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Editors

Primate Life Histories, Sex Roles, and Adaptability

Essays in Honour of Linda M. Fedigan

Springer

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ISSN 1574-3489 ISSN 1574-3497 (electronic)
Developments in Primatology: Progress and Prospects
ISBN 978-3-319-98284-7 ISBN 978-3-319-98285-4 (eBook)
https://doi.org/10.1007/978-3-319-98285-4

Library of Congress Control Number: 2018958642

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Chapter 11
Dietary Profile, Food Composition, and Nutritional Intake of Female White-Faced Capuchins

Mackenzie L. Bergstrom, Amanda D. Melin, Monica S. Myers, and Linda M. Fedigan

Abstract Seasonal variation in food availability and nutritional intake can ultimately affect female reproductive success. Although many primate studies have looked at foraging behaviour as a measure of diet, nutritional ecology and associated physiological consequences are a relatively new area of research. We present data on variation in the dietary profiles, foraging behaviour, and nutritional intake of female white-faced capuchins (*Cebus capucinus imitator*) in response to temporal variation in food abundance within the home ranges of three groups in the Área de Conservación Guanacaste, Sector Santa Rosa, Costa Rica. We estimated nutritional requirements based on published laboratory research and nutritional standards to determine whether females meet requirements in the face of seasonal variation in food abundance. Our results show that fruit contributed most to overall energy gain despite females devoting a greater proportion of foraging time to invertebrates; thus time spent foraging does not accurately reflect energy intake. On a dry matter basis, fruits provided the most important source of water-soluble carbohydrates, whereas high proportions of protein intake came from invertebrates, particularly when fruit availability was low. However, the greater weight of fruit items compared to invertebrates on a dry matter basis likely contributed to females' ability to consume macronutrients at higher rates while foraging on fruit due to higher mass intake per unit time. Requirement estimates and observed intake revealed that there are times

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Electronic supplementary material: The online version of this chapter (https://doi.org/10.1007/978-3-319-98285-4_11) contains supplementary material, which is available to authorized users.

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U. Kalbitzer, K. M. Jack (eds.), *Primate Life Histories, Sex Roles, and Adaptability*, Developments in Primatology: Progress and Prospects,
https://doi.org/10.1007/978-3-319-98285-4_11

during low-fruit seasons in which females do not appear to meet their minimum nutritional requirements, warranting further investigation into the physiological consequences of this shortfall.

Keywords Nutrition · Diet · Seasonal variation · Food availability · Neotropical primate

11.1 Introduction

Variation in the spatial and temporal abundance of food resources presents several challenges related to energy and nutrient availability that may ultimately affect the reproductive success of mammals living in seasonal habitats (Clutton-Brock and Harvey 1977; Clutton-Brock et al. 1982; Bronson 1985). Gaining access to the food resources necessary for important biological processes such as growth, maintenance of body condition, and reproduction greatly influences the survival and reproductive success of mammals, including primates (Altmann 1998). Therefore, primates may attempt to maximize overall energy intake, maximize specific nutrient intake (e.g. protein), avoid secondary plant metabolites (e.g. tannins), minimize the intake of factors that inhibit efficient digestion (e.g. fibre), and/or balance the intake of nutrients or modify behaviour to reduce energy expenditure to meet their nutritional goals (reviewed by Felton et al. 2009a). If unsuccessful at meeting nutritional requirements, consequences include weight loss, decelerated growth and development, decreased reproductive output, and increased mortality or population-level changes in density and distribution (van Schaik et al. 1993; Kay et al. 1997).

In addition to ecological variation in nutrient abundance, there is considerable variation in nutritional demands related to morphology that impact the growth and development of individuals as well as the care of offspring and reproductive success across an individual's lifespan. Males and females often have dietary differences due to the added metabolic demands of the larger body size of males in sexually dimorphic species and of energetically demanding reproductive states (i.e. late gestation and early lactation) for females (Bell 1971; Clutton-Brock et al. 1982). Nutritional intake and body condition can significantly affect female lifetime reproductive success by influencing the timing of reproductive maturation as well as the persistence of ovulatory cycling at regular intervals. Previous studies of human and non-human primates have shown that females who consume a high-quality diet and maintain better body condition, or time reproduction with food abundance, give birth at an earlier age and/or exhibit higher rates of reproduction and infant survival than do other females (e.g. reviewed in humans and apes, Bentley 1999; in humans, Voland 1998; in marmosets, Tardif and Jaquish 1997; in tamarins, Miller et al. 2006; in mangabeys, McCabe and Emery Thompson 2013; see Chapter by McCabe and Fernandez 2018, in this Volume). Maternal nutrient intake during gestation impacts foetal development (reviewed by Hinde and Milligan 2011), with consequences as extreme as impairment of foetal cerebral development due to maternal nutrient restriction (baboons, *Papio* spp.; Antonow-Schlorke et al. 2011). Nutritional intake by primates during infancy can influence the secretion of hormones and growth factors, also leading to long-term effects on growth, metabolism, and susceptibility to disease (Mott et al. 1990, 1991; Lucas 1998), which may ultimately impact reproductive success (Altmann 1991).

We investigate seasonal variation in foraging behaviour (i.e. actively searching for and consuming food items), dietary profile (i.e. the types of foods consumed by female capuchins), and nutritional intake as it relates to broad-scale estimates of the requirements in a wild population of white-faced capuchin monkeys (*Cebus capucinus imitator*). Capuchins are arboreal monkeys that make use of multiple forest strata to exploit a wide diversity of resources including fruit (also encompassing seeds, grasses, bromeliads, and arils), invertebrates, flowers, pith, and vertebrates (Chapman and Fedigan 1990; Fragaszy et al. 2004). They are broadly categorized as omnivorous in that they consume foods from multiple trophic levels, and they are specifically categorized as frugivore-insectivores since fruit and invertebrates make up the majority of their diet (Fragaszy et al. 2004). Capuchins are sexually dimorphic in body mass (*Cebus* spp. males = 3.1 kg, females = 2.3 kg; Ford and Davis 1992), and sex has been shown to be a strong predictor of differences in foraging activities and of the types of foods ingested. White-faced capuchin males and females differ in foraging strategies in that males spend more time foraging for invertebrates on the ground, whereas females spend more time foraging for embedded invertebrates (Melin et al. 2010). In other capuchin species, males have been reported to forage more on animal matter and females to focus more of their foraging efforts on plant-based food items (e.g. wedge-capped capuchins, *C. olivaceus*, Fragaszy and Boinski 1995).

To better understand the relationship between foraging behaviour and diet, it is important to estimate species-specific nutritional demands for maintenance, reproduction, and growth. Unfortunately, species-specific values and information on metabolizable energy (i.e. gross energy per food item minus the undigested energy lost in the faeces, urine, and combustible gases) are unknown for most non-human primate species (National Research Council [NRC] 2003). The dietary and morphological similarities between capuchins and humans (e.g. relatively large small intestine and small caecum) allow for broad-level cross-species inferences and comparisons regarding digestive processes contributing to nutrition and energy gain (Chivers and Hladik 1980; Milton 1987); however, humans can likely digest fibre to a greater extent due to slower gut passage time (Cummings et al. 1976; Milton 1981).

By estimating nutritional requirements and determining species-specific patterns of temporal variation in foraging behaviour and nutritional intake, we can better understand variation in reproductive success in primates living in seasonal habitats across the primate order. However, a number of factors complicate a simple presentation of how primates use food resources to meet nutritional needs, including seasonality of resources, variation in dietary food types, variation in intake rates as a result of food distribution and required processing, and differences in the energy and macronutrient availability across food types (Oftedal et al. 1991). It is therefore important to consider these confounding factors and directly assess the relationships among diet composition, nutritional intake, and behaviour rather than making assumptions regarding diet based on foraging behaviour alone. Here, we investigate the nutritional ecology of adult female white-faced capuchin monkeys in Sector Santa Rosa, Costa Rica, by measuring ecological variation (i.e. food abundance), foraging behaviour, and dietary profile, as well as the nutritional composition of food items and nutrient intake with respect to estimated nutritional requirements. We address the following sets of questions:

1. Characterization of female foraging budgets, dietary profile, and intake:
    (a) What percentage of total foraging time do females spend on different types of food (fruits, flowers, invertebrates, pith, and vertebrates)?
    (b) What is the dietary profile of female capuchins?
    (c) Is foraging time representative of intake?
2. Nutritional composition of capuchin foods:
    (a) Does the macronutrient composition and energy density of capuchin foods differ across food types (i.e. fruit, seeds, flowers, caterpillars, and other invertebrates)?
    (b) Do females consume macronutrients and energy at different rates depending on the type of food eaten?
3. Evaluation of nutritional requirements and intake:
    (a) What are the estimated energy intake requirements for female capuchins?
    (b) How do foraging behaviour, energy intake, and macronutrient intake differ in accordance with variation in fruit abundance?

By enhancing our understanding of the foraging behaviour and nutritional composition of foods eaten by white-faced capuchins, we can estimate whether they are meeting nutritional requirements, gain species-specific insight into the range of dietary flexibility exhibited by females, and identify limiting factors that may influence how they meet their nutritional goals. Knowledge of foraging behaviour and nutrition in wild populations may also help to inform captive management practices and in situ conservation efforts. More broadly, these data are valuable for making cross-species comparisons linking foraging ecology to reproductive success and patterns of sociality.

11.2 Methods

11.2.1 Study Site

We conducted this study in the highly seasonal tropical dry forest of Sector Santa Rosa (SSR; 10°50′30′′N, 85°37′0′′W), in the Área de Conservación Guanacaste, northwestern Costa Rica. The rainy season extends from mid-May until mid-November (see Chapter by Campos 2018, in this Volume). During the study period (2009–2011), the mean annual rainfall based on daily records was 2304 mm (SD = 737), only 32 mm of which fell during dry season months. The temperature ranged from a mean minimum of 22.9 °C (SD = 0.1) in the wet season to a mean maximum of 29.6 °C (SD = 0.8) during the dry season. We recorded daily temperature using a Kestrel Pocket Weather Tracker (Nielsen-Kellerman Co., Bloomberg, Pennsylvania) and daily rainfall using a standard cylindrical rain gauge.

11.2.2 Study Subjects

White-faced capuchins compete directly over fruit (Vogel 2005), a high-quality, clumped, and monopolizable food resource (Isbell 1991), but also show dietary flexibility by altering foraging behaviour to exploit alternate food resources in their seasonal environment (i.e. distinct rainy and dry seasons) where abundance, distribution, and nutritional quality of resources fluctuate. The SSR population shows considerable variation in diet and ranging patterns during an annual cycle (Chapman and Fedigan 1990; McCabe 2005; Campos et al. 2014; Melin et al. 2014b; Mosdossy et al. 2015). Reproductive events fluctuate with seasonal variation in food availability; although not strictly seasonal breeders, female births increase considerably between April and September (Carnegie et al. 2011a), but the role of nutrition and energy balance in the timing and success of reproduction is unknown.

We observed three study groups, LV, CP, and GN, over a period of 20 months between September 2009 and May 2011. The average annual home range size for capuchin groups in this study population is 197.77 ± 12.52 hectares (Campos et al. 2014). We collected data during three 4-month periods (Sep–Dec 2009, May–Aug 2010, and Jan–Apr 2011) to account for seasonal variation. With the aid of one to two field assistants per season, we followed groups from dawn until dusk on a rotational basis for 4 to 6 days per group per month [in total 575 focal hours: LV = 120 h, CP = 227 h, GN = 228 h); 2124 h of observational contact with the groups]. The size of the study groups ranged from 20 to 37 individually known subjects (LV, 20–23; CP, 26–33; GN, 33–37). Details of the demographics for study groups are reported in Bergstrom (2015).

We focused data collection on adult females because their reproductive success is thought to be more directly constrained by access to food relative to males (Wrangham 1980; Sterck et al. 1997; Koenig 2002). We classified females ≥ 6 years old as adults based on the average age at first conception (Carnegie et al. 2011b), unless they conceived before that time, in which case they were included as an adult at the beginning of the data collection season during which they gave birth to their first infant. We did not include females that disappeared or died during the study ($N = 3$) due to lack of data on these individuals. The number of female study subjects ranged from 24 to 25 (LV: 5; CP: 10; GN: 9–10) per season due to the maturation and inclusion of an additional female in GN group during the course of the study.

11.2.3 Estimating Capuchin Nutritional Requirements

We estimated the nutritional requirements of capuchins based on the general metabolic demands determined for mammals as well as published studies of the nutritional requirements for maintenance and growth of captive capuchins. Mean energy intake requirements for maintenance and growth can be estimated for animals by measuring energy intake, energy expenditure, and changes in body mass and have been documented for captive primates, including adult male capuchins (*Cebus albifrons*, body weight 1.5–3.0 kg) as 395 kJ/kg/day (range 250–500 kJ/kg/day) (Ausman and Hegsted 1980). Accordingly, the estimated intake requirement for *Cebus capucinus imitator* females, who weigh an average of 2.54 kg (Smith and Jungers 1997), is roughly 1000 kJ per day, assuming intake is proportional to the change in body size. We broadly categorized female reproductive state per month (cycling, gestating, and lactating; see Carnegie et al. 2011b and Bergstrom 2015 for details on reproductive state categorization). We assigned a monthly energy coefficient of 1.00 for cycling females, 1.25 for pregnant females, and 1.50 for lactating females based on the estimated energy demands of each reproductive state (Key and Ross 1999). The overall energy intake requirement of 1000 kJ/day was thus estimated to be 1.25 times higher in pregnant females (1250 kJ/day) and 1.5 times higher in lactating females (1500 kJ/day).

11.2.4 Behavioural Data Collection

We collected behavioural data using 10-min focal animal follows and ad libitum sampling (Altmann 1974). Often, two people worked together to record behavioural data to ensure accuracy of data collection; one person dictated behaviours, while another recorded data on a hand-held computer (Psion Workabout MX). To observe focal females, we followed a random rotation schedule, outlined in Bergstrom and Fedigan (2010) and following Perry (1996) to achieve a representative and as unbiased sample as possible. During follows, we continuously recorded the general state behaviours of the focal female (e.g. travel, forage, rest, feed, social, and solitary) and detailed foraging event behaviours (e.g. feeding rates) (Bergstrom 2015).

We used durations of behaviours gathered during focal follows to calculate time budgets as well as ingestion rates for each female. We calculated the mean percentage of time all females spent in six broad behavioural states [forage, social, rest, travel, and other (which included self-direct, vigilant, and allospecific association)] by summing the amount of time spent in each category, dividing by the total amount of time that all females were observed across the entire study period, and then multiplying this value by 100. To construct foraging time budgets, we determined the percentage of time females spent actively foraging on different types of resources (invertebrates, fruit, flowers, pith, small vertebrates, and water/other) as well as visually foraging (whereby females visually searched trees without continuously handling substrates such as bark or leaves).

To compare the consumption patterns of broad food categories, foraging time was further divided by food type; we calculated ingestion rates as the number of food items eaten per minute of observed feeding time by species (i.e. consistent targeting of and hand-to-mouth ingestion of food items) and then averaged values for all items within the two most commonly consumed food types, fruit (including seeds) and invertebrates to obtain a mean value for these two categories (O'Malley and Fedigan 2005; McCabe and Fedigan 2007). Feeding bouts, which ranged from seconds to the entire 10-min focal follow, were used to calculate ingestion rates per plant species. Fruit species or invertebrate groups for which we observed less than five items, two bouts, or 10 min of total feeding time (across samples) were excluded from the dataset as these items were eaten too infrequently to accurately quantify ingestion rates. If an item was partially eaten during an observation, only the proportion eaten (e.g. 0.1 items) was used in the calculation of total items consumed per minute. Food characteristics (e.g. size and abundance) greatly differ across plant species and affect variation in the rate at which each species can be ingested. For example, larger-sized food items take longer to ingest, on average, and are consequently eaten at slower rates, and species that are more spatially clumped and abundant may be located and ingested more rapidly. Accordingly, we calculated energy and macronutrient intake rates (items/minute) to compare the importance of different food types (i.e. fruit, seeds, flowers, caterpillars, non-caterpillar invertebrates) in terms of the nutrients ingested.

To estimate energy consumption per day, we extrapolated the total energy intake from the energy ingested during 10-min focal follows. Energy ingested by each individual, determined based on observed intake and the energy content of each item, was summed and divided by daily focal time to determine hourly energy intake rates, and these were used to extrapolate the total estimated energy consumed based on the number of active hours. Although there are limitations to extrapolating from 10-min follows in that they are a snapshot of activity, the benefit to using this shorter sampling scheme is that more data points can be collected per individual and across individuals, both throughout the day and over a series of days, that may be more representative of the true variation in activity than fewer, longer focals (e.g. full day) (see Chapter by Melin et al. 2018, in this Volume). Capuchins feed very regularly from dawn until dusk, and we aimed to collect a sufficient number of focal follows to be representative of this variation in activity.

11.2.5 Ecological Data Collection

For nutritional analysis, we collected samples from plant species (including fruit, seeds, flowers, and pith) and broad categories of invertebrates (single species or groups of related species) consumed by female capuchins in the field, and we processed and dried them in the laboratory at the field station. Sample size per species ranged from five to thousands of specimens, depending on size and weight, to achieve a total dry weight of at least 16 grams, which was the minimum mass required by the lab where we sent samples for analysis (Dairy One Forage Laboratory, New York, USA). If sample collection was not possible on the day the species was observed to be eaten, we collected samples later (≤3 days for fruit and flowers) from as many of the locations in which foraging was observed as possible. Invertebrate samples were an exception; we collected those samples during a season in May 2013 dedicated to this analysis. Capuchins often consume specific parts of food items (shell, flesh, and seed); therefore, when processing fruits with multiple parts, we separated the shell from the flesh and cut away the pulp from the seed. We only analysed the part of the food item that was consumed by the capuchins for nutritional content unless separation of components resulted in loss of the item's integrity and composition (e.g. water content). Subsequently, we dehydrated the samples at 30 °C using a food dehydrator (Nesco American Harvest Gardenmaster Pro, Model FD-1020) and stored them in airtight waterproof bags with silica until exported for analysis.

We could not always taxonomically identify invertebrates on a fine scale. Consequently, we grouped invertebrate samples into the following broader categories for nutritional analysis: peppered roaches (*Archimandrita tesselata*), cicadas (*Fidicina mannifera*), shield bugs (Pentatomidae), ants (Hymenoptera), satellite sphinx caterpillars (*Eumorpha satellitia*, mean wet mass = 1.47 g), medium-sized noctuid caterpillars (*Euscirrhopterus poeyi* and *Gerra Hallowach01*, mean wet mass = 0.26 g), medium-sized caterpillars from various families (Lepidoptera), small-sized caterpillars from various families (Lepidoptera, mean wet mass = 0.05 g), jumping bean moth larvae (*Cydia deshaisiana*), crickets (Gryllidae), grasshoppers and katydids (Caelifera), wasp larvae (*Polistes*), scorpions (*Centruroides limbatus*), and a bulk category that included unidentified small non-caterpillar invertebrates. We collected, flash-froze, and dehydrated the invertebrate samples at a temperature of 42 °C using a hot air oven for 2–6 days, depending upon size and density, to avoid moulding that may occur when drying animal matter at slower rates (DSO-3000DF, Digisystem Laboratory Instruments Inc.).

Nutritional samples were consistently monitored for contamination; any food items showing signs of fermentation or moulding were discarded, and new samples were collected (Harborne 1984; Conklin-Brittain et al. 2006). Due to the higher risk of contamination associated with dehydrated animal matter, we stored invertebrate samples in a temperature and humidity-controlled room until exported for analysis. All samples were transported to Dairy One Forage Laboratory to measure the macronutrient composition (e.g. crude protein, crude fat, water-soluble carbohydrates, neutral detergent fibre, total ash, and organic matter; see Appendix A).

Because there can be large differences in the nutritional composition of plant foods of the same species across space and time (Chapman et al. 2003), we collected samples from multiple trees (two to ten individuals per species based on rarity, fruit size and density, and distribution across home ranges), and the collection of these plant samples spanned the period in which each species was eaten. Thus, values should be more representative of a species average, rather than tied to a specific time and location. We consider the nutritional values subsequently obtained as applicable to this study, but caution should be used when using these values for broad application.

For laboratory nutritional sample analysis, specifics regarding analytical procedures performed by Dairy One can be found in Appendix A. Briefly, additional drying was done to accurately calculate total dry mass. Moisture content was determined by first subtracting the final dry matter weight (grams) from the initial weight of the wet fruit sample collected in the field and then dividing that value by the total wet weight to obtain an overall percentage (Conklin-Brittain et al. 2006). Crude protein (CP) was measured; however, this measure does not subtract bound proteins, which are metabolically unavailable, and thus may overestimate the amount of protein intake by capuchins in this study. Crude fat (CF), water-soluble carbohydrates (WSC), and neutral detergent fibre (NDF) were also measured.

We used the per item macronutrient values determined by the laboratory nutritional analyses to calculate the total energy density of food items as described below. Energy density is an estimate of the total amount of digestible energy (in kJ or kcal) per gram of dry matter. Mean gross energy concentrations for macronutrients determined using bomb calorimetry and published by the National Research Council (2003) are known: 4.1 kcal for carbohydrates, 5.6 kcal for protein, and 9.4 kcal for fat. In an attempt to approximate the digestible portion of gross energy, physiologically available energy conversion factors assigned based on early studies of food digestibility (Merrill and Watt 1955) have been published for humans as 4 kcal for carbohydrates, 4 kcal for protein, and 9 kcal for fat. Unfortunately, requirements based on metabolizable energy (gross energy minus the undigested energy lost in faecal matter) for each nutritional component have not yet been quantified for primates (NRC 2003); therefore, we used the values reported for humans. Here, we converted from kilocalories to kilojoules (kJ) using the factor 4.184 (16.74, 16.74, and 37.66, respectively). We used Formula 1 to calculate the energy density (kJ per gram dry matter) of each food item, where CP is the proportion of dry mass as crude protein, WSC is the proportion of dry mass as water-soluble carbohydrates, and CF is the proportion of dry mass as crude fat (Janson 1985; NRC 2003). We multiplied energy density by the dry mass per item to calculate the energy per food item (kJ/item).

Formula 1

$$\mathrm{Energy}\left(\mathrm{kJ}\right)=\left(16.74\times\left(\mathrm{CP}+\mathrm{WSC}\right)\right)+\left(37.66\times\mathrm{CF}\right).$$

We did not include fibre (measured in this study as neutral detergent fibre, NDF) in this calculation for a number of reasons. First, given their frugivorous-insectivorous diet, *Cebus* monkeys have a simple gastrointestinal system and a relatively short gut transit time of approximately 3.5 h, which is comparable to other frugivorous platyrrhines (e.g. *Ateles*, 4.4 h) but much shorter than that of folivorous platyrrhines (e.g. *Alouatta*, 20.4 h) (Milton 1981). Second, because capuchins lack a specialized digestive system, it is unlikely that they are able to extract significant amounts of energy from difficult to digest plant materials such as fibre. Regarding invertebrate consumption, crude protein is likely a more accurate estimate of the energy available from chitin than is fibre for species like capuchins that produce chitinase (Finke 2007).

We collected and analysed a total of 53 plant-based food items and 10 invertebrate categories during this project. For species that we could not collect during this study for nutritional analyses, we used published data on specimens collected from Sector Santa Rosa, Costa Rica, by McCabe (2005); collected from the nearby site of Lomas Barbudal Biological Reserve, Costa Rica, by Vogel (unpublished, 2004, 2005); and information for one fruit species published by the US Department of Agriculture (USDA) (2014). We estimated energy values for unknown plant species or plant species for which we were unable to conduct nutritional analyses or use literature values. Specifically, when possible, we used the energy values for congeners of species with unknown values ($N = 1$) or species with similar size and composition ($N = 2$; Appendix B, C). When using congener species was not possible, we used the median energy value (kJ/item) for fruit, the mean energy value for flowers, and an assigned energy value for pith (1 kJ per 1-inch unit). Similarly, we calculated energy and macronutrient values per item for two groups of invertebrates (shield bugs and crickets), which were not analysed by Dairy One, using the mean macronutrient values for the same order of invertebrates (Hemiptera and Orthoptera, respectively) multiplied by the dry mass per item (obtained during sample collection for this study).

11.2.6 Fruit Abundance: Fruit Biomass (kg/ha) and Ripe Fruit Energy Density (kJ/ha)

To determine the energy density of ripe fruit (kJ/ha) in the study area per monthly round of data collection, we first calculated the fruit abundance in terms of ripe fruit biomass (kg/ha) using phenological data in combination with biological transects and then applied energy values (kJ/gram wet mass) per fruit species.

Tree abundance data were obtained from 151 botanical transects covering a total area of 3.02 hectares and distributed across all group home ranges (for details see Melin et al. 2014a). Following Peters et al. (1988), for each tree in the transect, the biomass was calculated using Formula 2, where F is the estimated grams of fruit produced by a tree of a given DBH and 47 and 1.9 are coefficients based on regressions between plant height and fruit weight generated using a number of tree species.

Formula 2

$$\text{Tree fruit biomass}\left(\text{F}\right) = 47 \times \text{DBH}^{1.9}$$

Monthly phenological data are collected as part of a long-term and ongoing collaborative project at SSR. We assessed the monthly fruit coverage and maturity values for data collected from January 2009 through December 2011 for approximately 8 individual trees ($\bar{x}$ = 7.93, SD = 2.46) for 30 fruit species. Although it would be ideal to have monthly phenological data for all dietary plants, this is unfeasible, and these 30 species comprise ca. 80% of the capuchin annual diet (Melin et al. 2014a). We used a 5-point index (0 = absent, 0–25% = 1, 25–50% = 2, 50–75% = 3, and 75–100% = 4) to assess the score for the percentage of fruit coverage (*C*) and the score for the percentage of mature fruit (*M*) (Melin Meachem 2011). These species represented 44% (9394 of 21,347) of the fruit ingestion events recorded during focal observations. Many of the capuchin food species missing from this list were either wind-dispersed species (e.g. *Luehea candida* and *L. speciosa*), for which the Peters et al. (1988) equation (Formula 2) is not likely to provide an accurate fruit biomass estimate, or species for which it is difficult to gain accurate phenological information such as lianas, shrubs, palms, or bromeliads. Our overall calculations of fruit abundance underestimate total fruit abundance; however, as the most consumed species, we feel they provide an accurate measure of the relative abundance of ripe fruit in each month of our study. We calculated a combined index score (CI) for each tree (*i*) by multiplying the proportion coverage index (*C*/4), by the proportion maturity index (*M*/4) (Campos et al. 2014). Using this combined index, trees were assigned the minimum score of 0 when the coverage or maturity indices were 0, and trees received the maximum score of 1 when the coverage and maturity was considered 100% (Formula 3).

Formula 3

$$\text{Tree combined index score}\left(\text{CI}_i\right) = \left(\frac{C}{4} \times \frac{M}{4}\right)$$

Then, we calculated the mean monthly index (MI) for each species (*s*) as the mean combined index (CI_i) score for that species in that month. The fruit biomass score per species (B_s) in kilograms per hectare (kg/ha) per month was calculated as the sum of F (from Formula 2) divided by the sampled area (3.02 ha) and multiplied by 1000 to convert grams to kilograms (Formula 4).

Formula 4

$$\text{Species ripe fruit biomass}\left(B_s\right) = \text{MI}_s \times 1000 \times \left(\frac{\sum_{i=1}^{n} F_i}{3.02}\right)$$

The monthly total energy availability from ripe fruit (EA) in kilojoules per hectare (kJ/ha) was calculated as the sum of the species-specific fruit biomass score (B_s) multiplied by the species-specific energy content E_s (kJ/kg wet weight) for all fruit species (Formula 5). We categorized data collection months as high- and low-energy density based on these calculations.

Formula 5

$$\text{Total ripe fruit energy availability}\left(\text{EA}\right) = \sum_{s=1}^{n} B_s \times E_s$$

11.2.7 Statistical Analyses

11.2.7.1 Nutritional Composition of Capuchin Foods

To compare the dry and wet mass between ripe fruit and invertebrate food items (and thus water content), we performed independent-samples Mann-Whitney U tests ($\alpha = 0.05$, 2-tailed) because sample sizes were unequal, and Kolmogorov-Smirnov tests confirmed that the data were not normally distributed. We performed a non-parametric Kruskal-Wallis test with Dunn's post hoc tests to compare the nutritional composition among five food types (fruit, seed, flower, non-caterpillar invertebrate, and caterpillar), because sample size for some food categories was small and the data were not normally distributed. We report the standardized test statistic and adjusted significance (multiple comparisons) using the Dunn-Bonferroni for post hoc tests.

11.2.7.2 Evaluation of Nutritional Requirements in Light of Fruit Abundance

We ran linear mixed effects models to examine the effects of seasonal variation in fruit abundance on foraging and intake after confirming our data conformed to assumptions of normality of distribution and homoscedasticity visually and through exploratory statistics. In these models, we included ripe fruit energy density as the fixed effect (standardized as a unitless Z-score) and female ID as the random effect. We ran eight separate models, each with one of the following measurements as response variable using a monthly mean value per female: (a) the proportion of time spent foraging, (b) the proportion of energy intake from fruit, (c) mass intake rate (gDM/hr), (d) energy intake (kJ/hr), (e) crude protein intake (g/hr), (f) crude fat intake (g/hr), (g) water-soluble carbohydrates (g/hr), and (h) neutral detergent fibre (g/hr).

All statistical analyses were performed in SPSS 21.0 (IBM Corp., Armonk, NY) using an alpha of 0.05 except in the case of multiple post hoc analyses, where levels were adjusted for running multiple comparisons.

11.3 Results

11.3.1 What Percentage of Total Foraging Time Do Females Spend on Different Types of Food?

The mean annual time budget for all general activity indicates that females in LV, CP, and GN groups spent the majority of their time foraging (60.4%) followed by resting (18.1%) and socializing (12.7%). There was considerable variation in general activity patterns across study months. Although females spent the most time foraging relative to other behaviours throughout the annual cycle, they spent roughly the same amount of time foraging as resting in April, the month with the highest maximum temperature (33.6 °C) and high fruit abundance. Of the total time foraging, capuchins spent 70.3% foraging on invertebrates, which represented the majority of the average time spent foraging over the entire study period. They spent 20.0% foraging on fruit, 1.1% foraging on pith, 0.7% foraging on flowers, 0.4% foraging on vertebrates, 1.3% foraging for water, and 6.2% of their time visually foraging. Both the percentage of total time spent foraging and the contribution of fruit and invertebrates to the foraging budget varied across months (Fig. 11.1). Females spent the greatest percentage of time foraging on invertebrates during the early rainy season months of June and July, which coincided with a flush of caterpillars, whereas the peak in the percentage of time spent foraging on fruit occurred during the late dry season in March and April, which corresponded to a peak in fruit abundance.

11.3.2 What Is the Dietary Profile of Female Capuchins?

Female capuchins in Sector Santa Rosa consumed fruit (including arils, bromeliads, seeds, and grasses), flowers, pith, invertebrates, vertebrates, and a small number of other items (e.g. dirt) during the study. We identified 88 plant food items (fruit from multiple ripeness stages, flowers, and pith) from 41 plant families, including fruit, seeds, bromeliads, and grasses from 64 species, flowers from 7 species, and pith from 3 species. The species for a small proportion of ingested fruit (two species), flowers (one species), and pith (one species) could not be identified. However, using the average per item nutritional value of known species, we estimated that these species comprised less than 1% of the energy consumed during this study. The capuchins also consumed 29 identifiable types of invertebrates from 10 orders, including Araneae, Blattodea, Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera, Phasmatodea, and Scorpiones. Based on the subset of species analysed for nutritional content (Appendices B and C), fruit items were significantly heavier ($N = 55$, range = 0.01–19.24 gDM, $\bar{x} = 1.51 \pm 0.46$) than invertebrates ($N = 13$, range = 4.72×10^{-3} to 2.29 gDM, $\bar{x} = 0.38 \pm 0.18$) on a dry matter basis (Mann-Whitney; $U = 226.0$, $p = 0.040$). However, the wet mass of ripe fruit was not significantly greater ($N = 55$, range = 0.02 to 99.00 g, $\bar{x} = 6.52 \pm 2.39$) than that of invertebrates ($N = 13$, range = 0.01 to 7.29 g, $\bar{x} = 1.29 \pm 0.56$) (Mann-Whitney; $U = 240.0$, $p = 0.067$).

11.3.3 Is Foraging Time Representative of Food Consumption and Energy Intake?

Females not only spent the largest percentage of their time foraging on invertebrates; they also comprised the largest percentage of the annual diet in terms of the number of items ingested followed by fruit, flowers, and pith (Table 11.1). However, fruit made a notably higher contribution to the percentage of dry matter ingested and the overall energy intake than did invertebrates (Table 11.1).

Table 11.1 Contribution of different food types to the annual foraging profile (Values are displayed as mean ± SE for female white-faced capuchins at Sector Santa Rosa, Costa Rica)

Food type	Foraging time (%)	Items ingested (%)	Dry matter ingested (%)	Energy ingested (%)
Fruit	19.96 ± 0.20	30.19 ± 1.11	61.69 ± 1.93	57.58 ± 2.01
Invertebrate	70.34 ± 0.22	66.56 ± 1.04	35.77 ± 1.87	39.06 ± 1.90
Flower	0.74 ± 0.10	1.84 ± 0.36	1.20 ± 0.36	0.80 ± 0.28
Pith	1.12 ± 0.15	1.49 ± 0.29	Na	1.23 ± 0.27

The calculation of percentage dry matter ingested does not include pith, as we were unable to successfully measure dry mass per unit. Total energy ingested is only the sum of categories for which nutritional processing and estimation were possible and excludes vertebrates and miscellaneous items

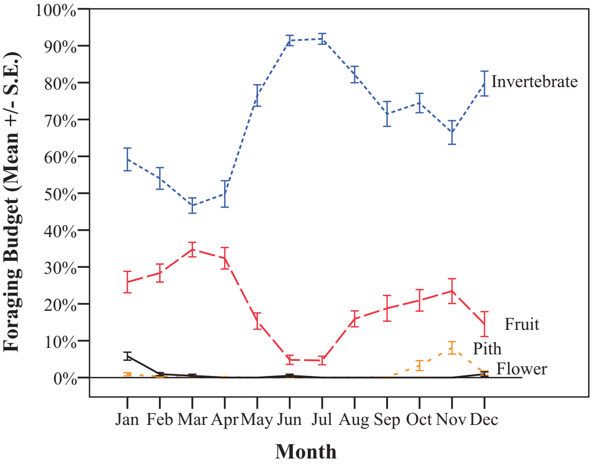

Fig. 11.1 Monthly foraging budget. The line graph depicts the mean ± SE percentage of time spent foraging on the four most common food types (invertebrates, fruit, pith, and flowers) by all three study groups

11.3.4 Does the Macronutrient Composition and Energy Density of Capuchin Foods Differ Across Food Types?

Nutritional composition varied greatly among food types (Table 11.2). Water content significantly differed by food type (Kruskal-Wallis; $N = 81$, $\chi^2(4) = 11.787$, $p = 0.019$). Flowers ($\bar{x} = 80.24\% \pm 3.76$) and caterpillars ($\bar{x} = 79.84\% \pm 5.38$) contained the most moisture, and seeds contained the least amount of moisture ($\bar{x} = 40.83\% \pm 13.35$). The difference in water content between caterpillars and seeds was significant (Dunn's test; $z = 2.957$, $p = 0.031$). Similarly, the percentage of crude protein significantly differed with respect to food type (Kruskal-Wallis; $N = 81$, $\chi^2(4) = 43.704$, $p < 0.001$). Fruit was significantly lower in crude protein compared to caterpillar (Dunn's test; $z = 3.790$, $p = 0.002$) and non-caterpillar invertebrates (Dunn's test; $z = -5.650$, $p < 0.001$). The water-soluble carbohydrates (WSC) significantly differed with respect to food type (Kruskal-Wallis; $N = 81$,

Table 11.2 Summary of macronutrient content per food type for food items eaten by adult females in the study groups

Food item	N species	% H_2O	% CP	% CF	% WSC	% NDF
Ripe fruit, seeds, and grasses	58	66.21 ± 2.47	8.86 ± 0.72	12.46 ± 2.13	35.85 ± 3.20	30.46 ± 2.47
Ripe fruit	53	68.60 ± 2.18	**8.11 ± 0.64**	12.06 ± 2.29	**38.21 ± 3.30**	30.45 ± 2.62
Seeds and grasses	5	**40.83 ± 13.35**	16.89 ± 3.65	16.64 ± 4.95	10.79 ± 3.52	30.62 ± 8.09
Flowers	3	80.24 ± 3.76	13.64 ± 3.13	3.94 ± 2.22	28.61 ± 8.65	21.25 ± 4.07
Invertebrates	13	72.99 ± 2.73	64.92 ± 4.27	16.17 ± 4.01	5.79 ± 1.67	21.65 ± 2.55
Non-caterpillar invertebrates	8	68.71 ± 1.89	**67.25 ± 5.16**	12.56 ± 1.82	**5.50 ± 2.63**	26.40 ± 2.82
Caterpillars	5	**79.84 ± 5.38**	**61.18 ± 7.87**	21.94 ± 10.13	**6.26 ± 1.55**	14.06 ± 2.22

CP crude protein, *CF* crude fat, *WSC* water-soluble carbohydrates, *NDF* neutral detergent fibre. Mean ± SE macronutrient values are listed as the percentage of dry mass. Species with estimated nutritional composition are excluded. Significant differences in composition as calculated by a pairwise comparisons using Dunn's test are highlighted in bold (please see Sect. 11.3.4 for details)

$\chi^2(4) = 33.833$, $p < 0.001$). Fruits contained significantly higher concentrations of water-soluble carbohydrates than did non-caterpillar invertebrates (Dunn's test; $z = 5.006$, $p < 0.001$) or caterpillars (Dunn's test; $z = -2.911$, $p = 0.036$). The differences in fat content across categories were not significant (Kruskal-Wallis; $N = 81$, $\chi^2(4) = 7.719$, $p = 0.102$). There were no significant differences in the percentage of neutral detergent fibre (NDF) across food types (Kruskal-Wallis; $N = 80$, $\chi^2(4) = 5.778$, $p = 0.216$).

Finally, food types differed in their total energy content per gram dry matter (Kruskal-Wallis; $N = 81$, $\chi^2(4) = 18.705$, $p = 0.001$; Fig. 11.2a). Non-caterpillar invertebrates contained significantly more energy than did fruits (Dunn's test; $z = -2.983$, $p = 0.029$). There was no significant difference in energy per gram dry matter between non-caterpillar invertebrates and flowers (Dunn's test; $z = -2.687$, $p = 0.072$) or between caterpillars and fruit (Dunn's test; $z = 2.746$, $p = 0.060$) and flowers (Dunn's test; $z = 2.805$, $p = 0.050$). When energy was assessed per gram wet mass to account for differences in water content, there were also significant differences across food types (Kruskal-Wallis; $N = 81$, $\chi^2(4) = 12.330$, $p = 0.015$; Fig. 11.2b), but none of the differences between pairs significantly differed from each other according to post hoc tests (Dunn's test; all p-values >0.074). When energy was assessed per item, there was a significant difference across food types (Kruskal-Wallis; $N = 81$, $\chi^2(4) = 16.234$, $p = 0.003$; Fig. 11.2c). Specifically, fruit contained significantly more energy (kJ) per item than did seeds (Dunn's test; $z = 3.093$, $p = 0.020$).

11.3.5 Do Females Consume Macronutrients and Energy at Different Rates Depending on the Type of Food Eaten?

The mean annual diet of female capuchins as a percentage of dry matter ingested, including all food types, was comprised of 27.15% (SE = 1.00) crude protein, 9.93% (SE = 0.27) crude fat, 35.75% (SE = 1.48) water-soluble carbohydrates, and 25.54% (SE = 0.07) neutral detergent fibre. As a percentage of metabolizable energy, protein comprised 30.15% (SE = 1.11), fat comprised 25.32% (SE = 0.60), and sugar comprised 43.36% (SE = 1.52).

The item intake rate for fruit and seeds was not significantly different from the intake rate for invertebrates (Mann-Whitney; $U = 164.000$, $p = 1.000$; Table 11.3; for item-specific rates, see Appendix D). However, the energy intake rate (kJ/min) was significantly higher for fruits and seeds than invertebrates (Mann-Whitney; $U = 21.000$, $p < 0.001$). The difference in energy consumption was a result of the significantly higher nutrient intake rate (g/hr) of sugar (Mann-Whitney; $U = 15.000$, $p < 0.001$) and fat (Mann-Whitney; $U = 55.000$, $p = 0.003$) during fruit and seeds versus invertebrate consumption, as the difference in the intake of protein between fruit and seeds and invertebrates was not significant (Mann-Whitney; $U = 122.000$,

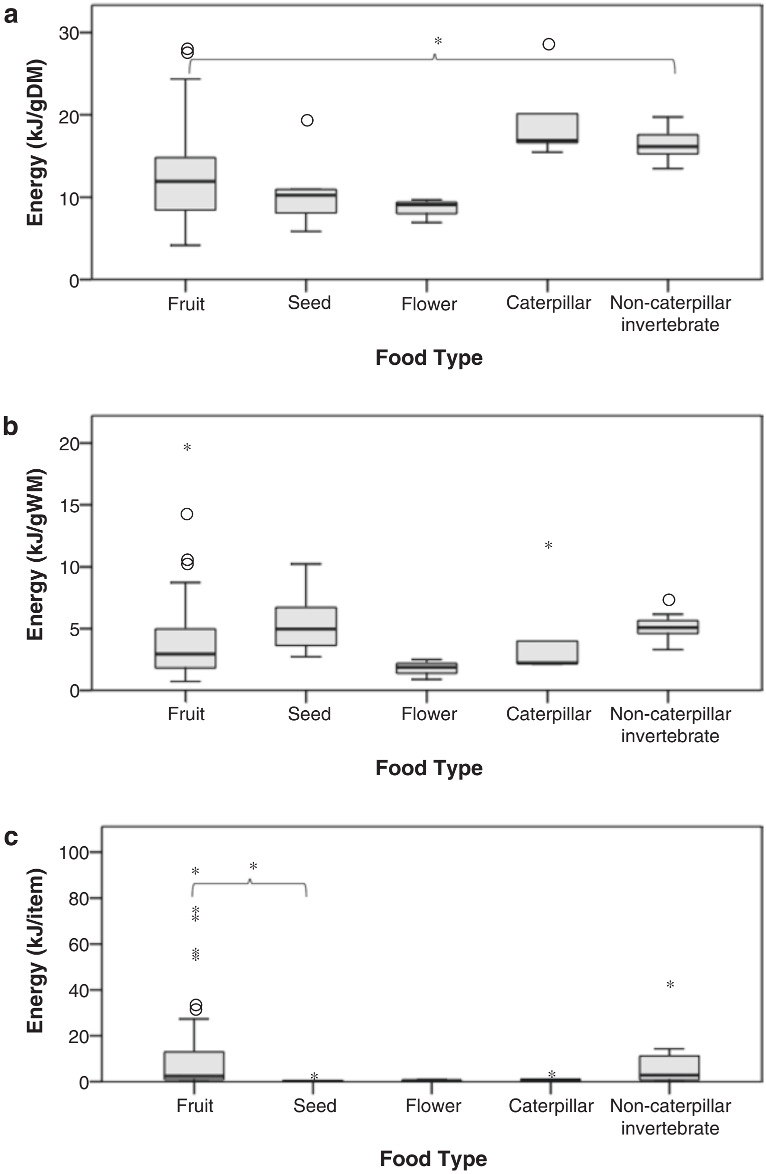

Fig. 11.2 Box plots of the nutritional composition of energy consumed by adult female study subjects. Graphs depict (**a**) energy per dry matter (kilojoules/gram), (**b**) energy per wet mass (kilojoules/gram), and (**c**) energy per item (kilojoules/item). Open circles and stars represent outliers >1.5 times the IQR and >3 times the IQR, respectively. Pairwise comparisons were conducted using Dunn's post hoc tests, and significant results are depicted by brackets and * for $p < 0.05$

Table 11.3 Intake rate and nutritional profitability of two food types (fruit and seeds and invertebrates) eaten by female capuchins

	Food type	
Variable	Fruit and seeds (mean ± SE)	Invertebrates (mean ± SE)
Species (N)	44	8
Item intake rate (N/min)	4.82 ± 0.77	3.89 ± 1.15
Energy intake (kJ/min)	**10.70 ± 1.36**	**1.75 ± 0.57**
Protein (CP)	5.71 ± 0.85	3.58 ± 1.12
Fat (CF)	**7.18 ± 1.34**	**0.84 ± 0.25**
Sugar (WSC)	**28.89 ± 5.13**	**0.77 ± 0.56**
Fibre (NDF)	**29.13 ± 5.68**	**1.27 ± 0.52**

Food items included in calculations are a subset of the larger nutritional dataset for which the targeting of specific species while foraging allowed for measurement of foraging bout length. Macronutrient intake (protein, fat, sugar, and fibre) is measured in grams per hour. Significant differences are highlighted in bold (see Sect. 11.3.5 for details)

$p = 0.256$). There was also significantly higher intake in fibre during fruit and seeds versus invertebrate consumption (Mann-Whitney; $U = 22.000$, $p < 0.001$).

11.3.6 What Are the Estimated Energy Intake Requirements for Female Capuchins?

Based on the number of females that were gestating and lactating during each month and assigning the factors of 1.25 and 1.50, respectively, for increased demands of these two reproductive states, the mean monthly reproductive demand for females during this study was 1.40 (SE = 0.01) times the requirements for a non-cycling female. Thus, the mean daily energy requirement for all females, who spend a disproportionate amount of the annual cycle in a lactational state (mean weaning completion age = 20.50 mo., Fragaszy et al. 2004; mean interbirth interval = 26.36 mo., Fedigan and Rose 1995), was estimated as 1400 kJ/day.

11.3.7 How Does Foraging Behaviour, Energy Intake, and Macronutrient Intake Differ with Variation in Food Abundance?

During this study, biannual peaks in ripe fruit energy density (kJ/ha) occurred from February–March to September–October (Fig. 11.3). Although fruiting patterns are variable interannually, these peaks coincided with the mean annual variation in fruit biomass collected between 2007 and 2013 at this field site (Campos et al. 2014). Monthly mean ripe fruit energy density (kJ/ha) was 557,763 kJ/ha (SEM = 94,514).

The highest energy density occurred during February 2011 (1,066,184 kJ/ha), whereas the lowest occurred during December 2009 (74,030 kJ/ha).

11.3.7.1 Differences in Foraging Behaviour and Energy Intake in Relation to Fruit Abundance

Ripe fruit energy density was a significant predictor of the mean proportion of time spent foraging across study months (Table 11.4). Females spent a lower proportion of their total activity budget foraging when fruit energy density was high compared to periods when fruit energy density was low (Fig. 11.4a). As expected, ripe fruit energy density was also significantly related to the proportion of energy intake from fruit (Table 11.4), whereby the more fruit energy that was available, the higher the proportion of fruit-based energy intake by females (Fig. 11.4b). Females consumed the highest average proportion of energy from fruit during April 2011 ($\bar{x} = 0.861 \pm 0.036$) and the lowest proportion of energy intake from fruit during May 2010 ($\bar{x} = 0.132 \pm 0.042$). Neither the rate of food intake (grams of dry matter per hour) nor the rate of total energy intake was significantly predicted by ripe fruit energy density (Table 11.4, Figs. 11.4c and 11.5d). However, the lowest mean monthly food intake rate ($\bar{x} = 3.251$ g/hr ± 0.433) and energy intake rate ($\bar{x} = 53.097$ kJ/hr ± 6.270) did occur during June 2010, a month with very low ripe fruit abundance (256,209 kJ/ha compared to the mean of 557,763 kJ/ha). The

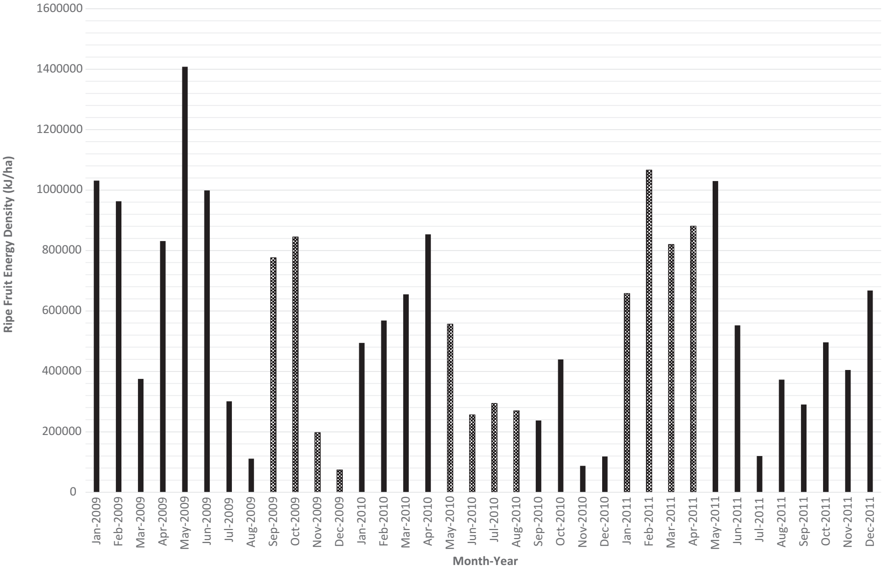

Fig. 11.3 Energy density from ripe fruit (kJ/ha) based on 30 fruiting species important to the diet of white-faced capuchins at Sector Santa Rosa, Costa Rica. Data associated with data collection periods for this study are indicated by patterned bars

Table 11.4 Summary of linear mixed effects models analysing the effect of monthly ripe fruit energy density (kJ/ha) on variation in mean feeding time and nutrient intake

								95% confidence interval	
Response variable	Fixed effect	Intercept	Estimate	Standard error	df	*t*	*p*-value	Lower	Upper
Feeding time (proportion)	**Energy density**	**0.573**	**−0.075**	**0.009**	**270.565**	**−8.065**	**<0.001**	**−0.094**	**−0.057**
Proportion of intake from fruit	**Energy density**	**0.583**	**0.167**	**0.018**	**270.546**	**9.184**	**<0.001**	**0.131**	**0.202**
Intake (gDM/hr)	Energy density	10.856	0.768	0.573	294.000	1.340	0.181	−0.360	1.897
Energy intake (kJ/hr)	Energy density	142.121	7.637	6.446	270.368	1.185	0.237	−5.054	20.329
Crude protein (g/hr)	**Energy density**	**1.832**	**−0.323**	**0.050**	**269.815**	**−6.475**	**<0.001**	**−0.421**	**−0.225**
Crude fat (g/hr)	Energy density	0.851	−0.001	0.046	294.000	−0.020	0.984	−0.091	0.090
Water-soluble carbohydrates (g/hr)	**Energy density**	**4.656**	**0.834**	**0.300**	**270.375**	**2.775**	**<0.01**	**0.242**	**1.425**
Neutral detergent fibre (g/hr)	Energy density	2.820	0.331	0.180	294.000	1.842	0.067	−0.023	0.685

Macronutrient weight is shown as grams dry matter. Female ID was included as a random effect. Significant effects are highlighted in bold

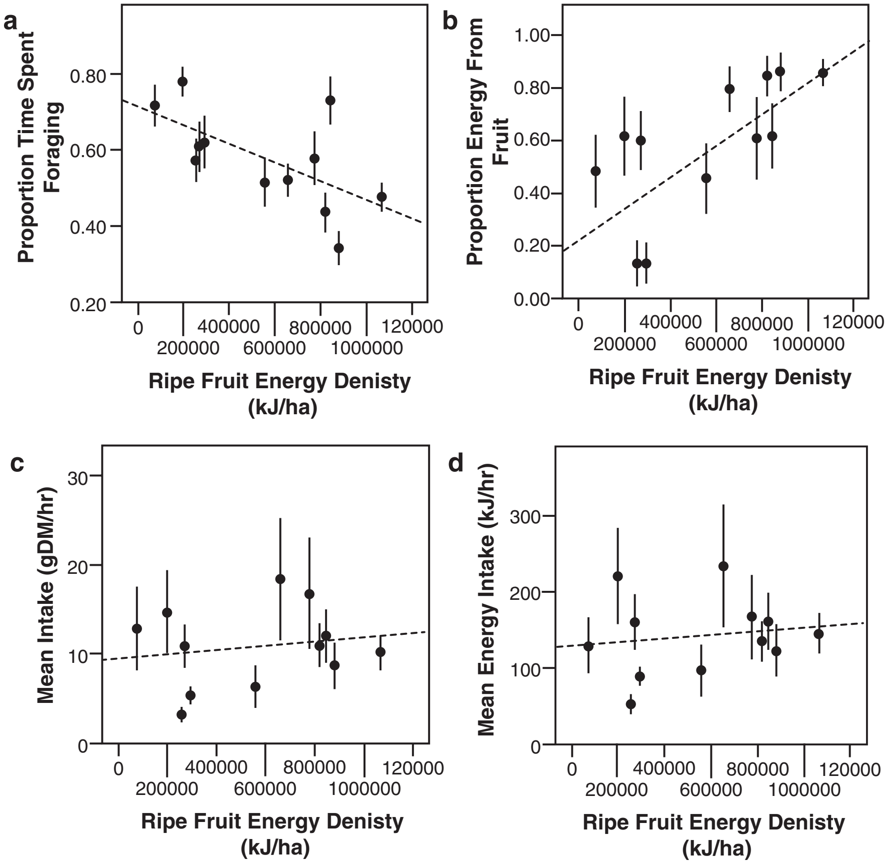

Fig. 11.4 Monthly variation in foraging time and intake by females. Points with error bars show the monthly mean values ± 95% confidence interval for (**a**) foraging time, (**b**) the proportion of energy intake from fruit (kJ/hr), (**c**) mass ingested (grams dry matter per hour), and (**d**) energy intake (kJ/hr) plotted against monthly ripe fruit energy density for 25 white-faced capuchin females at Sector Santa Rosa, Costa Rica. The dashed line depicts the predicted relationship between the variables according to the linear mixed effects models (see Table 11.4)

highest food intake rate (18.451 ± 3.336 g/hr) and energy intake rate (233.329 ± 39.669 kJ/hr) occurred during a month with higher than the annual mean ripe fruit abundance in January 2011 (657,730 kJ/ha). Based on these data, mean daily (12-h) energy intake is estimated to have reached as high as 2800 kJ/day and as low as 637 kJ/day.

11.3.7.2 Differences in Macronutrient Intake According to Fruit Abundance

Ripe fruit energy density significantly predicted protein intake rate (g/hr, Table 11.4). Females consumed protein at lower rates when fruit abundance was high compared to months when fruit abundance was low (Fig. 11.5a). Ripe fruit energy was

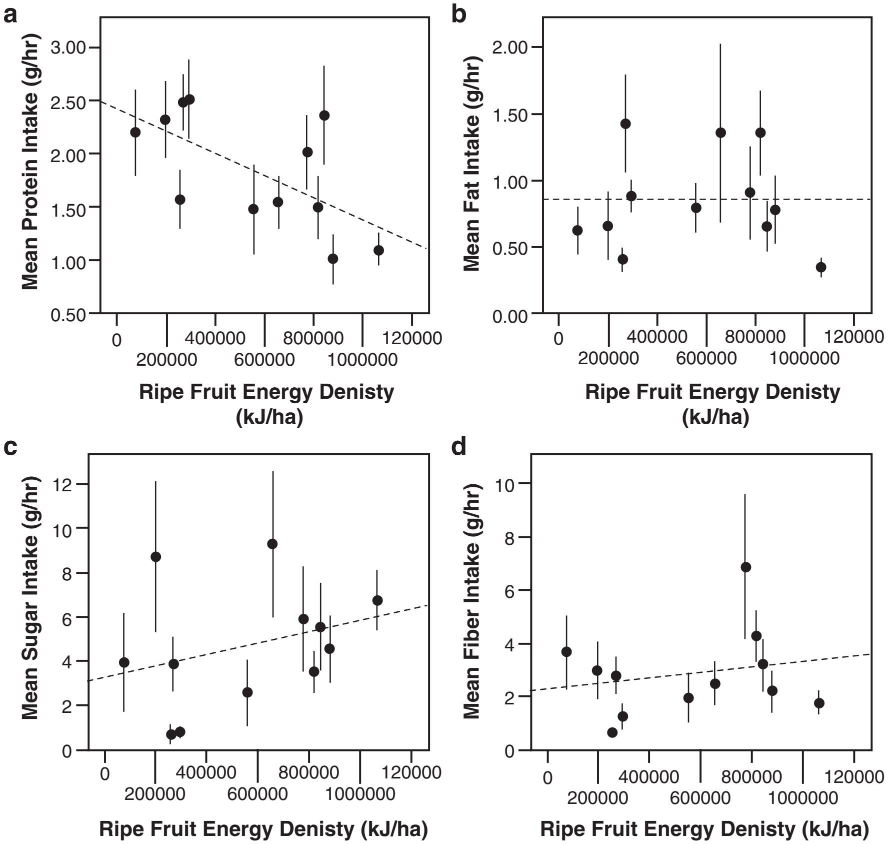

Fig. 11.5 Monthly variation in macronutrient intake by female capuchins. Points with error bars show the mean values ± 95% confidence interval for monthly intake, reported in grams intake per hour, for (**a**) crude protein, (**b**) crude fat, (**c**) water-soluble carbohydrates (WSC), and (**d**) neutral detergent fibre (NDF) plotted against monthly ripe fruit energy density for 25 female white-faced capuchins at Sector Santa Rosa, Costa Rica. The dashed line depicts the predicted relationship between the variables according to the linear mixed effects models (see Table 11.4)

significantly related to the rate of sugar intake (Table 11.4), whereby females consumed sugar at higher rates during months with higher ripe fruit energy density compared to month with lower ripe fruit energy density (Fig. 11.5c). Finally, ripe fruit energy was not significantly related fat intake or fibre intake (Table 11.4, Fig. 11.5b, d).

11.4 Discussion

The objectives of this study were to characterize female capuchin diet through assessment of the foraging budget, dietary profile, and nutritional composition of different food types, as well as to evaluate temporal variation in feeding behaviour, energy intake, and macronutrient intake in light of nutritional requirements. This is important for gaining a better understanding of the behavioural flexibility that capuchins exhibit in the face of seasonal changes in food availability and the physiological consequences (i.e. reproductive output) during seasons with low food abundance.

Female foraging budgets Adult female capuchins spent over half of their time foraging, during which they consumed a diversity of food items from two key dietary categories, plants and invertebrates. Despite interannual variation in food abundance and diet, the food item diversity is comparable to previous studies with documented foraging behaviour conducted at this field site (Chapman and Fedigan 1990; MacKinnon 2006). The observed foraging budget of 60.4% is also comparable to previous studies at this site (e.g. females, 53%, Rose 1994; all individuals, 53%, Melin et al. 2009), as well as the range of 41–58% across *Cebus* and *Sapajus* species (van Schaik and van Noordwijk 1989; Fragaszy 1990; Moura 2004; Matthews 2009; Izar et al. 2012).

Dietary profile Although there is variation in diet across the annual cycle, fruit and invertebrates make the most significant contribution to capuchin foraging time, number of items ingested, and overall energy gain across all months, as has been previously found in several capuchin studies (Chapman and Fedigan 1990; Rose 1994; Fragaszy et al. 2004; McCabe and Fedigan 2007; Melin et al. 2014b). Our results also indicate that invertebrates are arguably a more important food source when considering the amount of time that females spent foraging on them and the number of items ingested, which is comparable to other capuchin species (*C. albifrons* and *C. apella*) as well as more insectivorous common squirrel monkeys (*Saimiri sciureus*) and emperor tamarins (*Saguinus imperator*) (Terborgh 1983). However, fruit contributes substantially more to the annual dry matter ingested than do invertebrates. Fruit also comprises a larger percentage of the total annual energy consumed by females than do invertebrates.

Foraging time and intake Differences between foraging time and energetic contribution highlight the importance of including nutritional analyses in assessments and comparisons of diet and behaviour, as well as considering the nutritional values of food items with respect to a food item's weight and moisture content rather than making comparisons of nutrients on a dry matter basis alone (Rothman et al. 2014). While this insight seems rather obvious, due to lack of available nutritional data, studies that do not include nutritional analysis must base data analysis on the assumption that the amount of food eaten and/or the energy ingested is proportional to the time spent eating or the number of items ingested. This point is particularly important when making comparisons across food types with the largest size/weight disparities (e.g. between fruit and invertebrates), since distribution, size, handling time, and food processing all may affect energy and macronutrient intake rates (Hladik 1977; Milton 1984; Schulke et al. 2006).

Nutritional composition by food type We analysed the variation in the nutritional composition among different food types (fruit, seed, flower, pith, non-caterpillar invertebrate, and caterpillar). Invertebrates were higher in protein and energy than fruit and seeds, although fruit and seeds contained higher levels of water-soluble carbohydrates. These values are expected given that invertebrates are primarily composed of protein, fat, and chitin (Rothman et al. 2014). They are also comparable to other studies that have analysed the nutritional composition of primate foods, including those specific to platyrrhines (reviewed by Norconk et al. 2009).

The energy and nutritional composition of invertebrates may be considerably offset by their significantly smaller weight when compared to fruits on a dry matter basis (Rothman et al. 2014). The more dispersed distribution of invertebrates in the environment relative to the generally more highly clumped distribution of fruits produced by angiosperms may also greatly affect intake rate and profitability in terms of nutritional gain per unit time foraging.

Future research that expands the nutritional dataset to include (1) liana fruits (which were not quantified in our phenological data collection or estimates of fruit abundance and energy availability), (2) fruits that are available but not consumed by capuchins, (3) invertebrate abundance, (4) mineral concentrations, and (5) plant defence compounds such as tannins and polyphenols would help to better determine nutritional factors important to food selection and how selection may vary in relation to overall nutrient and energy availability. Whether a resource is “important” in terms of energy, macronutrient, and mineral intake and how these factors affect ranging patterns and resource defence may not only relate to a food’s nutritional composition but also to the availability of alternative resources (Janson 1988; Vogel and Janson 2006).

Nutritional intake by food type Females consumed fruit at a slightly higher rate than invertebrates on a per item basis; however, the energy intake rate (kJ/min) and sugar and protein intake rates (g/hr) were significantly higher from fruit versus invertebrate foraging. It is therefore important to emphasize that time spent foraging does not accurately reflect energy intake, at least for capuchins, due to the large degree of variation in weight and nutrient content across food items. Although there was no significant difference in fat content of invertebrates compared to other broad food-type categories, further investigation should be done to determine if capuchins might be consuming invertebrates to increase fat intake in addition to using them as a source of protein during the high-fruit season.

Evaluation of nutritional requirements and intake Like many other free-living animals, capuchins in Sector Santa Rosa face temporal variation in the abundance of food resources and exhibit variation in both foraging and intake patterns across study months. As expected, ripe fruit abundance significantly predicted both the overall proportion of time spent foraging and the proportion of energy intake from ripe fruit. As fruit abundance increased, the proportion of time spent by females foraging decreased, but the amount of energy consumed from fruit increased. With increased availability, they were likely able to find and consume this high-energy food type more quickly. When the range for 12-h mean energy intake of 637 kJ/day–2800 kJ/day for females is placed in the context of the minimum estimated requirement of 1000 kJ/day, and the requirement of *Cebus capucinus* females adjusted for the reproductive demands of 1400 kJ/day (inferred from studies of captive capuchins by Ausman and Hegsted 1980), there is the potential for female capuchins to far exceed or fall short of daily energy intake requirements at this field site. Although females appeared to meet estimated energy intake requirements during many months, and greatly exceed them in others when fruit abundance and intake rates were much higher than average (November 2009 and January 2011), it is important to note that they did not meet estimated requirements during the month with the lowest intake rate in June 2010. During this month, ripe fruit abundance was relatively very low, and consequently, females were focusing greater than 90% of their foraging time on invertebrates. Since invertebrates are low in mass and require additional time to search and capture (as indicated by intake rates), it is likely that females were simply unable to consume enough food during this period. Although less mass and energy were ingested in low-fruit months, the ingestion of protein-rich invertebrates led to an increase in protein intake during those months and potentially maintained fat intake; however, sugar and fibre intake did decrease during that time. Future analyses will assess variation in energy and macronutrient intake in more detail to advance our understanding of dietary variation when the abundance of fruit is low.

Analysis of plant toxins was out of the scope of this project, and therefore, we did not test the hypothesis that capuchin nutritional goals could be driven by the avoidance of secondary plant metabolites. Females did not seem to minimize energy expenditure as fruit abundance decreased, but instead increased the proportion of time spent foraging. When fruit abundance was high, females seemed to “overconsume” carbohydrates based on intake rates, but also seemingly exceeded protein requirements. In contrast, during periods of fruit scarcity, females increased the foraging of invertebrates and “overconsumed” protein to meet overall energy requirements. These patterns suggest that females may be attempting to maximize caloric intake in response to a decrease in fruit abundance. Further analyses, including those specific to assessing the intake geometry of various nutritional components, may help to elucidate patterns of capuchin foraging and the role of specific capuchin foods (Raubenheimer and Simpson 1993; Simpson and Raubenheimer 1993; Raubenheimer 2011), as has been successfully implemented in other primate studies (Felton et al. 2009b; Rothman et al. 2011; Johnson et al. 2013; Raubenheimer et al. 2014; Irwin et al. 2015).

In summary, female white-faced capuchins at Sector Santa Rosa, Costa Rica, focused foraging efforts on fruit and invertebrate food items. Fruit contributed the most to the overall energy gain despite the greater proportion of time devoted to searching for and consuming invertebrates. Although the nutritional composition of food types is variable, fruits were the most important source of sugar, whereas high proportions of protein intake came from invertebrates, particularly as fruit abundance decreased. Females were able to consume macronutrients at a much higher rate while foraging for fruit, likely due to the higher weight of food items compared to invertebrates. There was temporal variation in the types of foods consumed and in the ability of female capuchins to meet energy requirements, warranting a more detailed investigation into capuchin foraging patterns, variation in the utilization of other food types, and nutritional intake during this study.

In the context of the nutritional ecology of capuchin monkeys, this study adds to the documentation of behavioural responses to variation in fruit availability and the nutritional properties of food. Our understanding of behaviour and physiology in this context will continue to grow as we place our findings into a larger multi-year framework that is compared across field sites and species. Such a framework will help to determine the consistency of these responses, how they are linked to the fitness of individuals, and then how they were shaped by evolutionary pressures.

Acknowledgements Thank you to the Ministry of Environment, Energy and Technology (MINAET) of Costa Rica and the Animal Care Committee at the University of Calgary for permissions to conduct research. This project was also supported by Sr. R Blanco, MM Chavarria, and the staff of the Área de Conservación Guanacaste. Many field assistants and friends aided in the collection of valuable data for this project including M Myers, B Thankey, H Clouse, C Lees, B Kowalzik, Dr. C Turner Hogan, and S Chevez. R Espinoza, A Guadamuz, J Vargas, and R Franco provided valuable assistance with the identification of plant and invertebrate samples. We thank G Bridgett for logistical help with permits and Dr. J Addicott and J McQuade for assistance with data organization and database design. Thank you to Dr. E Vogel for contributing nutritional data and Drs. E Wikberg and F Campos for statistical guidance. The authors were supported by the following funding organizations: To MLB: The Leakey Foundation, Alberta Innovates Technology Futures, International Primatological Society, Animal Behaviour Society, Sigma Xi, and University of Calgary. To ADM: Natural Sciences and Engineering Research Council of Canada (NSERC) and Canada Research Chairs Program. To LMF: NSERC and Canada Research Chairs Program.

References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–265

Altmann SA (1991) Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. Proc Natl Acad Sci U S A 88(2):420–423

Altmann SA (1998) Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago

ANKOM Technology (2011) Method 6: neutral detergent fiber in feeds - filter bag technique (for A200 and A200I). https://www.ankom.com/sites/default/files/document-files/Method_6_NDF_A200.pdf. Accessed 31 Jan 2017

Antonow-Schlorke I, Schwab M, Cox LA, Li C, Stuchlik K, Witte OW, Nathanielsz PW, McDonald TJ (2011) Vulnerability of the fetal primate brain to moderate reduction in maternal global nutrient availability. Proc Natl Acad Sci U S A 108(7):3011–3016

AOAC International (2012a) AOAC official method 942.05 ash of animal feed. In: Latimer G (ed) Official methods of analysis of AOAC International, 19th edn. AOAC International, Gaithersburg

AOAC International (2012b) Official method 2003.05 crude fat in feeds, cereal grains, and forages. In: Latimer G (ed) Official methods of analysis of AOAC International, 19th edn. AOAC International, Gaithersburg

AOAC International (2012c) Official method 992.23 crude protein in cereal grains and oilseeds: generic combustion method. In: Latimer G (ed) Official methods of analysis of AOAC International, 19th edn. AOAC International, Gaithersburg

AOAC International (2012d) Official method 992.15 crude protein in meat and meat products including pet foods. In: Latimer G (ed) Official methods of analysis of AOAC International, 19th edn. AOAC International, Gaithersburg

AOAC International (2012e) Official method 930.15 loss on drying (moisture) for feeds (at 135 for 2 hours), dry matter on oven drying for feeds (at 135 for 2 hours). In: Latimer G (ed) Official methods of analysis of AOAC International, 19th edn. AOAC International, Gaithersburg

AOAC International (2012f) Official method 990.03 protein (crude) in animal feed: combustion method. In: Latimer G (ed) Official methods of analysis of AOAC International, 19th edn. AOAC International, Gaithersburg

Ausman LM, Hegsted DM (1980) Protein requirements of adult cebus monkeys (*Cebus albifrons*). Am J Clin Nutr 33(12):2551–2558

Bell RHV (1971) A grazing ecosystem in the Serengeti. Sci Am 225:86–93

Bentley GR (1999) Aping our ancestors: comparative aspects of reproductive ecology. Evol Anthr 7(5):175–185

Bergstrom ML, Fedigan LM (2010) Dominance among female white-faced capuchin monkeys (*Cebus capucinus*): hierarchical linearity, nepotism, strength and stability. Behaviour 147(7):899–931

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

Bronson FH (1985) Mammalian reproduction: an ecological perspective. Biol Reprod 32(1):1–26

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

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

Carnegie SD, Fedigan LM, Melin AD (2011a) Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Area de Conservación Guanacaste), Costa Rica. Int J Primatol 32(5):1076–1090

Carnegie SD, Fedigan LM, Ziegler TE (2011b) Social and environmental factors affecting fecal glucocorticoids in wild, female white-faced capuchins (*Cebus capucinus*). Am J Primatol 73(9):861–869

CEM Corportation (2014) Method notes: digestion of alfalfa. http://cem.com/en/digestion-of-alfalfa-80ml-quartz. Accessed 31 Jan 2017

CEM Corportation (2016) Methods notes: digestion of feed grain. http://cem.com/en/digestion-of-feed-grain. Accessed 31 Jan 2016

Chapman CA, Fedigan LM (1990) Dietary differences between neighboring *Cebus capucinus* groups: local traditions, food availability or responses to food profitability? Folia Primatol 54:177–186

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR (2003) Variation in the nutritional value of primate foods: among trees, time periods, and areas. Int J Primatol 24(2):317–333

Chivers DJ, Hladik CM (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. J Morphol 166:337–386

Clutton-Brock TH, Harvey PH (1977) Species differences in feeding and ranging behavior in primates. In: Clutton-Brock TH (ed) Primate ecology. Academic Press, London, pp 557–584

Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. Edinburgh University Press, Edinburgh

Conklin-Brittain NL, Knott CD, Wrangham RW (2006) Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding ecology in apes and other primates. Cambridge University Press, Cambridge, pp 445–471

Cummings JH, Jenkins DJ, Wiggins HS (1976) Measurement of the mean transit time of dietary residue through the human gut. Gut 17:210–218

Fedigan LM, Rose LM (1995) Interbirth interval variation in three sympatric species of neotropical monkey. Am J Primatol 37(1):9–24

Felton AM, Felton A, Lindenmayer DB, Foley WJ (2009a) Nutritional goals of wild primates. Funct Ecol 23(1):70–78

Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley WJ, Wood JT, Wallis IR, Lindenmayer DB (2009b) Protein content of diets dictates the daily energy intake of a free-ranging primate. Behav Ecol 20(4):685–690

Finke MD (2007) Estimate of chitin in raw whole insects. Zoo Biol 26(2):105–115

Ford SM, Davis LC (1992) Systematics and body size: implications for feeding adaptations in New World monkeys. Am J Phys Anthropol 88(4):415–468

Fragaszy DM (1990) Sex and age differences in the organization of behavior in wedge-capped capuchins, *Cebus olivaceus*. Behav Ecol 1(1):81–94

Fragaszy DM, Boinski S (1995) Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (*Cebus olivaceus*). J Comp Psychol 109(4):339–348

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

Hall MB, Hoover WH, Jennings JP, Miller Webster TK (1999) A method for partitioning neutral detergent-soluble carbohydrates. J Sci Food Agr 79:2079–2086

Harborne JB (1984) Phytochemical methods: a guide to modern techniques of plant analysis. Chapman and Hall, London

Hinde K, Milligan LA (2011) Primate milk: proximate mechanisms and ultimate perspectives. Evol Anthropol 20:9–23

Hladik CM (1977) A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In: Clutton-Brock TH (ed) Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys and apes. Academic Press, London, pp 324–353

Isbell LA (1991) Contest and scramble competition: patterns of aggression and ranging behavior among primates. Behav Ecol 2:143–155

Irwin MT, Raharison J, Raubenheimer DR, Chapman CA, Rothman J (2015) The nutritional geometry of resource scarcity: effects of lean seasons and habitat disturbance on nutrient intakes and balancing in wild sifakas. PLoS One 10(6):e0128046

Izar P, Verderane MP, Peternelli-dos-Santos L, Mendonça-Furtado O, Presotto A, Tokuda M, Visalberghi E, Fragaszy D (2012) Flexible and conservative features of social systems in tufted capuchin monkeys: comparing the socioecology of *Sapajus libidinosus* and *Sapajus nigritus*. Am J Primatol 74(4):315–331

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behav Ecol Sociobiol 18:125–138

Janson CH (1988) Experimental evidence for spatial memory in wild brown capuchin monkeys (*Cebus apella*). Anim Behav 55:1229–1243

Johnson CA, Raubenheimer D, Rothman JM, Clarke D, Swedell L (2013) 30 days in the life: daily nutrient balancing in a wild chacma baboon. PLoS One 8(7):e70383

Kay RF, Madden RH, Van Schaik C, Higdon D (1997) Primate species richness is determined by plant productivity: implications for conservation. P Natl Acad Sci USA 94(24):13023–13027

Key C, Ross C (1999) Sex differences in energy expenditure in non-human primates. P R Soc London B Bio 266(1437):2479–2485

Koenig A (2002) Competition for resources and its behavioral consequences among female primates. Int J Primatol 23:759–783

Lucas A (1998) Programming by early nutrition: an experimental approach. J Nutr 128(2):401S–406S

MacKinnon KC (2006) Food choice by juvenile capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. In: Estrada A, Pavelka M, Garber P, Luecke L (eds) New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation. Springer Press, New York, pp 349–366

Matthews L (2009) Activity patterns, home range size, and intergroup encounters in *Cebus albifrons* support existing models of capuchin socioecology. Int J Primatol 30(5):709–728

McCabe GM (2005) Diet and nutrition in white-faced capuchins (*Cebus capucinus*): effects of group, sex and reproductive state. Thesis, University of Calgary

McCabe GM, Fedigan LM (2007) Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female *Cebus capucinus* at Santa Rosa, Costa Rica. Int J Primatol 28:837–851

McCabe GM, Emery Thompson M (2013) Reproductive seasonality in wild Sanje mangabeys (*Cercocebus sanjei*), Tanzania: relationship between the capital breeding strategy and infant survival. Behaviour 150(12):1399–1429

McCabe G, Fernàndez D (2018, this volume) Patterns of infant mortality and seasonality in wild Sanje mangabeys, *Cercocebus sanjei*. 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 57–70

Melin, AD, Webb SE, Williamson RE, Chiou K (2018) Data Collection in Field Primatology: A Renewed Look at Measuring Foraging Behaviour. 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 161–187

Melin A, Fedigan L, Hiramatsu C, Hiwatashi T, Parr N, Kawamura S (2009) Fig foraging by dichromatic and *trichromatic Cebus capucinus* in a tropical dry forest. Int J Primatol 30(6):753–775

Melin AD, Fedigan LM, Young HC, Kawamura S (2010) Can color vision variation explain sex differences in invertebrate foraging by capuchin monkeys? Curr Zool 56(3):300–312

Melin AD, Hiramatsu C, Parr NA, Matsushita Y, Kawamura S, Fedigan LM (2014a) The behavioral ecology of color vision: considering fruit conspicuity, detection distance, and dietary importance. Int J Primatol 35(1):258–287

Melin AD, Young HC, Mosdossy KN, Fedigan LM (2014b) Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. J Hum Evol 71(0):77–86

Melin Meachem AD (2011) Polymorphic colour vision and foraging in white-faced capuchins: insights from field research and simulations of monkey vision. Dissertation, University of Calgary

Merrill AL, Watt BK (1955) Derivation of current calorie factors. In: USDA ARS (ed) Agricultural handbook no. 74: energy value of foods, basis and derivation. U.S. Government Printing Office, Washington D.C., p 24–43. https://naldc.nal.usda.gov/download/CAT40000007/. Accessed 31 Jan 2017

Miller KE, Bales KL, Ramos JH, Dietz JM (2006) Energy intake, energy expenditure, and reproductive costs of female wild golden lion tamarins (*Leontopithecus rosalia*). Am J Primatol 68(11):1037–1053

Milton K (1981) Food choice and digestive strategies of two sympatric primate species. The Am Nat 117(4):496–505

Milton K (1984) The role of food-processing factors in primate food choice. In: Rodman PS, Cant JGH (eds) Adaptations for foraging in nonhuman primates: contributions to an organismal biology of prosimians, monkeys and apes. Columbia University Press, New York, pp 249–279

Milton K (1987) Primate diets and gut morphology: implications for hominid evolution. In: Harris M, Ross EB (eds) Food and evolution: toward a theory of food habits. Temple University Press, Philadelphia, pp 93–115

Mosdossy KN, Melin AD, Fedigan LM (2015) Quantifying seasonal fallback on invertebrates, pith and bromeliad leaves by white-faced capuchin monkeys (*Cebus capucinus*) in a tropical dry forest. Am J Phys Anthropol 150:67–77

Mott GE, Jackson EM, McMahan CA, McGill HC Jr (1990) Cholesterol metabolism in adult baboons is influenced by infant diet. J Nutr 120(3):243–225

Mott GE, Lewis DS, McGill HC Jr (1991) Programming of cholesterol metabolism by breast or formula feeding. Ciba Found Symp 156:56–76

Moura ACdA (2004) The capuchin monkey and the Caatinga dry forest: a hard life in a harsh habitat. Dissertation, University of Cambridge

National Research Council (2003) Nutrient requirements of nonhuman primates. National Academy Press, Washington, DC

Norconk MA, Wright BW, Conklin-Brittain NL, Vinyard CJ (2009) Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American primates: comparative perspectives in the study of behavior, ecology, and conservation. Springer Science+Business Media, LLC, New York, pp 279–319

O'Malley R, Fedigan L (2005) Variability in food-processing behaviour among white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Am J Phys Anthropol 128:63–73

Oftedal OT, Whiten A, Southgate DAT, Van Soest P (1991) The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. Philos T R Soc B 334(1270):161–170

Perry S (1996) Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. Am J Primatol 40(2):167–182

Peters RH, Cloutier S, Dubé D, Evans A, Hastings P, Kaiser H, Kohn D, Sarwer-Foner B (1988) The allometry of the weight of fruit trees and shrubs in Barbados. Oecologia 74(4):612–616

Raubenheimer D (2011) Toward a quantitative nutritional ecology: the right-angled mixture triangle. Ecol Monogr 81(3):407–427

Raubenheimer D, Simpson SJ (1993) The geometry of compensatory feeding in the locust. Anim Behav 45:953–964

Raubenheimer D, Rothman JM, Pontzer H, Simpson SJ (2014) Macronutrient contributions of insects to the diets of hunter–gatherers: a geometric analysis. J Hum Evol 71(0):70–76

Rose LM (1994) Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). Int J Primatol 15(1):95–114

Rothman JM, Raubenheimer D, Chapman CA (2011) Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biol Lett 7:847–849

Rothman JM, Raubenheimer D, Bryer MAH, Takahashi M, Gilbert CC (2014) Nutritional contributions of insects to primate diets: implications for primate evolution. J Hum Evol 71:59–69

Schulke O, Chalise MK, Koenig A (2006) The importance of ingestion rates for estimating food quality and energy intake. Am J Phys Anthropol 68:951–965

Simpson SJ, Raubenheimer D (1993) A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. Philos T R Soc B 342(1302):381–402

Smith RJ, Jungers WL (1997) Body mass in comparative primatology. J Hum Evol 32(6):523–559

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiol 41:291–309

Tardif SD, Jaquish CE (1997) Number of ovulations in the marmoset monkey (*Callithrix jacchus*): relation to body weight, age and repeatability. Am J Primatol 42(4):323–329

Terborgh J (1983) Five New World primates. Princeton University Press, Princeton

United States Department of Agriculture (2014) The PLANTS Database. http://plants.usda.gov. Accessed 7 Jul 2014

van Schaik CP, van Noordwijk MA (1989) The special role of male cebus monkeys in predation avoidance and its effect on group composition. Behav Ecol Sociobiol 24(5):265–276 van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu Rev Ecol Syst 24(1):353–377

Van Soest PJ, Robertson JB, Lewis BA (1991) Methods for dietary fiber, neutral deterent fiber, and nonstarch polysaccharides in relation to animal nutrition. J Dairy Sci 74(10):3583–3597

Vogel ER (2004) The ecological basis of aggression in white-faced capuchin monkeys, *Cebus capucinus*, in a Costa Rican dry forest. Dissertation, Stony Brook University

Vogel ER (2005) Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. Behav Ecol Sociobiol 58:333–344

Vogel ER, Janson CH (2006) Predicting the frequency of food related agonism in white-faced capuchin monkeys (Cebus capucinus), using a novel focal tree method. Am J Primatol 69(5):533–550

Voland E (1998) Evolutionary ecology of human reproduction. Annu Rev Anthropol 27:347–374

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