 100 kg/ha of fruit to be available each month. The interquartile ranges for 5/12 months (June, July, August, November, December) are below this mean, while only 1 month (April) has an interquartile range above this (Fig. 10.1b). June and July have the smallest interquartile ranges, and they, along with December, do not overlap with February's or April's ranges. The most productive year, 2009, was especially productive during the wet season (May–October, except for August), and the single highest monthly production occurred during this

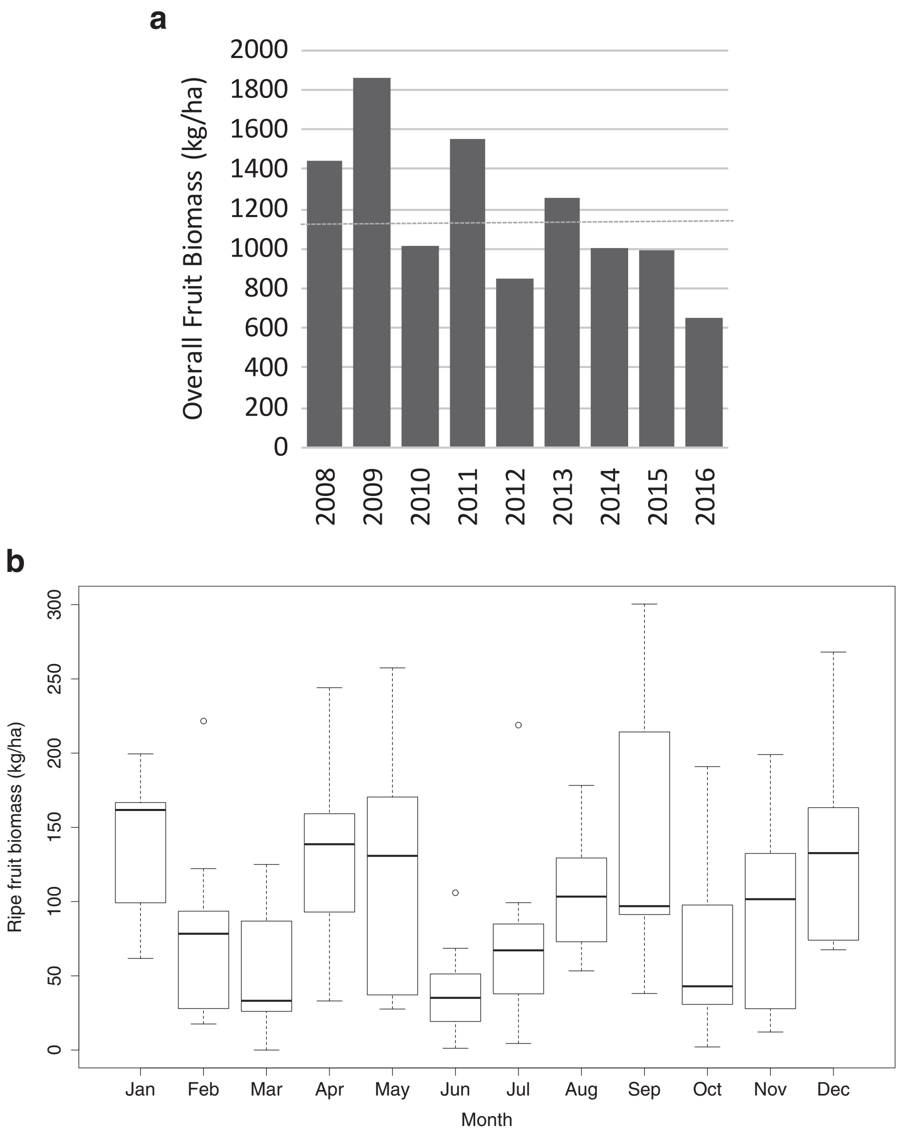

Fig. 10.1 The (**a**) annual and (**b**) monthly biomass estimates (kg/ha) for 38 capuchin food species in 2008–2016. Monthly variation across years is displayed via boxplots: for each month, the bolded central line represents the median biomass estimate for all years, the boxes encapsulate the interquartile range, dashed lines are the maximum and minimum values, and open circles are outliers

same year (300 kg/ha in May). Conversely, 2016, which had the lowest annual production, also had the lowest production for 8/12 months, including the entire wet season. December 2016 is also the only month for any year with no recorded ripe fruit production.

10.3.2 Fruiting Seasonality of Capuchin Food Species

Almost all (36/38) trees in our phenology system were seasonal, as they produced fruit significantly more frequently in one part of the year (Fig. 10.2, Table 10.2). However, the probability of a species producing fruit in a specific month was low: the peak fruiting month (i.e., the month with the highest expected number of individuals in fruit for a given species) for 26 of 38 species had a fruiting probability of <50%, and only two species (*Guazuma ulmifolia* and *Karwinskia calderoni*) were at least 75% likely to produce fruit in their peak months (Table 10.2).

10.3.3 Plant Diet Diversity and the Importance of Specific Plant Food Items

Capuchins were observed to be feeding on an identifiable food item during 15% of scan records. A total of 90 different plant food items were recorded to be consumed during scan sampling over the course of both sampling periods (Fig. 10.3). Nearly half (42/90) of plant food items were unique to one sampling period. These unique foods were typically rarely used, and combined they accounted for 10% of the plant

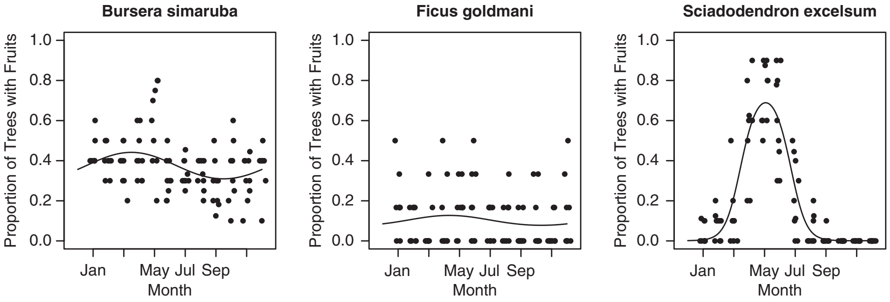

Fig. 10.2 Monthly probability of fruit production for three species of capuchin fruit foods: the weakly seasonal but persistently fruiting *Bursera simaruba*, the aseasonal, asynchronous fig species *Ficus goldmani*, and the highly seasonal, highly synchronous *Sciadodendron excelsum*. Each point represents the proportion of fruiting trees for that species monthly, with monthly data from nine consecutive years. A light horizontal jitter was applied to the figure to increase the visibility of overlapping points

Table 10.2 The degree of seasonality of fruit production, peak fruit month, and the peak probability of fruit production for 38 capuchin fruit foods representing over 90% of the annual capuchin plant diet. Data is derived from generalized linear mixed models with sinusoidal terms of months as predictor variables, using 8 years of phenological data. Chi-square and p values are derived from comparisons between the seasonal and null models; a *p* value <0.05 indicates fruit is more likely to be produced in a particular time period annually

Species	χ^2	*p*	Peak month	Probability of fruiting in peak month (%)
Manilkara chicle	73.4	<0.001	January	25
Guazuma ulmifolia	198.6	<0.001	March	85
Luehea candida	13.8	<0.001	March	15
Malvaviscus arboreus	46.9	<0.001	March	30
Simarouba glauca	270.7	<0.001	March	55
Bursera simaruba	9.9	<0.01	April	40
Dipterodendron costaricense	156.8	<0.001	April	50
Genipa americana	158.5	<0.001	April	55
Sloanea terniflora	94.0	<0.001	April	55
Vachellia collinsii	97.7	<0.001	April	20
Sciadodendron excelsum	431.3	<0.001	May	70
Zuelania guidonia	297.7	<0.001	May	50
Byrsonima crassifolia	172.7	<0.001	June	50
Ficus hondurensis	30.7	<0.001	June	45
Ficus ovalis	24.2	<0.001	June	40
Sebastiana pavoniana	57.1	<0.001	June	25
Tabebuia ochracea	8.3	<0.05	June	10
Cecropia peltata	144.9	<0.001	July	60
Jacquinia nervosa	63.7	<0.001	July	60
Psidium guajava	65.9	<0.001	July	50
Trichilia martiana	164.4	<0.001	July	50
Allophylus occidentalis	146.8	<0.001	August	40
Ficus cotinifolia	54.7	<0.001	August	30
Guettarda macrosperma	190.0	<0.001	August	40
Maclura tinctoria	379.7	<0.001	August	65
Spondias mombin	426.1	<0.001	August	70
Stemmadenia obovata	72.4	<0.001	August	30
Cordia panamensis	26.1	<0.001	September	15
Sapium glandulosum	61.0	<0.001	September	30
Randia thurberi	20.8	<0.001	October	30
Alibertia edulis	137.7	<0.001	November	60
Diospyros salicifolia	82.9	<0.001	November	35
Randia monantha	45.1	<0.001	November	25
Annona reticulata	42.7	<0.001	December	30
Karwinskia calderoni	375.6	<0.001	December	75
Trichilia americana	10.4	<0.01	December	25

(continued)

Table 10.2 (continued)

Species	χ^2	*p*	Peak month	Probability of fruiting in peak month (%)
Ficus goldmani	2.2	0.3306	April	15
Ficus morazaniana	1.6	0.4501	September	15

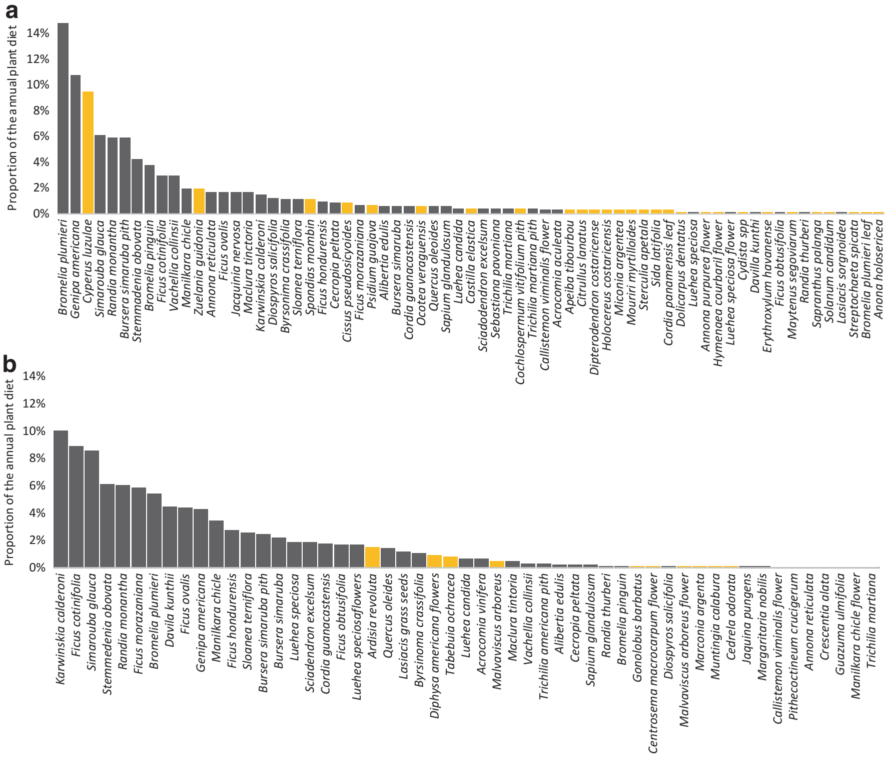

Fig. 10.3 The frequency of plant feeding records for each food item in (**a**) 2007–2008, and (**b**) 2013–2014. Lighter bars indicate foods that were not consumed in the other sampling period ($n = 42$); these "unique" foods account for 10% of the total plant food diet

food diet. Of these foods only used in one sampling period, only one, *Cyperus luzulae*, was amongst the ten most important food species (3rd, 2007–2008). It is important to note that this study does not reflect the total range of plant foods utilized by capuchins and that scan sampling is known to underestimate rare, fleeting behaviours, a shortcoming that can be compensated for via all-occurrences sampling (Leighton 1993; Melin et al. 2014).

Capuchins had high levels of diversity in their plant diet in both sampling periods, with 67 plant foods consumed in 2007–2008 and 53 in 2013–2014. Most food items that were consumed constituted less than 5% of the annual plant diet, and only four foods (*Bromelia plumieri*, 15% in 2007–2008; *Genipa americana*, 11% in 2007–2008; *Cyperus luzulae*, 10% in 2007–2008; *Karwinskia calderoni*, 10% in 2013–2014) accounted for 10% or more of the annual diet during either season.

The most important food items remained relatively static interannually. In both sampling periods, the top 10 foods accounted for approximately 2/3 of the plant food diet, and six of the top 10 foods annually remained consistent during both sampling periods. The 43 species included in phenology transects accounted for over 90% of the plant diet. Of the plant foods not currently included in phenology transects, very few were consumed in large quantities, the exceptions being grass seeds of *Cyperus luzulae* (3rd ranked 2007–2008), pith of *Bursera simaruba* (6th 2007–2008), and the fruits of *Davilla kunthii* (8th 2013–2014), a liana.

10.3.4 How Scale Affects Dietary Diversity and Importance Measures

Diet diversity varied greatly throughout the 2013–2014 sampling period, during which observation periods were broken into equal 2-week cycles. The number of different plant food items consumed by all three capuchin groups within a 2-week cycle varied from a low of 2 to a high of over 20 (Fig. 10.4). However, during 2-week cycles with high levels of diversity, typically only a few plant foods

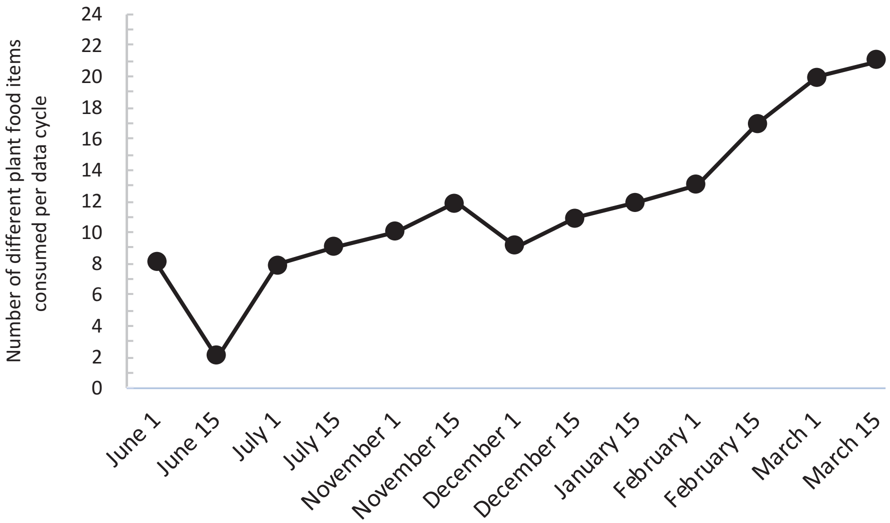

Fig. 10.4 Dietary diversity of white-faced capuchins within 2-week behavioural observation periods ("cycles") during 2013–2014. The date listed on the x-axis is the start of the 2-week window for a given cycle. Data were not collected August–October 2013

were consumed with high frequencies. For example, during 12 of 13 cycles, the top two foods accounted for over half the scan records for that period (Fig. 10.5). The diversity of plant food use by white-faced capuchins was lowest in the early wet season (June) and peaked in the late dry season (March). This pattern appeared to be inversely related to invertebrate foraging: during the period of highest invertebrate reliance, the diversity of the plant diet was lowest (Fig. 10.6). It is important to note that diet diversity is measured at the group level per cycle and is a binary presence/absence response; therefore it does not measure the importance of any food items in the diet or how frequently any item was consumed.

The timescale of the study period affects which foods ranked as the most important in the capuchin diet: several foods were very important for at least one 2-week cycle yet did not show up amongst the most important foods annually (Table 10.3). The timing of a cycle also affected importance: very few foods remained important in the capuchin diet for multiple cycles, and only one species (*Ficus cotinifolia*) was the most important food for multiple cycles. Figs (*Ficus* spp.) in general were extremely important throughout the year and were a top 3 food item in 8/13 cycles.

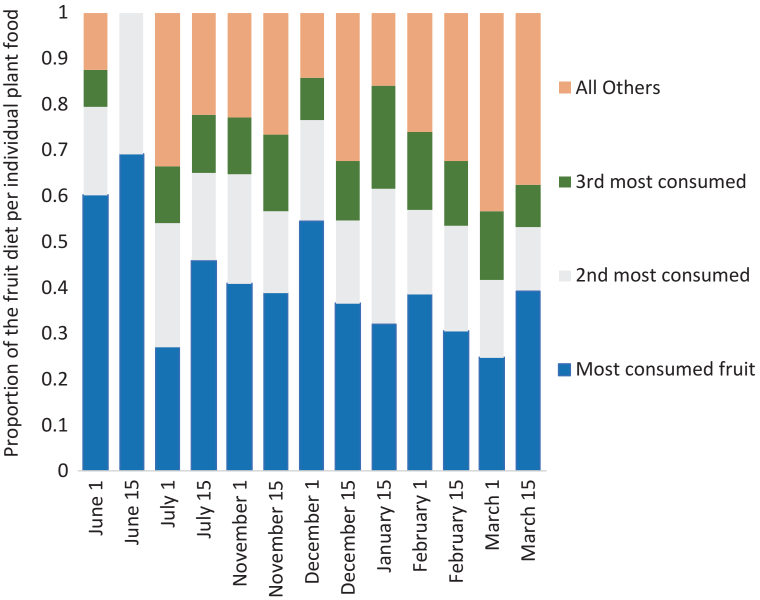

Fig. 10.5 Proportion of the capuchin plant food diet comprised of the three most consumed food items and all other plant foods (i.e., fourth up to 21st) within each 2-week study cycle. At short (2-week) timescales, the capuchin diet is dominated by just a few food items

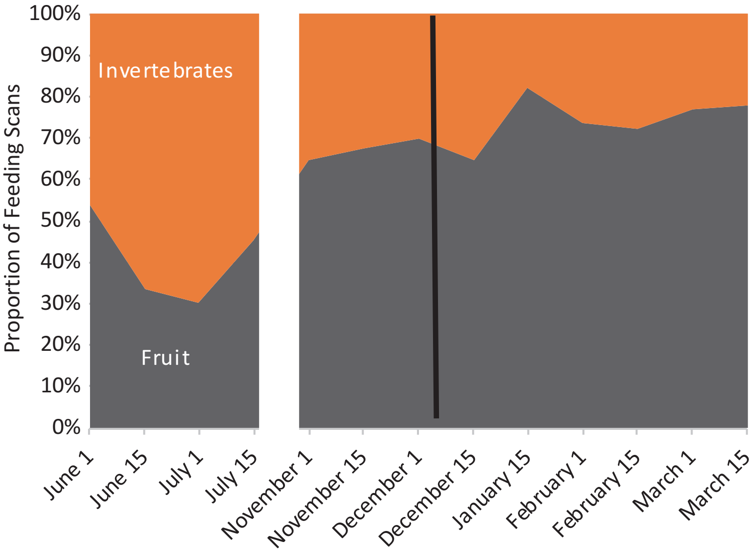

Fig. 10.6 Proportion of scan samples where capuchins were foraging for an identifiable type of invertebrate (light area) or plant food (dark area) during the 2013–2014 sampling period ($n = 2680$ scan samples). The vertical black bar is a rough estimate of the onset of the dry season in late 2013. Data collection did not occur August–October 2013

Table 10.3 The three most important (most frequently consumed) capuchin plant foods observed for each 2-week behavioural observation period ("cycle") in 2013–2014. Species highlighted in bold are foods that were also a top 10 food item in terms of annual importance

	Importance rank of food per cycle		
Cycle midpoint	1st	2nd	3rd
June 1	***Genipa americana***	*Tabebuia ochracea*	*Acrocomia vinifera*
June 15	*Sciadendron excelsum*	***Genipa americana***	n/a
July 1	***Ficus ovalis***	***Genipa americana***	*Quercus oleoides* *Byrsonima crassifolia*
July 15	*Cordia guanacastensis*	*Byrsonima crassifolia*	*Maclura tinctoria*
November 1	***Stemmadenia obovata***	*Bursera simaruba* (pith)	***Ficus cotinifolia***
November 15	*Ficus hondurensis*	***Stemmadenia obovata***	*Lasiacis* species (grass)
December 1	***Ficus cotinifolia***	***Stemmadenia obovata***	*Quercus oleoides*
December 15	***Ficus cotinifolia***	*Luehea speciosa* (flowers)	***Ficus morazaniana***
January 15	***Ficus ovalis***	***Karwinskia calderoni***	***Manilkara chicle***
February 1	***Karwinskia calderoni***	***Ficus morazaniana***	***Randia monantha***
February 15	***Randia monantha***	***Karwinskia calderoni***	***Bromelia plumieri***
March 1	***Davilla kunthii***	***Bromelia plumieri***	***Ficus morazaniana***
March 15	***Simarouba glauca***	*Sloanea ternifolia*	*Bursera simaruba*

10.4 Discussion

10.4.1 How Does Fruit Phenology Vary, and How Does This Variation Affect Capuchin Foraging?

Our study reveals that while most plant species predictably produce fruit around the same annual time period, there is relatively low probability of fruit production for most species for any given month and large interannual variation in the overall monthly and annual fruit abundance. The fruit production patterns observed here for most species (seasonal production but low monthly predictability) are consistent with other field sites (Chapman et al. 1999). Such interannual phenological variation provides a natural experiment, allowing for comparison of food selectivity during periods when several plants are concurrently productive and years in which one or more species are unproductive in the same timeframe.

Many of the top annual food items (e.g. *Karwinskia calderoni, Spondias mombin, Zuelania guidonia*) are very large trees with large, fleshy fruit crops that can hold an entire capuchin group repeatedly over multiple days (Melin et al. 2014; Parr et al. 2011). These important large-crop species that fruit during low-resource abundance period are likely the most crucial individual food item for capuchins, and their absence in a given year is likely the most detrimental. For example, in May, which is the transition period between the dry and wet seasons in Santa Rosa, only *Zuelania guidonia* and *Sciadendron excelsum* are in their peak fruiting windows, and ripe fruit biomass data indicates that May is extremely variable for fruit productivity, with occasional productive years tempered by more typical low-productivity years (median of 100 kg/ha; Fig. 10.1b). Although early May was not included in the sampling period during the 2013–2014 field season, this study also demonstrates that capuchin plant diet diversity is at its lowest immediately after this time, with <10 plant foods consumed in late May (and only two in mid-late June). *Zuelania guidonia* and *Sciadendron excelsum* are large and two of the most predictably seasonal and synchronous fruiting species (Table 10.2). Should both species fail to produce in a particularly bad year, capuchins could be faced with a severe food shortage. While starvation to the point of population crashes is thought to be rare, it has been observed elsewhere, in one instance reducing the local white-faced capuchin population by an estimated 70% (Milton and Giacalone 2014). Future research at this field site will be telling as to how plastic the capuchin diet truly is: Santa Rosa experienced extreme drought in 2015 (Fedigan unpublished data), leading to the lowest recorded biomass estimates for capuchin foods since the inception of phenology data collection. Many fruit crops (e.g. *Spondias mombin*, *Sloanea terniflora, Zuelania guidonia*) that are typically very important annually (i.e. amongst the ten most consumed foods annually) failed to produce altogether. Knowing which foods capuchins switch to in times of preferred food shortages will provide great insight into the limits of their foraging plasticity and may help to predict their success adapting to escalating climactic and environmental variation.

10.4.2 How Diverse Is the Capuchin Diet, and How Does It Vary at Different Timescales?

Over the course of two sampling periods comparing the same time periods, we observed 90 different plant foods being consumed by capuchins, half of which were only used in one of two periods, and the most important food item accounted for no more than 15% of the annual plant diet. While studies reporting on the types of foods consumed at the species level remain rare, our results are typical for a frugivorous primate, although studies from other field sites inhabited by capuchins (both *Cebus and Sapajus* species) reveal slightly less plant diet diversity (Guillotin et al. 1994; Perry and Ordonez Jimenez 2006; Simmen and Sabatier 1996). Possibly this is an artefact of different study lengths and methods, but an alternative hypothesis is that because Santa Rosa is regenerating tropical dry forest, it is less productive than wetter, more established forests studied elsewhere, leading to reduced consumption of any one plant species and the inclusion of lower-quality foods. One study across three sites in Costa Rica suggests that while the vast majority of foods are consumed by white-faced capuchins at different sites, there are “cultural” differences that result in some edible species being ignored by a population (Panger et al. 2002). As long-term data become available at other field sites, comparative studies of capuchin foraging strategies investigating the differences in the long-term diet and forest structure will be illuminating.

When compared to most primates, the capuchin diet appears to be more diverse than average. Of the eight sympatric primate species inhabiting Gabon rainforest observed over 10 years, only western lowland gorillas (*Gorilla gorilla gorilla*, 188 items) and central chimpanzees (*Pan troglodytes troglodytes*, 161 items) utilized more plant food types than Santa Rosa’s capuchins, while primates more similarly sized to capuchins had much less diverse plant diets (Tutin et al. 1997). Furthermore, many of the food items consumed by these two ape species were leaves, likely primarily as a protein source (Felton et al. 2009). Capuchins rarely consume leaves, instead focusing their protein intake efforts on invertebrates. To accurately compare the diversity of diets requires a holistic approach including all food classes and accounting for macro- and micronutrient requirements. However, due to the size of most invertebrate foods, the speed with which capuchins locate and consume them, and their patchiness in the environment, it is currently impossible to accurately assess the diversity of invertebrates consumed by capuchins at the level of detail possible for plant parts. Recent advances in DNA barcoding techniques of faecal samples are promising and may prove to be the key to better understanding the overall dietary diversity of insectivorous primates (Mallott et al. 2016).

The importance of different food items within different timeframes also varied considerably, demonstrating the scale-dependent nature of the diet. For example, in 2013, only two plant foods were included in the diet in early June, and there are strong indications of an inverse relationship between the diversity of the plant diet and the consumption of invertebrates. Typically during this time period, which was near the start of the rainy season, much of the capuchin day is spent gleaning invertebrates off plant surfaces, and a significant proportion of the diet is comprised of Lepidoptera larvae (Bergstrom 2015; Mallott et al. 2016). Fruit biomass estimates also indicate this time period to be a period of relatively low fruit availability for capuchins (Fig. 10.5b), which suggests that caterpillars may be essential to their ability to survive a lean "crunch" period, an interpretation supported by recent work on capuchin metabolism (Bergstrom et al. 2017; Milton and Giacalone 2014). Whether capuchins are consuming less fruit (and fewer species of fruit) because there is a fruit food shortage, or simply because they prefer to eat caterpillars, is a question worthy of future investigation.

Overall, which specific food items are important, and even how important food classes (e.g. fruits) are to the capuchin diet, is variable depending on the length of time investigated as well as the specific time the investigation occurs. This finding highlights the need for longitudinal studies that encompass multiple years and different seasons to reliably capture the full range of foraging behaviours of which this species is capable. Capuchins have a very narrow diet at times and are surprisingly dependent on a small selection of food items over short timescales. Whether this is driven by preference for maximum exploitation of a resource while it is available or a lack of other options needs to be further explored. It is likely that the phenology and abundance patterns of certain important food species are influential.

10.4.3 Conclusion and Future Directions

Perhaps a better question than "what characteristics do capuchin foods share" is "what plant foods are present that capuchins do NOT eat, and what stops them from doing so?" This question need not be limited to phenological differences between foods and non-food plant species. Food quality is determined by many factors beyond the characteristics examined in this study, including accessibility, availability, nutritional quality, and the intrinsic characteristics of the consumer (Felton et al. 2009; Lambert and Rothman 2015). One important question yet to be answered is whether dietary fruits share morphological or chemical characteristics that make them attractive to capuchins and whether this may even vary between study sites due to environmental characteristics. For example, two hard-shelled fruits common to Costa Rican dry forest (*Guazuma ulmifolia* and *Sterculia apetala*) are typically not consumed by Santa Rosa capuchins, whereas both are consumed in high proportions by capuchins living in the nearby Lomas Barbudal Biological Reserve (Panger et al. 2002). Comparing the physical qualities (particularly hardness) of these fruits between sites, as well as the overall forest phenological patterns during the times these species are in fruit at both field sites, could further strengthen our understanding of capuchin food choice. The interaction effects between fruiting patterns and fruit quality are also likely to prove important. For example, capuchins may consume fruits that appear unpredictably and for short time periods only if they are of particularly high quality. Fortunately, vegetation transect work in Santa Rosa has resulted in an extensive tree database, cataloguing nearly 50,000 trees to the species level within capuchin home ranges. From this dataset, future research can be directed towards determining which non-food species are most abundant but not consumed and from there to conduct a comparison of characteristics that are not shared with important dietary plant species.

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References

Altmann SA (2009) Fallback foods, eclectic omnivores, and the packaging problem. Am J Phys Anthropol 140:615–629. https://doi.org/10.1002/ajpa.21097

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67. https://doi.org/10.18637/jss.v067.i01

Bergstrom ML (2015) Seasonal effects on the nutrition and energetic condition of female white-faced Capuchin monkeys. University of Calgary

Bergstrom ML, Emery Thompson M, Melin AD, Fedigan LM (2017) Using urinary parameters to estimate seasonal variation in the physical condition of female white-faced capuchin monkeys (*Cebus capucinus imitator*). Am J Phys Anthropol. https://doi.org/10.1002/ajpa.23239

Bergstrom ML, Melin AD, Myers MS, Fedigan LM (2018) Dietary profile, food composition, and nutritional intake of female white-faced capuchins. In: Kalbitzer U, Jack KM (eds) Primate life histories, sex roles, and adaptability – essays in honour of Linda M. Fedigan., developments in primatology: progress and prospects. Springer, New York, pp 213–238

Boyle WA, Bronstein JL (2012) Phenology of tropical understory trees: patterns and correlates. Rev Biol Trop 60:1415–1430

Brugiere D, Gautier J-P, Moungazi A, Gautier-Hion A (2002) Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. Int J Primatol 23:999–1024

Campera M, Serra V, Balestri M, Barresi M, Ravaolahy M, Randriatafika F, Donati G (2014) Effects of habitat quality and seasonality on ranging patterns of collared Brown Lemur (Eulemur collaris) in littoral Forest fragments. Int J Primatol 35:957–975. https://doi.org/10.1007/s10764-014-9780-6

Campos FA (2018, this volume) A synthesis of long-term environmental change in Santa Rosa, Costa Rica. In: Kalbitzer U, Jack KM (Eds) Primate life histories, sex roles, and adaptability – essays in honour of Linda M. Fedigan, developments in primatology: progress and prospects. Springer, New York, pp 331–354

Campos FA, Fedigan LM (2009) Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Am J Phys Anthropol 138:101–111. https://doi.org/10.1002/ajpa.20908

Campos FA, Bergstrom ML, Childers A, Hogan JD, Jack KM, Melin AD, Mosdossy KN, Myers MS, Parr NA, Sargeant E, Schoof VAM, Fedigan LM (2014) Drivers of home range characteristics across spatiotemporal scales in a Neotropical primate, Cebus capucinus. Anim Behav 91:93–109. https://doi.org/10.1016/j.anbehav.2014.03.007

Chapman CA (1995) Primate seed dispersal: coevolution and conservation implications. Evol Anthropol 4:74–82

Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. J Trop Ecol 15:189–211

Dahlgren JP, von Zeipel H, Ehrlén J (2007) Variation in vegetative and flowering phenology in a forest herb caused by environmental heterogeneity. Am J Bot 94:1570–1576

DeGama-Blanchet HN, Fedigan LM (2006) The effects of forest fragment age, isolation, size, habitat type, and water availability on monkey density in a tropical dry forest. In: New perspectives in the study of Mesoamerican primates. Springer, New York, pp 165–188

Felton AM, Felton A, Lindenmayer DB, Foley WJ (2009) Nutritional goals of wild primates. Funct Ecol 23:70–78. https://doi.org/10.1111/j.1365-2435.2008.01526.x

Fenner M (1998) The phenology of growth and reproduction in plants. Perspect Plant Ecol Evol Syst 1:78–91

Fragaszy DM, Visalberghi E, Fedigan LM (2004) The complete capuchin: the biology of the genus *Cebus*. Cambridge University Press, Cambridge/New York

Gautier-Hion A, Duplantier J-M, Quris R, Feer F, Sourd C, Decoux J-P, Dubost G, Emmons L, Erard C, Hecketsweiler P et al (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65:324–337

Guillotin M, Dubost G, Sabatier D (1994) Food choice and food competition among the three major primate species of French Guiana. J Zool 233:551–579

Hilje B, Calvo-Alvarado J, Jiménez-Rodríguez C, Sánchez-Azofeifa A (2015) Tree species composition, breeding systems, and pollination and dispersal syndromes in three Forest successional stages in a tropical dry Forest in Mesoamerica. Trop Conserv Sci 8:76–94. https://doi.org/10.1177/194008291500800109

Hogan JD, Melin AD, Mosdossy KN, Fedigan LM (2016) Seasonal importance of flowers to Costa Rican capuchins (*Cebus capucinus imitator*): implications for plant and primate. Am J Phys Anthropol 161:591. https://doi.org/10.1002/ajpa.23059

Janzen DH (1988) Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson EO (ed) Biodiversity. National Academy Press, Washington, DC, pp 130–137

Lambert JE, Rothman JM (2015) Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. Annu Rev. Anthropol 44:493–512. https://doi.org/10.1146/annurev-anthro-102313-025928

Leighton M (1993) Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. Int J Primatol 14:257–313

Mallott EK, Garber PA, Malhi RS (2017) Integrating feeding behavior, ecological data, and DNA barcoding to identify developmental differences in invertebrate foraging strategies in wild white-faced capuchins (Cebus capucinus). Am J Phys Anthropol 162(2):241–254. https://doi.org/10.1002/ajpa.23113

Marshall AJ, Boyko CM, Feilen KL, Boyko RH, Leighton M (2009) Defining fallback foods and assessing their importance in primate ecology and evolution. Am J Phys Anthropol 140:603–614. https://doi.org/10.1002/ajpa.21082

Marshall AJ, Beaudrot L, Wittmer HU (2014) Responses of Primates and other frugivorous vertebrates to plant resource variability over space and time at Gunung Palung National Park. Int J Primatol 35:1178–1201. https://doi.org/10.1007/s10764-014-9774-4

Melin AD, Hiramatsu C, Parr NA, Matsushita Y, Kawamura S, Fedigan LM (2014) The behavioral ecology of color vision: considering fruit conspicuity, detection distance and dietary importance. Int J Primatol 35:258–287. https://doi.org/10.1007/s10764-013-9730-8

Milton K, Giacalone J (2014) Differential effects of unusual climatic stress on capuchin (*Cebus capucinus*) and howler monkey (*Alouatta palliata*) populations on Barro Colorado Island, Panama: Climatic stress and differential mortality. Am J Primatol 76:249–261. https://doi.org/10.1002/ajp.22229

Nagy-Reis MB, Setz EZF (2016) Foraging strategies of black-fronted titi monkeys (Callicebus nigrifrons) in relation to food availability in a seasonal tropical forest. Primates. https://doi.org/10.1007/s10329-016-0556-9

Panger MA, Perry S, Rose L, Gros-Louis J, Vogel E, Mackinnon KC, Baker M (2002) Cross-site differences in foraging behavior of white-faced capuchins (Cebus capucinus). Am J Phys Anthropol 119:52–66. https://doi.org/10.1002/ajpa.10103

Parr NA, Melin AD, Fedigan LM (2011) Figs are more than fallback foods: the relationship between *Ficus* and *Cebus* in a tropical dry Forest. Int J Zool 2011:1–10. https://doi.org/10.1155/2011/967274

Perry S, Ordonez Jimenez JC (2006) The effects of food size, rarity, and processing complexity on white-faced capuchins' visual attention to foraging conspecifics. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding ecology in apes and other Primates. Ecological, physical and behavioral aspects. Cambridge University Press, Cambridge, pp 203–236

Peters RH, Cloutier S, Dube D, Evans A, Hastings P, Kaiser H, Kohn D, Sarwer-Foner B (1988) The allometry of the weight of fruit on trees and shrubs in Barbados. Oecologia 74:612–616

Pewsey A, Neuhauser M, Ruxton G (2013) Circular statistics in R, 1st edn. Oxford University Press, New York

Rose L (1997) Vertebrate predation and food-sharing in *Cebus* and *Pan*. Int J Primatol 18:727–765

Simmen B, Sabatier D (1996) Diets of some French Guianan primates: food composition and food choices. Int J Primatol 17:661–693

Snow AA, Whigham DF (1989) Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). Ecology 70:1286–1293

Sussman RW (1991) Primate origins and the evolution of angiosperms. Am J Primatol 23:209–223

Sussman RW, Rasmussen DT, Raven PH (2013) Rethinking primate origins again: primate origins again. Am J Primatol 75:95–106. https://doi.org/10.1002/ajp.22096

Tutin CE, Ham RM, White LJ, Harrison MJ (1997) The primate community of the Lopé reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. Am J Primatol 42:1–24

Valenta K, Nevo O, Martel C, Chapman CA (2016) Plant attractants: integrating insights from pollination and seed dispersal ecology. Evol Ecol. https://doi.org/10.1007/s10682-016-9870-3

Wright SJ, van Schaik CP (1994) Light and the phenology of tropical trees. Am Nat 143:192–199