

Research Article

Figs Are More Than Fallback Foods: The Relationship between *Ficus* and *Cebus* in a Tropical Dry Forest

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In many studies on primate feeding ecology, figs (*Ficus* spp.) are characterized as fallback foods, utilized only when preferred sources of food are unavailable. However, for white-faced capuchin monkeys (*Cebus capucinus*) living in northwestern Costa Rica, figs are a consistently important resource and may increase groupwide energy intake. We investigated whether visits to figs affect ranging and behavioural patterns of capuchins. Although daily range length and average travel speed do not differ on days when fig trees are visited, capuchins spend more time in directed travel and more time stationary on “fig days”. Capuchins also increase time spent foraging for fruit and decrease time spent foraging for invertebrates on days when figs trees are visited. Capuchins experience higher energy intake and lower energy output on “fig” days. Thus, the patterns of foraging for figs support an energy-maximization strategy and constitute an important nutritional resource for capuchins.

1. Introduction

Fig syconia (hereafter referred to as figs or fig fruits) produced by *Ficus* trees are important resources for a plethora of tropical mammal, bird, reptile, and invertebrate species [1, 2]. Many of these animals are in turn important to fig trees, acting as seed dispersers. Three major types of fig-eating frugivores have been identified: birds, bats, and arboreal mammals. The evolution of the physical characteristics of different fig species is linked to particular types of seed dispersers [3]. Bat-dispersed figs tend to be larger, cryptically coloured (greenish), and highly odorous while bird-dispersed figs are small, conspicuously coloured (reddish), and less odorous [3, 4]. There is no specific fig dispersal syndrome that is linked with all arboreal mammals, but there is significant overlap in the fig species consumed by monkeys and birds [2]. Many Neotropical primates, including capuchins, have trichromatic vision and, like birds, are attracted to conspicuously coloured figs [5].

Figs are often described as fallback foods for tropical primates, eaten only when preferred foods are unavailable [6], or not eaten at all [7]. Rarely are figs described as consistent or preferred food items for primates (but see [8, 9]).

However, the characterization of figs as fallback foods has been strongly influenced by feeding studies of gibbons and orangutans [10–12] and may not be ubiquitous across the order Primates. In particular, there is evidence that fig fruits are both a consistent and preferred resource for many New World primates (Valenta and Melin, in review). Neotropical monkeys are frequent consumers of figs [6, 8, 9, 13–16] and are likely candidates as seed dispersers thereof.

Ecologists propose that nutritional needs explain food preferences and selection, including energy- and protein-maximization and the avoidance of plant secondary metabolites (PSMs; [17]). Figs are palatable, easily digested, contain few PSMs, and exhibit protein contents that are high enough to influence food selectivity in some Neotropical primates [1, 18]. Published nutritional data for *Ficus* fruits are highly variable, depending on the fig species analyzed and whether or not fig seeds were removed prior to analysis [19–24]. Proper assessment of nutritional uptake for a given fruit requires not only data on the nutritional content of single fruits, but information on the fruit intake rate as well. Figs eaten by capuchins and howler monkeys are most often small and conspicuously coloured and are consumed at higher rates than other fruits [8, 25].

Energy maximization is a key concept in optimal foraging theory [26, 27], which proposes that animals will maximize their net energy uptake during foraging and feeding behaviour [17]. Thus, according to optimal foraging theory, animals should travel to the next food patch at the most energy-efficient pace when the food energy available in their current patch is below a threshold level, and they should stop moving to feed when the available energy rises above this threshold [28]. Therefore, in food patches with high energy yields primates should feed more and move less [29].

While optimal foraging and patch depletion theories describe net energy maximization in regards to food acquisition, they do not predict behaviours after animals have become satiated, which likely occurs in very large fruit patches. If food acquisition is a primary motivation for primate movement, a higher proportion of stationary behaviours, such as resting and socializing, would be expected after satiation at large fruit patches. For example, primates in a Peruvian national park rested more and traveled less when seasonal fruit availability was highest [6]. Because fig trees produce extremely large fruit crops, fruit availability in fig trees can be high even if habitat-wide fruit availability is low. Therefore, we should expect more rest and less travel when primates visit fig trees.

An increase in resting or stationary behaviours should be reflected in short-term ranging measures such as day range length. An abundance of food may allow primates to relax their search efforts, leading to shorter day range lengths or an overall reduction in the amount of time dedicated to foraging movements [30, 31]. Additionally, the energy available in easily acquired, abundant foods may permit primates to expend extra energy on movement, such as increasing travel speeds between food patches.

Our objective is to combine data from previous studies of capuchin nutritional ecology [19, 21] with new data on ranging behaviour, foraging rates, duration of visits to fruit trees, monkey carrying capacities of fruit trees, and activity budgets to achieve a multifactor assessment of the relationship between capuchin monkeys and *Ficus* trees in Sector Santa Rosa, Costa Rica. We test the hypothesis that if *Ficus* trees provide a uniquely rich resource, in terms of energy gain per minute for all group members, then capuchins will alter their ranging and foraging behaviours in a way that that is more energy optimal on the days that they feed from fig trees (“fig days”) than on days that fig trees are not visited.

2. Materials and Methods

2.1. Study Site. This study took place in the Santa Rosa Sector (SSR) of the 153,000-hectare Área de Conservación Guanacaste (ACG), in Guanacaste province, Costa Rica. SSR is approximately 108 km² of evergreen and semideciduous tropical dry forest with a highly seasonal climate [32]. Sections of the forest were cleared for cattle pasture over the past 300 years and currently exhibit various stages of regeneration following the establishment of Santa Rosa as a national park in 1971. The area experiences an intense dry season from mid-December to mid-May, which is

characterized by high ambient temperatures, strong winds, little to no rainfall, and the defoliation of many nonriparian trees [33]. Most of the natural water sources in the area dry up towards the end of the dry season. The wet season occurs from the second half of May through November, with the majority of the 1500 mm of annual rainfall occurring during September and October. A short but relatively drier period (the “veranito”) occurs between mid-July and mid-August, dividing the early and late wet seasons [34], a pattern that is typical of tropical forests at this latitude [35].

2.2. Subjects. Capuchin monkeys are frugivore-insectivores and live in matrilineal social groups [36]. We studied the movement and foraging behaviours of one small group (EX: 8–11 individuals), two medium-sized groups (LV: 20–23; CP: 24–26), and one large group (GN: 33–35) of free-ranging white-faced capuchins (*Cebus capucinus*) for 22 months (January through April 2007, September 2007 through January 2008, May through August 2008, January through August 2009). All groups were habituated to human presence, and two have been studied intensively for over 20 years (e.g., [37, 38]). Each group was followed, on average, for three consecutive days each month.

2.3. Data Collection

2.3.1. Energy Acquisition. We recorded a “fruit patch visit” (FPV) whenever we observed a monkey to enter a new fruit source. For each FPV, we recorded the plant species, GPS location, trunk circumference at breast height (CBH) and, whenever possible, the carrying capacity of the patch (maximum number of monkeys simultaneously feeding) and the duration of the FPV (time elapsed from entry of the first monkey until the exit of the last monkey). We designated all days that included at least one FPV in a *Ficus* tree as a “fig day”.

To calculate invertebrate capture rates, we collected behavioural data using 10-minute continuous focal animal samples [39] of all adult, subadult, and large juvenile capuchins in each of the four study groups. We recorded behaviour states and foraging events whenever they occurred and attempted to identify all consumed insects. Insect capture rates were calculated by dividing the number of captures for each insect, or set of insects, by the total time spent in the “visually foraging” state (“scanning nearby substrates”; [40]). We used previously published nutritional data for insects consumed by capuchins [19] to calculate nutrient uptake from insect foraging.

We conducted 1- to 5-minute continuous focal animal samples [39] of all independently foraging group members (i.e., not infants) to record feeding events when we observed them feeding in fruit trees. The durations of the focal samples were dependent on visibility. We counted a feeding event whenever the focal animal swallowed a fruit whole or took at least two bites from it. The total number of individual fruits ingested was divided by the total duration of the foraging state to calculate the feeding rate for each fruit tree species.

We reviewed the literature to obtain nutritional data for *Ficus* species and found great variation in the results.

While capuchins likely chew and digest some seeds, they are predominantly “gentle” fig eaters, squeezing the pulp and juice out of figs and rarely masticating the seeds [41]. Therefore, we decided that Jordano’s [24] nutritional data for figs are most applicable to our study because Jordano did not include the nutritional value of seeds and also because his study took place in Sector Santa Rosa, as did ours. We obtained nutritional data for other fruits consumed by capuchins from the published literature as well [19, 21, 22] to compare with figs.

To calculate the energy uptake rate (KJ/minute) for each fruit species, we multiplied the feeding rate (fruits/minute) by the energy content (KJ/fruit). We only calculated energy uptake rates for 31 fruit species with available nutritional data (Table 1). We have additional feeding rates, FPV durations and carrying capacities for another 45 plant species.

2.3.2. Ranging Data. We used Garmin GPSMAP 76Cx handheld GPS units to record group locations on the hour and half hour throughout the day ($N = \text{approx. } 25$ per day), and at the sleep sites in the morning and evening. Best efforts were made to record the location of the centre of the group. Analysis for this study only included data from full-day follows of monkey groups ($N = 186$), when we were with the group from their wake site in the morning to their sleep tree in the evening. We sampled evenly between the dry ($N = 90$) and wet ($N = 96$) seasons.

Day range lengths were calculated using Garmin MapSource software (Garmin, USA) by summing the vector distances between consecutive location points over the course of the day. We measured stationary time daily by counting the number of half-hour intervals in which the travel distance was less than 10 metres. Travel speed was calculated by dividing the average distance traveled for each half-hour interval by the length of the interval (30 minutes). For each day, we averaged travel speed by summing the travel speeds for each interval and dividing by the number of intervals. Travel speed calculations only included intervals where the distance traveled was ≥ 10 metres. Any travel distance < 10 metres was considered to be stationary. This distance was chosen as the cut-off point because it was the maximum error range (± 10 m) of the GPS unit, and it allowed us to account for the fact that the monkeys could be spread out within the crown of especially large fruit trees that could reach 10 metres in diameter.

2.3.3. Activity Budgets. Every half hour we conducted group scan samples and assigned a behaviour class to each monkey we could locate within 10 minutes. We calculated daily activity budgets as the proportion of scans devoted to each behaviour class (Table 2).

2.4. Statistical Analyses. We used general (GLM), and generalized linear mixed models (GLMM) to test the effect of fig day on the ranging parameters: day range length (GLM), travel speed (GLM) and stationary time (GLMM; negative binomial distribution). To analyze the group scan data relating to activity budgets, we classified and subclassified

each variable (Table 2). We first compared foraging to nonforaging behaviours and then compared the types of behaviours to the others within each of these larger classifications (i.e., fruit foraging behaviours to the remaining foraging behaviours.) To maintain adequate sampling, we removed days from the analysis if they had < 10 scans in the category of interest. We included group size (small, medium, large) and season (wet, dry) as covariates in all analyses, as these variables affect ranging patterns and activity budgets of capuchins in Sector Santa Rosa. For all statistical models, significance was set at $P < 0.05$. All statistical analyses for this study were performed using SAS software, Version 9.1.3 (SAS Institute Inc., Cary, NC).

3. Results

We observed the capuchins eating the fruits of 117 plant species including eight different fig species: *Ficus bullenii*, *F. citrifolia*, *F. cotinifolia*, *F. goldmani*, *F. hondurensis*, *F. morazaniana*, *F. obtusifolia*, and *F. ovalis*. Four of these fig species (*F. citrifolia*, *F. cotinifolia*, *F. hondurensis*, *F. ovalis*) are conspicuous, while the other four species have cryptically-coloured fruits characteristic of bat dispersal. Among the conspicuous *Ficus* species, *F. citrifolia* is rare in SSR; to date we have recorded only two trees in the monkeys’ home ranges. Thus, data on this fig species should be interpreted with caution, as the sample size is low for all our measures. 88% of capuchin fig foraging time was dedicated to the four conspicuous figs. One fig species in particular, *Ficus cotinifolia*, was consumed approximately three times more often than any of the other conspicuous figs. As *F. cotinifolia* fruits are similar in size and colour to other conspicuous figs, and this species is the only conspicuous fig in SSR for which nutritional data have been published, we use this species as a representative of all conspicuous fig species in our discussion.

3.1. Energy Obtained for Foraging Visits to Figs. Fig trees in SSR fruit both asynchronously and aseasonally (Fedigan, unpub. data). Hence, we observed the consumption of figs by capuchins during every month of the year. Fig trees in SSR had the largest carrying capacities of any species (Table 1). The single highest maximum carrying capacity recorded during our study was for the entire CP group (26 monkeys) cofeeding in a single *Ficus ovalis* tree. Four of the five maximum carrying capacities belonged to *Ficus* species, with several other *Ficus* species ranking closely behind. *Ficus* species also had among the highest average carrying capacities, nearly filling the top 10 spots.

Along with large carrying capacities, *Ficus* trees also had the longest FPV durations recorded. One visit to a *F. cotinifolia* resulted in four hours of continuous foraging as group members took turns feeding. *Ficus* species occupied the top three spots for FPV duration, as well as the 7th spot.

Of the 76 fruit tree species for which we could calculate feeding rates, the conspicuous *Ficus hondurensis*, *F. cotinifolia*, *F. ovalis*, and *F. citrifolia* ranked 5th, 7th, 10th, and 23rd, respectively. The feeding rate for *F. citrifolia* is likely an underestimate, not only because our sample size for this

TABLE 1: Fruit patch data, nutritional information, feeding rates, and nutrient intake rates for 31 fruit species consumed by *Cebus capucinus* at Sector Santa Rosa, ACG, Costa Rica. FPV = fruit patch visit.

Family	Tree information		Carrying capacity		FPV duration (min.)		Nutrition (fruit ⁻¹)		Intake Rate (fruits/min)		Nutritional intake (min ⁻¹)	
	Tree species	Avg. DBH	Maximum	Mean	Maximum	Mean	Energy (KJ)	Protein (g)	Energy (KJ)	Protein (g)	Energy (KJ)	Protein (g)
Anacardiaceae	<i>Spondias purpurea</i> ²	28.3	—	—	—	—	11.623	—	3.3	37.811	—	—
Apocynaceae	<i>Stemmadenia obovate</i> ²	12.7	4	1.3	3.1	28	189.779	—	0.5	103.986	—	—
Araliaceae	<i>Sciadodendron excelsum</i> ^{1,2}	57.0	8	2.5	10.7	64	1.231–1.331	0.006	12.3	15.165–16.408	0.074	0.074
Bignoniaceae	<i>Tabebuia ochracea</i> ²	26.9	5	2.4	9.8	33	14.574	—	7.9	115.233	—	—
Burseraceae	<i>Bursera simaruba</i> ^{1,2}	35.2	11	2.0	7.1	52	0.431–3.710	0.015	7.1	3.094–26.511	0.107	0.107
Elaeocarpaceae	<i>Sloanea ternifolia</i> ²	92.7	16	4.7	29.3	142	1.545	—	5.0	7.792	—	—
Erythroxylaceae	<i>Erythroxylum havanense</i> ^{1,2}	6.1	4	1.5	7.1	44	0.239–0.611	0.004	24.8	5.874–15.152	0.099	0.099
Fabaceae	<i>Vachellia collinsii</i> ¹	4.2	7	1.4	1.6	8	6.305	0.082	4.3	27.214	0.354	0.354
Flacourtiaceae	<i>Casearia arguta</i> ²	11.0	4	1.6	2.9	7	5.870	—	6.7	39.130	—	—
	<i>Casearia sylvestris</i> ²	12.7	6	2.0	8.0	40	0.159	—	22.1	3.521	—	—
Malpighiaceae	<i>Bunchosia ocellata</i> ¹	14.2	4	2.4	7.4	22	6.778	0.036	9.4	63.635	0.338	0.338
	<i>Byrsonima crassifolia</i> ^{1,2}	29.9	5	1.8	6.7	28	7.189–8.826	0.333	5.3	38.050–46.725	1.763	1.763
Malvaceae	<i>Malvaviscus arboreus</i> ¹	5.5	2	1.1	0.7	3	5.330	0.038	6.2	33.285	0.237	0.237
Meliaceae	<i>Trichilia martiana</i> ¹	27.9	9	2.0	13.3	95	4.878	0.017	10.3	50.112	0.175	0.175

TABLE 1: Continued.

Family	Tree information Tree species	Avg. DBH	Carrying capacity		FPV duration (min.)		Nutrition (fruit ⁻¹)		Intake Rate (fruits/min)		Nutritional intake (min ⁻¹)	
			Maximum	Mean	Maximum	Mean	Energy (KJ)	Protein (g)	Intake Rate (fruits/min)	Energy (KJ)	Protein (g)	
Moraceae	<i>Ficus bullene</i> ⁴	102.4	—	—	—	—	0.098	—	3.9	—	—	0.384
	<i>Ficus citrifolia</i>	19.3	7	3.7	12	8.0	—	—	7.8	—	—	—
	<i>Ficus cotinifolia</i> ³	129.3	15	5.4	273	46.5	0.007	2.261	14.5	—	33.687	0.104
	<i>Ficus goldmani</i>	89.1	12	5.7	18	10	—	—	5.3	—	—	—
	<i>Ficus hondurensis</i>	86.0	11	5.6	222	46.1	—	—	16.2	—	—	—
	<i>Ficus morazaniana</i>	120.2	13	5.9	177	42.9	—	—	3.9	—	—	—
	<i>Ficus obtusifolia</i> ⁴	84.2	8	3.2	41	11.5	—	0.128	2.6	—	—	0.334
	<i>Ficus ovalis</i>	113.4	26	5.5	117	27.3	—	—	12.5	—	—	—
	<i>Psidium guajaba</i> ¹	12.1	8	1.8	28	6.2	14.302	0.254	1.3	—	18.593	0.330
	<i>Karwinskia caldronii</i> ¹	43.6	10	2.9	91	12.7	0.695	0.010	12.0	—	8.345	0.120
Rhamnaceae	<i>Alibertia edulis</i> ¹	6.2	5	1.2	7	1.7	16.801	0.131	1.6	—	26.830	0.209
	<i>Genipa americana</i> ^{1,2}	20.8	7	1.8	38	4.4	27.964–60.462	1.359	0.5	13.982–30.231	0.680	—
Rubiaceae	<i>Guettarda macrocarpa</i> ²	29.9	7	2.4	17	6.0	1.437	—	10.4	—	14.988	—
	<i>Randia monantha</i> ¹	8.0	7	1.9	44	7.0	18.093	0.268	0.9	—	17.090	0.253
Simaroubaceae	<i>Simaruba glauca</i> ^{1,2}	29.6	8	2.5	57	13.2	1.676–3.474	0.038	4.5	7.535–15.621	0.171	—
Solanaceae	<i>Solanum hazenii</i> ¹	9.5	4	1.8	17	5.9	1.111	0.035	4.2	4.678	0.147	—
Sterculiaceae	<i>Guazuma ulmifolia</i> ²	35.4	2	1.2	6	1.8	5.448	—	2.3	—	12.259	—

Nutritional data from ¹McCabe 2005, ²Vogel 2006, ³Jordano 1983, ⁴Milton 2008. FPV: fruit patch visit.

TABLE 2: Ethogram of the behaviour classes recorded during behavioural scan samples of *Cebus capucinus* in Sector Santa Rosa, ACG, Costa Rica.

Type	Behaviour class	Description	
Fruit foraging	Extractive foraging fruit	Extracting edible part of fruit from husk/shell within a fruit patch	
	Visually foraging fruit	Scanning for or consuming bite-sized fruit within a fruit patch	
	Feeding on fruit	Dedicated feeding (duration > 1 sec) on fruit within a fruit patch	
	Insect foraging	Extractive foraging invertebrate	Extracting invertebrates from bark, branches, leaves; stationary insect foraging
		Visually foraging invertebrate	Scanning for and consuming bite-sized invertebrates, often coincident with slower group travel
		Feeding on invertebrate	Dedicated feeding (duration > 1 sec) on invertebrates; stationary insect feeding
Other foraging	Feeding on other	Dedicated feeding (duration > 1 sec) on vertebrates or woody plant parts	
Nonforaging behaviours	Low Intensity	Resting	
		Social	
	Active	Directed travel	
		Other	

species is significantly lower than the other three species, but also because we only observed capuchins foraging for *F. citrifolia* twice and in both cases very few of the figs were ripe. The average feeding rate for ripe conspicuous figs was 14.5 figs per minute. Feeding rates for cryptic figs were lower (ranks 39, 48, and 60 for *F. goldmani*, *F. morazaniensis*, and *F. obtusifolia*, respectively), averaging 4.9 figs per minute.

At the level of an individual fruit, *Ficus cotinifolia* figs are not exceptionally nutritious (Table 1). However, given the high feeding rates, figs are at par with most other fruits for energy uptake rate given the nutrition of the pulp. Importantly, however, figs also contain fig wasps and other animal matter, which contain a relatively high amount of energy and increase the protein content by up to 30% [20].

3.2. Effect of Figs on Ranging Behaviour. Our study groups traveled 2357 ± 506 m daily (range: 1200–3892 m). Day range lengths varied significantly among group size classes ($F = 7.13$, $N = 186$, $df = 2, 11$, $P = 0.0103$) and between the wet and dry seasons ($F = 5.17$, $N = 186$, $df = 1, 11$, $P = 0.0440$). Day range lengths were 110 m shorter on average on fig days, but this was not a statistically significant difference ($F = 0.42$, $N = 186$, $df = 1, 11$, $P = 0.53$).

There was considerable variation in the time that capuchin groups spent stationary during our study. Occasionally ($N = 21$ days) we observed the capuchins to remain stationary for more than five half-hour intervals per day while on other days ($N = 34$) the groups did not stop travelling for even one interval. We did find a significant effect of fig visits on stationary time. The capuchins spent nearly twice as much time stationary on days when they visited figs, than nonfig days ($F = 19.26$, $N = 186$, $df = 1, 179$, $P < 0.0001$). Capuchin groups traveled 13.2 metres/hour faster on fig days, although the effect was not significant ($F = 0.02$, $df = 1, 11$, $P = 0.8841$) because of the large intraday varia-

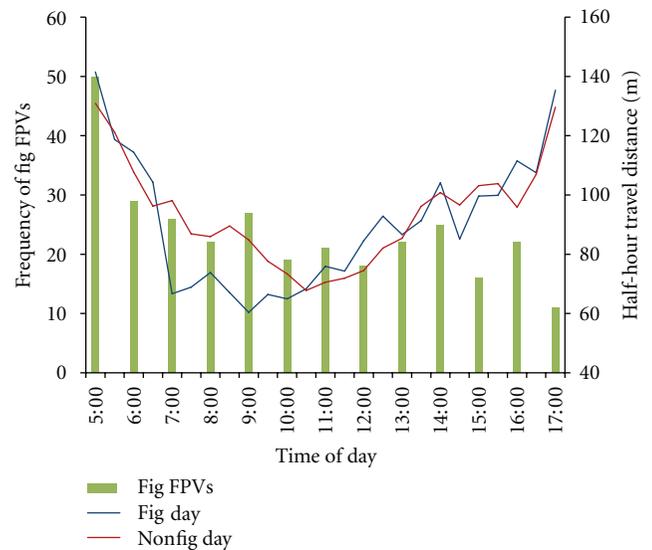


FIGURE 1: Average travel distance and fig fruit patch visit (FPV) frequency by time of day for *Cebus capucinus* in Sector Santa Rosa, Costa Rica.

tion in travel speed. Capuchins travelled further in 30-minute intervals (i.e., more quickly) in the early morning, when fig visitation rates were the highest, and more slowly as midday approached relative to days on which figs were not visited (Figure 1). Travel rates during the latter half of the day were more similar between fig days and nonfig days.

3.3. Effect of Figs on Activity Budgets. Time spent in foraging versus nonforaging behaviours was not affected by whether the group went to a fig tree. However, among the foraging behaviours, capuchins dedicated significantly more time to fruit foraging ($F = 28.85$, $N = 114$, $df = 1, 111$, $P < 0.0001$) and correspondingly less time to invertebrate foraging on

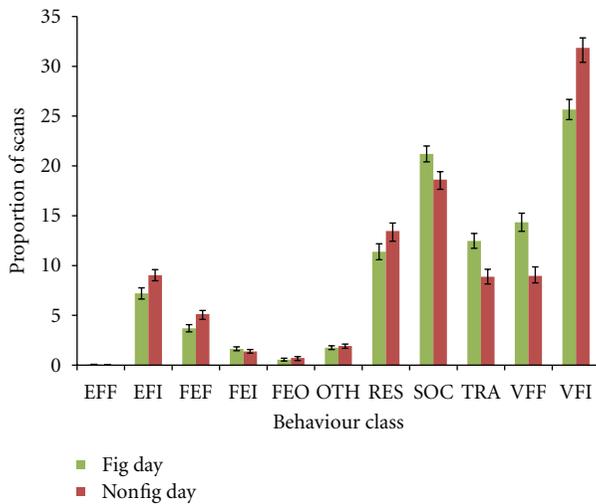


FIGURE 2: Proportion of scan samples taken at 30-minute intervals dedicated to different behaviour classes by white-faced capuchin monkeys in Sector Santa Rosa, ACG, Costa Rica. EFF: extractive foraging fruit; EFI: extractive foraging invertebrate; FEF: feeding fruit; FEI: feeding invertebrate; FEO: feeding other; OTH: other behaviour; RES: resting; SOC: social; TRA: traveling; VFF: visually foraging fruit; VFI: visually foraging invertebrate.

fig days (Figure 2). Among the nonforaging behaviours, capuchins spent more time in directed travel ($F = 5.46$, $N = 113$, $df = 1$, 97 , $P = 0.0215$) on fig days (Figure 2). The proportion of time dedicated to different low-intensity behaviours (resting, social) was not significantly affected by fig day ($F = 0.23$, $N = 113$, $df = 1$, 110 , $P = 0.6291$).

4. Discussion

4.1. Figs Are more than a Fallback Resource for *Cebus* monkeys. The eight fig species in Santa Rosa supply 31% of the fruit in the capuchin diet. This is similar to the proportion of figs in the diet of *Cebus albifrons* (37.5%), but higher than in the tufted capuchin, *Cebus apella* (20%; [6]). 87% of capuchin fig-foraging time dedicated to conspicuous figs [8] and more than half of this time was spent consuming figs from *Ficus cotinifolia* [42]. We recorded 365 visits to *Ficus* trees over a period of 22 months and *Ficus* trees were visited in each month of the year, during which time the overall availability of fruits eaten by capuchins varies considerably (Santa Rosa capuchin database, unpubl. data). Thus, we conclude that figs are consistently important resources in the diet of white-faced capuchins in SSR due to their year-round consumption by capuchins, and we would not characterize them as fallback foods for capuchins.

4.2. Energy Obtained during Foraging Visits to Figs. Some previous nutritional studies have downplayed the importance of figs to Neotropical primates due to their low nutritional content [20]. However, these studies have not taken into account the high feeding rates of primates in fig trees, and other researchers have found that figs represent a relatively well-rounded nutritional source [43]. We found

that fig intake rates are one of the highest among all fruits eaten by white-faced capuchins and are comparable to previously published fig consumption rates for howler monkeys and capuchins [21, 25, 44]. Three conspicuous fig species rank within the top 10 of our list of 76 fruits for which we could calculate feeding rates. Although the small single fruits from *Ficus cotinifolia* contain little energy (2.26 KJ; [24]) capuchins obtain substantial amounts of energy in short periods of time from these figs due to high intake rates.

Perhaps the most important feature of fig trees is their ability to provide an abundant source of food for entire groups of capuchin monkeys in SSR. *Ficus* trees have high visitation rates, the longest foraging visit durations, and the highest monkey carrying capacities of any fruit source in SSR, which ensures that most or all of the group members can feed in the same location. Compared to smaller canopy trees, capuchin feeding rates in figs are less affected by aggression levels and are only slightly higher for dominant individuals than for subordinates [44]. When capuchins forage in large-crowned trees, individuals are able to spread out and reduce competition and aggression [45, 46]. Therefore, in large food patches, like fig trees, the form of feeding competition may shift from contest to scramble with dominant individuals feeding in areas of the tree with higher concentrations of easily consumable fruits [21]. The energy obtained through the easy acquisition and low processing times of fig fruits by entire capuchin groups supports the claim that figs are the most important resource for tropical frugivores [2].

4.3. Effect of Figs on Ranging Behaviour. Foraging on figs does not affect the ranging behaviour of white-faced capuchins *per se*. Capuchin groups travel similar distances and at the same average speed on fig and nonfig days. Travel speed and distance may be affected by other factors such as access to water and territorial monitoring and intergroup encounters [47], but the time spent stationary by capuchins is significantly affected by trips to fig trees. Capuchin groups spend significantly more time stationary on fig days. With constant day range lengths, we would expect capuchins to travel faster on fig days to make up the distance lost during their long stationary bouts. The likely explanation is in the distribution of half-hour travel speeds. Many primates eat fruits early in the day to ensure they acquire the energy that will sustain their behaviour later in the day [22]. Capuchins travel their furthest distances during the first few hours of the day (Figure 1). On fig days, capuchin groups travel even faster during these hours and travel slower over the next few hours than they do on nonfig days. The early morning also coincides with the highest rate of visits to fig trees, which suggests that capuchins travel directly to reach fig trees as early as possible in the day.

4.4. Effect of Figs on Activity Budget. While a large amount of time spent in a large fruit patch is not unexpected [29], the behaviour differences on fig versus nonfig days are noteworthy. Capuchins increase their fruit foraging by ten percent on fig days, which corresponds with a ten percent decrease in invertebrate foraging. This dietary shift could have several

TABLE 3: Energy, fat, and protein intake rates for *Ficus cotinifolia* and common invertebrate prey of capuchins in Sector Santa Rosa, ACG, Costa Rica.

Species	Intake/h	g/h		
		KJ/h Energy	Fat	Protein
Invertebrates				
Cockroach (<i>Blaberus giganteus</i>) ¹	0.054	2.437	0.020	0.089
Cicada (<i>Fidicina</i> spp.) ¹	0.108	2.319	0.010	0.083
Small shelled insects (Insecta spp.) ¹	27.42	43.396	0.192	1.371
Caterpillars (Lepidoptera spp.) ¹	12.46	4.279	0.025	0.112
Grasshoppers/Katydid (Orthoptera spp.) ¹	0.987	11.556	0.118	0.404
Ants (Formicidae spp.) ¹	0.230	0.033	<0.000	0.001
Scorpions (<i>Scorpiones</i> spp.) ¹	0.014	0.134	0.001	0.005
All invertebrates		64.150	0.367	2.064
Figs				
<i>Ficus cotinifolia</i> (pulp only) ²	894	2021.220	3.576	6.258
<i>Ficus cotinifolia</i> (pulp + animal matter) ^{2,3}	894	2099.823	4.184	7.581

Source: ¹McCabe 2005, ²Jordano 1983, ³Urquiza-Haas et al. 2008. Nutritional values for animal matter in *F. cotinifolia* are estimated from the percentage dry weight of animal matter in *F. perforata*.

implications for the health and nutrition of capuchins. First, invertebrate foraging is an energy-expensive behaviour. Although, individually, invertebrates are high in protein and fat [19], they are much more difficult to acquire than fruit. Capuchins utilize many techniques to acquire invertebrate prey, including breaking and chewing through branches, chasing and catching, and sifting through leaf litter, all of which are sure to be more energy expensive than fig foraging. Second, invertebrate foraging is potentially more dangerous for capuchins. Defense tactics of some invertebrate prey (e.g., stinging scorpions, biting ants, and acid-releasing beetles) aside, invertebrate foraging likely increases the risk of predation to capuchins. In SSR, capuchins often forage for invertebrates on, or near, the forest floor, especially when fruit availability is low [48], which increases their susceptibility to predation by terrestrial hunters, including snakes, cats, and other carnivorous mammals. Third, invertebrate capture rates are quite low compared to fruit intake rates in general, and to fig intake rates specifically. Usually capuchins supplement their frugivorous diet with invertebrate prey, but they may require less supplementation if the protein intake at fig trees is high enough. For example, the protein acquired by consumption of a scorpion is equivalent to only six minutes of fig foraging based on published nutritional estimates [19, 20, 24] and invertebrate intake rates (Table 3). Similarly, it takes only 50 seconds of fig foraging to equal the protein intake for a small, shelled invertebrate (e.g., stink bug), the capuchins' most common invertebrate prey. We calculated that capuchins ingest ~2.1 g protein per hour from invertebrates and ~6.3 g per hour of protein from figs. Therefore, fig foraging may allow the capuchins to significantly decrease the amount of time spent searching for and capturing invertebrates.

Capuchins spent significantly more time involved in directed travel on fig days. Directed travel is defined as fast-speed movement (adults walk/jump quickly or lope, and juveniles usually run) that does not include visual

foraging. During other group movement, capuchins often travel more slowly and forage for invertebrates while moving between fruit trees, water sources, or favourite rest trees. This "foraging locomotion" is decreased on fig days. Although directed travel is expected to have higher thermoregulatory costs than foraging travel, it is noteworthy that the highest travel speeds occur early in the morning and later in the day, when thermoregulation costs of travelling in a tropical environment are decreased [33].

5. Conclusions

Fig trees are one of the most important resources for white-faced capuchins in the tropical dry forests of Costa Rica. They provide a superabundance of food, simultaneous foraging space for many group members and lower predation risk, allowing monkeys to spend less time in solitary searching for invertebrates close to the forest floor. Additionally, group cohesiveness and close proximity in fig trees allows for better vigilance and protection from aerial predators. The fruit biomass in fig trees provides enough energy to satiate an entire capuchin group, despite the fact that energy uptake rates from *Ficus cotinifolia* are not significantly higher than other fruit species. Finally, figs fruit asynchronously and year round, making them a dependable resource for capuchins living in a tropical dry forest where fruit availability is highly seasonal.

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