Nutritional Ecology of *Ateles chamek* in lowland Bolivia: How Macronutrient Balancing Influences Food Choices

**Annika M. Felton · Adam Felton · Jeff T. Wood ·
William J. Foley · David Raubenheimer ·
Ian R. Wallis · David B. Lindenmayer**

Abstract All free-living animals must make choices regarding which foods to eat, with the choices influencing their health and fitness. An important goal in nutritional ecology is therefore to understand what governs animals' diet selection. Despite large variation in the availability of different food items, Peruvian spider monkeys (*Ateles chamek*) maintain a relatively stable daily protein intake, but allow total energy intake to vary as a function of the composition of available food items. This is referred to as protein-dominated macronutrient balancing. Here we assess the influence of this nutritional strategy on daily and seasonal nutritional intakes,

A. M. Felton · A. Felton · J. T. Wood · D. B. Lindenmayer
Fenner School of Environment and Society, The Australian National University, Canberra 0200, Australia

A. M. Felton (✉)
Instituto Boliviano de Investigación Forestal (IBIF), Cuarto Anillo Casilla Postal 6204, Santa Cruz de la Sierra, Bolivia
e-mail: Annika.Felton@anu.edu.au

W. J. Foley · I. R. Wallis
Department of Botany and Zoology, The Australian National University, Canberra 0200, Australia

D. Raubenheimer
Institute of Natural Sciences, Massey University, Albany, Private Bag 102 904, Auckland, New Zealand

D. Raubenheimer
New Zealand Institute for Advanced Study, Massey University, Albany, Private Bag 102 904, Auckland, New Zealand

estimate the nutritional value of different foods, and interpret unusual food choices. We conducted continuous all-day observations of focal spider monkeys inhabiting a semideciduous forest in Bolivia. We recorded feeding events, collected foods, and analyzed their nutrient content. By using the Geometric Framework for nutrition, we show that individuals reached their daily end-point in nutrient space —balance between protein and nonprotein energy intake— by consuming nutritionally balanced foods or by alternating between nutritionally complementary foods. The macronutritionally balanced figs of *Ficus boliviana* were their primary staple food and therefore dominated their overall nutritional intake. Our results also demonstrate that spider monkeys consumed a diverse array of ripe fruits to overcome periods of fig scarcity rather than vice versa; they could obtain sufficient protein on a diet of pure fruit; and unripe figs constituted a nutritionally rewarding and reliable food resource. We hope that the approaches taken and the conclusions reached in this study will catalyze further inquiries into the nutritional ecology of frugivorous primates.

Introduction

Primates must make choices regarding which foods to include in their daily diet, with these choices influencing their nutritional state and ultimately their health and fitness (Altmann 1998; Beehner *et al.* 2006). The food choices made will be determined primarily by the animal's regulatory phenotype, but constrained by the nutritional, chemical, and structural composition of the foods in the environment (Lambert 2007; Milton 1993). Quantifying the underpinnings of diet selection is challenging, especially in studies of wild animals, because it requires precise feeding observations of individuals over continuous periods, relevant analyses of all foods consumed, and a framework to analyze the complex, multivariate nature of the data.

The Geometric Framework for nutrition (GF) is an analytical technique that enables an understanding of the nutritional strategies of animals (Simpson and Raubenheimer 1993; Raubenheimer and Simpson 2004) and the interpretation of food choices that are otherwise difficult to explain (Robbins *et al.* 2007). Researchers have successfully applied the framework to a range of vertebrate and invertebrate taxa (Chambers *et al.* 1995; Felton *et al.* 2009b; Raubenheimer and Simpson 2006; Robbins *et al.* 2007; Ruohonen *et al.* 2007; Simpson and Raubenheimer 2001, 2005). The GF describes feeding behavior within an *n*-dimensional space delineated by axes representing nutrients of interest (Raubenheimer and Simpson 2004). It is possible to identify an animal's nutritional intake target within this nutrient space and to relate this target to the nutritional content of the foods available (Felton *et al.* 2009a).

Spider monkeys (genus *Ateles*, subfamily Atelinae) are arboreal primates that inhabit the canopies of Neotropical forests and primarily consume ripe fruit (Di Fiore *et al.* 2008; Kinzey 1997). Energy is often proposed to be the primary driver behind atelines' diet selection (Di Fiore and Rodman 2001; Rosenberger and Strier 1989; Strier 1992), because they frequently select and ingest large volumes of fruits that are rich in lipids and soluble carbohydrates (Castellanos 1995; Dew 2005). In

contrast to this view and other major schools of thought in nutritional ecology (Dearing *et al.* 2005; Freeland and Janzen 1974; Mattson 1980; Schoener 1971; White 1993), Felton *et al.* (2009b) determined that spider monkeys (*Ateles chamek*) in La Chonta, Bolivia, select diets that supply a set amount of protein, rather than attempting to maximize the ingestion of energy or protein, or to regulate plant secondary metabolites. Daily protein intake was regulated more tightly than carbohydrates or fats, and thus disproportionately influenced total energy intake. Further, protein intake did not vary across seasons despite dramatic fluctuations in food availability (Felton *et al.* 2009b). Research on the spider monkeys in La Chonta further showed that although their diet contained as much fruit as other *Ateles* species, it differed in 2 respects (Felton *et al.* 2008). First, figs (*Ficus*) were a staple food all through the year. There are no similar reports of a comparable reliance on *Ficus* by this primate genus even though all spider monkeys eat figs (Di Fiore *et al.* 2008). Second, the spider monkeys in La Chonta spent much time consuming unripe figs, even when ripe figs and other ripe fruits were abundant (Felton *et al.* 2008).

Here we build on the knowledge that diet selection of the La Chonta spider monkey community is governed by protein-dominated macronutrient balancing. We use the Geometric Framework to assess the influence of this nutritional strategy on daily and seasonal nutritional states of individuals by analyzing the intake trajectories of individuals and the macronutritional balance of foods consumed. We also estimate the nutritional value of different foods, and interpret the unusual food choices described in the preceding text in nutritional terms.

Methods

The lead author together with field assistants collected data in the lowland subtropical semihumid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. The study area (S: 15°36′26′′ to 15°37′45′′ and W: 62°46′59′′ to 62°47′56′′) was located in an unlogged section of the 100,000 hectare forestry concession La Chonta, owned by Agroindustría Forestal La Chonta Ltda. The average annual temperature and precipitation for La Chonta are 25°C and 1580 mm, with 4 dry months (<100 mm rain; May–September).

Tall forest dominates the study area, with small sections of low vine forest, chaparral, and swamp (Felton *et al.* 2008). There were 3 distinct phenological periods (seasons) during the study, including a period of high ripe fruit abundance (late wet season; February to mid-April) followed by a 10-wk period of fruit scarcity (early–mid dry season; mid-April to June) before ripe fruits became more abundant again (late dry–early wet season; July to September; Felton *et al.* 2008).

We established a network of trails in the focal individuals' 360–400 ha territory and used it for daily observations of focal individuals, monthly phenological surveys, and 1 vegetation survey. We collected basal area information from all trees >10 cm diameter at breast height (DBH) within 71 0.1-ha plots distributed throughout the home range. A detailed description of the design and sampling of our phenology surveys appears in Felton *et al.* (2008).

We spent 5 mo habituating the study community, and thereafter (February 2004– September 2004) systematically collected feeding data via continuous observations

of a focal animal (FA) from dawn to dusk. We observed a total of 18 adult FAs: 8 males and 10 females. Females were either lactating or pregnant while caring for a juvenile. When possible, we followed 10–15 of the FAs for a whole day each month, over 20 d, alternating daily between males and females. For the purpose of the detailed dietary analyses used here, we include 51 full days during which we successfully observed the individual the entire day and, at most, only brief moments of feeding were unrecorded (32 d of observations of 8 females, 19 d of 8 males; see Table III for the distribution of follow days between seasons). We also use data from an additional 19 partial follow days when presenting the nutritional content of commonly eaten food items. Because there are no significant differences in macronutrient intake between sexes or individuals (Felton *et al.* 2009b), it is unlikely that the greater number of female follow days represented a bias in our analysis.

We recorded the time of the start and end of each feeding event, and the foods eaten from the categories of ripe fruit/fig, unripe fruit/fig, flower, young leaf, mature leaf, or other. We took detailed notes on which parts of the fruits subjects consumed. We used differences in fruit size, color, and consistency to differentiate between immature and ripe fruits. We calculated feeding rates (number of items consumed/ minute) for all food types. We identified and tagged all plants from which the monkeys ate. Within 1 or 2 days of feeding observations, we collected and dried (40–50°C) samples of the food items from these trees (Felton *et al.* 2009b). During the 51 full day follows, we observed monkeys eating 84 different foods, 69 of which we collected and analyzed. FAs spent <1% of their total feeding time eating items we did not analyze.

We used near infrared reflectance spectroscopy (NIRS; Foley *et al.* 1998) to estimate the concentrations of total nitrogen, lipid, starch, neutral detergent fiber, ash, polyethylene glycol (PEG) binding capacity, and *in vitro* digestible nitrogen and dry matter (DM) in all food items. We did this by using standard NIRS procedures (ANON 1995). We refer to Felton *et al.* (2009b) for descriptions of chemical analyses of total nitrogen (total N), water-soluble carbohydrates, starch, and neutral detergent fiber. We combine values for water-soluble carbohydrates and starch and present them as total nonstructural carbohydrates (TNC). We assayed tannins as the amount of PEG bound per unit DM and we estimated the effect of tannins on nitrogen and DM availability via the *in vitro* digestion procedure described by De Gabriel and others (2008). We estimated available protein as (total N) × (*in vitro* N digestibility) × 6.25. There is some uncertainty whether 6.25 is the best conversion factor for tropical fruits (Milton and Dintzis 1981), but we use it here to allow for comparison with other studies. We assumed that lipids were 100% available. We present dry matter digestibility (DMD) as DMD in the absence of PEG (DMD-PEG).

The *in vitro* measure of protein availability (and DMD) may not accurately represent *in vivo* availability, but it at least allowed us to estimate the proportion of total nitrogen available to the consumer versus how much was bound up by dietary tannins. To highlight the disparity between concentrations and intakes of available protein (available N×6.25) and crude protein (total N×6.25), we include both measures in the tables. We did not analyze termites but instead used the nutrient concentrations reported by Dufour (1987).

We applied the Geometric Framework to our data (Raubenheimer and Simpson 1997; Simpson and Raubenheimer 1995). The framework unifies several nutrition-

ally relevant measures within simple geometrical models, thus allowing for a comparison between observed patterns and predicted reference patterns. For the purpose of our analysis, TNC and lipids can be regarded as interchangeable energy sources (Ruohonen *et al.* 2007), because when TNC and lipids are plotted separately against protein intake, they contribute similarly to the nonprotein energy curve. We therefore combined TNC and lipids into one axis (nonprotein energy), with available protein on the other axis. We refer to this 2-dimensional space as the nutritional space. For uniformity, we plotted protein in energy units (mega joule, MJ), although we could have also used mass units. We calculated the energetic value of each food, using the following conversion factors: 16.7 kJ/g TNC, 37.7 kJ/g lipid, and 16.7 kJ g available protein.

Data Analysis

We estimated nutrient intake from each feeding event by multiplying the ingestion time with the corresponding feeding rate and the nutrient content of the item (Felton *et al.* 2009b). We summed all daily events to obtain the daily nutrient intake. To compare differences in nutrient gain versus time spent feeding (nutrient intake efficiency) on ripe and unripe figs of *Ficus boliviana*, we divided the estimated total intake of nutrient x (g) from item i with the total time spent feeding (minutes) on item i.

We used linear regression to assess the relationship between feeding rates (population means of #items consumed/min) and wet weight of immature and ripe figs belonging to *Ficus boliviana* and *F. trigona*. We used 1-way ANOVA to test differences in nutrient intake efficiency between unripe and ripe figs of *Ficus boliviana*. We assessed whether the mean observed intake ratio was purely a product of the dominance of figs in their diet or whether the nutrient intake balance of individuals was the same regardless of the presence of figs. For this purpose, we used 1-way ANOVA to test whether mean intake ratio of days when figs were included in the diet ($n=25$) was different from the observed daily intake ratio of days when figs were not consumed at all ($n=13$).

We plotted daily cumulative intake (x = available protein; y = TNC + lipids) of individual spider monkeys and placed these intakes into 3 different categories based on the following visual characteristics: 1) straight intake trajectories toward the mean intake ratio (population mean of x/y); 2) zigzagging intake trajectories toward the mean intake ratio; and 3) straight intake trajectories toward a point representing a greater intake of nonprotein energy than average. We used 1-way ANOVA to assess the relationship between the type of intake strategy and habitat-wide food availability (scores originating from phenology surveys). We also used 1-way ANOVA to test the relationship between the type of intake strategy and diet composition (% ripe nonfig fruit and % figs). For the 2 latter statistical tests we included data from 38 full follow days where we had complete observational and nutritional data of everything the focal individuals consumed.

Results

Nutritional Composition of Food Items

Ripe fruit usually contained almost 50% more TNC and lipids than did immature fruit, which instead had lower DMD and contained more fiber and ash, but similar

concentrations of available protein (Fig. 1). Young leaves contained more available protein and had higher DMD than did mature leaves (Fig. 1). For figs, we refer to the emerging buds, immature figs, and medium-ripe figs collectively as unripe figs, because they had similar composition that was unlike that of ripe figs. Individuals consumed different combinations of wall/pulp of ripe figs depending on the species of *Ficus*. The nutritional composition of the most commonly eaten combinations of figs and other items is provided in Table I.

Feeding Rates

We recorded 775 different feeding rates (including several replicates per feeding event), thereby supplying information on the rate of ingestion of 76 different food items. We used this information in calculations of daily nutrient intake. Spider monkeys consumed small figs, i.e., less mature for interspecific comparisons, faster than they did larger figs (data for *Ficus boliviana* and *F. trigona*, $R^2=0.70$, $n=7$, $p=0.011$).

Daily Nutrient Intake and Major Sources of Nutrients

We recorded 904 different feeding events, amounting to 175 h of observation. Spider monkeys ate 0.4–2.4 kg (mean 1.0 kg ; SE 0.07 kg) of fresh food per day, which corresponded to an average of 262 g of DM (Table II). The daily intake of available protein remained steady across all 3 phenological seasons, whereas the intake of crude protein fluctuated by 75%.

On only 8 of the 51 full follow days did monkeys not eat fruits or leaves of *Ficus*, with 7 of these days occurring during the period of general fruit scarcity. Spider monkeys predominantly consumed food items from *Ficus boliviana* and *F. trigona*, but also ate figs from 4 less common *Ficus* sp. (Table I). *Ficus* trees represented 23% of all food trees, and FAs spent 50% of their feeding time eating various items from *Ficus* (Table II). This resulted in *Ficus* supplying the spider monkeys with the majority of their protein, lipids, fiber, and water (Table II). Other main sources of nutrients were *Pseudolmedia laevis* and *Myrciaria* sp. (locally called sahuinto; Table II).
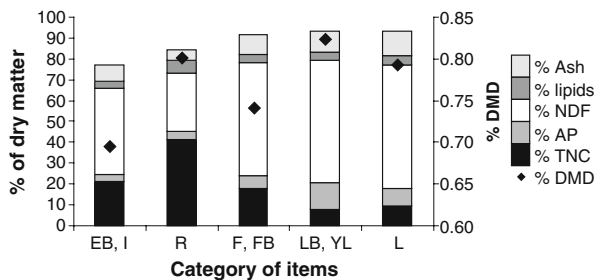
Fig. 1 Average nutritional composition of food categories eaten by *Ateles chamek* in La Chonta. EB = emerging buds; I = immature fruits; R = ripe fruits; F = flowers; FB = flower buds; LB = leaf buds; YL = young leaves; L = mature leaves; NDF = neutral detergent fiber; AP = available protein; TNC = total nonstructural carbohydrates. The secondary axis shows *in vitro* dry matter digestibility (%DMD), which is represented in the figure with black diamonds.

Table 1 Nutritional contents of food items consumed by *Ateles chamek* in La Chonta, in order of family

Species name	Family	Type	% BA	% Time	% H₂0	% Ash	% CP	% AP	% TNC	% Lipids	% NDF	% DMD	P: (TNC+L)	n
Spondias mombin	Anacardiaceae	R	1.5	1.69	83	5.2	3.3	1.3	57.2	2.5	9.9	80	0.03	2
Rollinia herzogii	Annonaceae	R	<0.01	a	61	6.9	7.2	3.6	24.7	2.3	55.2	46	0.17	1
Dendropanax arboreus	Araliaceae	R	1.4	2.69	58	1.2	5.4	3.0	10.6	21.8	53.5	28	0.07	1
Didymopanax morototoni	Araliaceae	R	0.1	0.13	65	2.5	6.2	6.8	19.4	33.2	14.5	50	0.10	2
Astrocarium murumuru	Arecaceae	R	0.7	0.64	68	4.4	3.0	2.4	58.1	3.4	20.9	72	0.05	3
Socratea exhorriza	Arecaceae	R	7.0	0.66	85	4.1	6.8	3.1	35.9	0.4	42.3	70	0.12	1
Syagrus sancona	Arecaceae	F	0.02	0.11	95	7.5	15.0	4.7	32.0	3.6	55.3	57	0.17	2
Marsdenia macrophylla	Asclepiadaceae	L	–	0.19	76	14.5	14.0	10.1	8.4	5.0	50.6	84	0.73	2
Melloa quadrivalvis	Bignoniaceae	L	–	0.08	64	8.0	19.2	14.3	3.3	2.5	67.8	42	2.25	1
M. quadrivalvis	Bignoniaceae	YL	–	0.93	79	7.1	28.0	25.8	8.0	3.0	38.7	76	2.47	3
Cordia alliodora	Boraginaceae	R	1.3	a	66	5.0	3.8	1.8	67.4	1.3	26.8	98	0.04	1
Jacaratia spinosa	Caricaceae	R	0.8	0.87	82	3.7	7.8	6.1	64.4	1.7	18.6	113	0.13	4
J. spinosa	Caricaceae	L	0.8	0.12	77	11.9	14.5	6.1	9.8	4.4	65.1	51	0.44	1
J. spinosa	Caricaceae	YL	0.8	a	83	8.8	18.2	6.5	7.4	4.2	59.1	57	0.56	1
J. spinosa	Caricaceae	FLB	0.8	0.43	85	10.8	19.1	9.7	7.6	4.5	55.8	70	0.77	1
Cecropia concolor	Cecropiaceae	R	0.03	a	62	12.6	11.0	6.4	17.3	7.0	59.2	70	0.27	3
Hura crepitans	Euphorbiaceae	I	8.6	a	–	7.8	11.9	6.6	19.8	1.7	28.8	78	0.40	1
Sapium glandulosum	Euphorbiaceae	R	0.8	0.73	18	2.0	8.7	12.1	19.7	34.4	0.0	54	0.18	1
Machaerium oblongifolium	Fabaceae	YL	–	1.29	79	5.8	19.1	13.5	7.2	5.4	74.9	71	0.99	4
Inga edulis	Leguminosae	R	0.4	1.17	73	1.8	4.2	3.8	72.3	0.8	13.0	114	0.07	3
I. edulis	Leguminosae	MR	0.4	a	–	3.7	9.7	6.2	35.9	1.9	52.1	83	0.22	4
Ceiba pentandra	Malvaceae	YL	0.2	0.26	74	11.8	23.8	15.4	6.7	5.6	67.5	66	1.14	1
Batocarpus amazonicus	Moraceae	R	0.2	a	70	4.8	4.6	4.0	65.6	2.9	12.9	98	0.08	1

Table I (continued)

Species name	Family	Type	% BA	% Time	% H$_2$O	% Ash	% CP	% AP	% TNC	% Lipids	% NDF	% DMD	P: (TNC+L)	n
B. amazonicus	Moraceae	LB/YL	0.2	2.64	77	8.9	16.5	5.6	10.4	3.8	63.3	57	0.42	2
Brosimum guadichaudii	Moraceae	R	0.2	a	71	4.4	7.0	4.7	56.3	1.6	25.6	104	0.11	4
B. guadichaudii	Moraceae	L	0.2	0.05	73	8.5	12.4	4.8	11.2	3.6	56.6	45	0.35	2
Ficus boliviana	Moraceae	I (1)	6.9	9.02	70	10.8	6.5	4.3	9.9	3.3	50.5	53	0.35	2
F. boliviana	Moraceae	R (0.3)	6.9	7.51	55	7.9	8.1	2.2	24.0	2.7	41.6	54	0.11	5
F. boliviana	Moraceae	L	6.9	0.01	72	14.4	9.7	2.6	20.1	7.1	51.4	39	0.10	1
F. boliviana	Moraceae	LB	6.9	5.26	67	11.1	15.6	9.2	7.2	3.6	52.1	65	0.85	3
F. boliviana	Moraceae	YL	6.9	0.13	62	11.0	16.2	8.0	6.4	3.3	55.0	63	0.81	2
F. boliviana	Moraceae	EB	6.9	4.09	76	11.2	16.2	5.3	4.8	3.0	b	69	0.66	3
Ficus pertusa	Moraceae	R (1)	0.8	0.15	75	8.5	5.8	2.4	38.8	1.9	b	66	0.08	2
Ficus eximia	Moraceae	R (1)	<0.01	0.23	71	10.4	1.3	2.6	53.1	2.6	b	69	0.06	1
Ficus sp.	Moraceae	R 1	0.01	a	86	10.2	2.8	8.1	5.4	3.0	b	74	0.95	1
Ficus trigona	Moraceae	R (0)	7.0	18.54	82	6.5	4.1	0.9	24.8	2.2	b	54	0.04	9
F. trigona	Moraceae	I (1)	7.0	1.00	82	9.8	5.5	1.8	11.5	3.4	b	41	0.13	8
Pseudolmedia laevis	Moraceae	R	9.8	2.77	77	3.5	5.2	2.6	69.0	0.9	17.4	102	0.05	2
P. laevis	Moraceae	MR	9.8	1.30	78	4.6	7.1	3.0	48.4	1.9	34.7	103	0.08	1
P. laevis	Moraceae	FLB	9.8	5.18	65	10.6	10.0	3.6	14.7	3.2	51.8	53	0.23	3
P. laevis	Moraceae	I	9.8	1.08	86	7.0	10.4	3.5	12.1	3.2	47.2	73	0.26	4
P. laevis	Moraceae	IB	9.8	0.09	67	7.0	11.0	2.4	10.0	4.3	67.3	56	0.18	1
Virola sebifera	Myristicaceae	R	0.01	0.59	34	0.0	2.7	3.0	40.6	22.1	8.8	56	0.05	1
Myrciaria sp.	Myrtaceae	R	0.7	9.95	70	4.0	3.1	1.0	35.4	0.6	30.6	66	0.04	3
Myrciaria sp.	Myrtaceae	MR	0.7	0.72	70	4.5	4.2	1.1	41.0	0.4	25.3	65	0.04	1
Quiina florida	Quinaceae	R	0.01	0.05	60	2.1	2.9	1.0	49.1	2.0	38.8	97	0.03	1

Species	Family	Type	%BA	%time										n
Paullinia elegans	Sapindaceae	R	–	0.64	46	1.5	2.2	1.4	32.0	1.4	13.7	92	0.06	5
Pouteria nemorosa	Sapotaceae	I	2.6	0.66	90	4.1	2.6	2.0	63.0	3.7	5.8	113	0.04	1
P. nemorosa	Sapotaceae	R/MR	2.6	2.41	94	8.7	3.2	1.8	39.2	4.4	9.9	100	0.05	7
Guazuma ulmifolia	Sterculiaceae	R	0.6	3.44	35	2.7	4.4	1.7	25.8	1.1	57.7	50	0.09	2
Heliocarpus americanus	Tiliaceae	L	0.2	2.01	73	11.3	16.2	7.1	10.3	4.9	65.5	51	0.48	6
H. americanus	Tiliaceae	YL	0.2	0.06	76	11.7	19.0	9.5	8.7	5.0	70.1	53	0.68	1
Ampelocera ruizii	Ulmaceae	YL	6.9	0.22	77	10.9	23.4	22.3	6.3	3.1	48.9	89	2.38	5
Celtis iguanea	Ulmaceae	R	–	1.69	48	5.8	7.8	7.1	71.2	0.0	2.6	96	0.14	2
Urera baccifera	Urticaceae	L	2.0	0.13	69	15.2	17.0	10.4	5.1	3.0	59.3	63	1.25	1
Vitaceae sp. 1	Vitaceae	AR	–	0.01	86	11.3	10.3	7.5	7.7	5.9	56.4	80	0.50	1
Caterpillar[c]		A		[a]	86	12.9	30.5	27.8	1.8	3.5	60.2	94	4.09	1
Unid epiphyte		S		[a]	93	13.3	3.5	3.2	27.5	2.1	34.2	100	0.14	1
Minimum				0.01	18	0.0	1.3	0.9	1.8	0.0	0.0	28.4	0.03	
Average				3.15	71	7.6	10.2	6.2	26.9	4.7	41.1	71.3	0.47	
Maximum				9.75	95	15.2	30.5	27.8	72.3	34.4	74.9	114	4.09	

We did not include seeds in fruit in the nutritional analysis.

Column headings: Type: EB = whole emerging fruit bud; I = whole immature fruit; MR = pulp of medium ripe fruit; R = pulp of ripe fruit (and aril if present); F = whole flower; FLB = whole flower bud; LB = whole leaf bud; YL = whole young leaf; L = mature leaf exl petiole; AR = aerial root; A = animal matter; S = stalk; % BA = species specific percentage of estimated total basal area (m²/ha) of trees DBH >10 cm (Felton et al. 2008). For members of Arecaceae, % of total density (trees/ha) is presented. (-) = no basal area or density information available for lianas; % time = percentage of the total feeding time recorded for focal animals during full-day follows (51 d); %H_2O = proportion of fresh weight composed of water; CP = crude protein (tot N ×f 6.25); AP = available protein estimated from *in vitro* assay (available N×6.25); TNC = total nonstructural carbohydrates (water-soluble carbohydrates + starch); NDF = neutral detergent fiber; P:(TNC+L) = ratio between protein and nonprotein energy (TNC+Lipids); % DMD = measure of dry matter digestibility (see Methods); %DMD = 100 indicates 100% digestibility of total dry matter; n = number of individual plants sourced for samples. In many cases several samples were taken from the same plant individual at different occasions.

[a] Feeding time not quantified but observed during partial-follow days.

[b] NDF values of fig pulp may have been overestimated by the NIRS and are therefore not displayed.

[c] Nutritional values of caterpillars should be interpreted with caution. Because this was the only sample consisting of animal material NIRS may not have been able to accurately predict levels of chemical attributes.

Table II Relative contributions of ingested nutrients from the 10 plant species most commonly consumed and daily intakes of different nutrients

Species	Item	% DM	% Water	% Ash	% AP	% TNC	% Lipids	% NDF	% Time
Top 10 species (of 47), representing 84% of all consumed dry weight.									
Ficus boliviana	EB, I,MR, R, LB, YL, L	22.8	15.6	34.2	23.2	10.1	25.6	31.6	28.0
Myrciaria sp.	MR, R	18.5	15.4	12.6	5.9	19.5	4.2	15.5	10.7
Pseudolmedia laevis	EB, I, MR, R, FB, YL	16.4	19.1	11.6	14.4	27.9	8.4	11.3	10.4
Ficus trigona	EB, I, MR, R, LB, YL	7.2	17.0	8.4	4.0	4.4	7.0	7.9	22.1
Spondias mombin	R	5.1	5.3	4.4	2.2	8.4	4.9	1.4	1.7
Guazuma ulmifolia	R	4.6	1.4	2.1	2.5	3.4	2.0	7.4	3.4
Jacaratia spinosa	R, F, L	4.1	5.3	3.4	8.6	6.4	3.5	3.0	1.4
Pouteria nemorosa	I,MR, R	3.6	6.1	2.8	2.2	6.2	5.2	0.6	3.1
Heliocarpus americanus	LB, YL, L	3.4	2.3	6.3	7.7	1.0	6.2	6.2	2.1
Batocarpus amazonicus	LB, YL	2.0	1.7	3.0	3.6	0.6	2.9	3.6	2.7
Ficus sp.	All items	31.3	33.2	43.6	27.7	15.4	33.3	40.2	50.8
		DM	Water	Ash	AP (CP)[a]	TNC	Lipids	NDF	
Mean daily intake		262 g	1487 g	15.7 g	11.5 g (17.2 g)	88.4 g	6.6 g	94.5 g	
SE of mean		15	103	0.9	0.8 (0.7)	10	0.5	6	
% of daily mean dwt intake				6.0%	4.4% (6.6%)	34%	2.5%	36%	

Data include 51 full-day follows over the entire study with plant species sorted by the relative amount of dry matter ingested.

[a] Crude protein (CP = total N×6.25) intake presented for comparison.

EB = emerging fruit bud; I = immature fruit; MR = medium ripe fruit; R = ripe fruit; F = flower; FB = flower bud; LB = leaf bud; YL = young leaf; L = mature leaf; DM = dry matter; water = proportion of fresh weight; AP = available protein estimated from *in vitro* assay (available N×6.25); TNC = total nonstructural carbohydrates (water-soluble carbohydrates + starch); NDF = neutral detergent fiber; % time: percentage of total feeding time.

Seasonal Differences in Sources of Nutrients

The relative contributions of different food categories to spider monkeys' nutrient intake varied among the 3 phenological seasons (Fig. 2), although ripe fruit was prominent in all seasons. During the period of relative ripe fruit scarcity (dry season), monkeys relied more on immature fruit and mature leaves than during the previous peak fruiting season (Fig. 2b vs. 2a). At the beginning of the next peak fruiting season (early wet season), individuals changed from eating mature leaves to young leaves, but immature fruit (of which unripe figs constituted 84% of feeding time) still provided >20% of all nutrients except TNC (Fig. 2c). The effects of these dietary differences are reflected in the average nutritional state of individuals during the study (Fig. 2d). While protein intake remained stable across seasons, the abundance of TNC- and lipid-rich fruit in the habitat during the late peak fruiting season resulted in monkeys ingesting an average of 52% more nonprotein energy than they did in the period of fruit scarcity (the latter being their fall-back diet; Fig. 2d). Some individuals consumed almost 6 times more energy per day during the peak fruiting season versus the fruit-scarce period.

Fig Nutrition and Macronutritional Balance of Food Items

Figs were major sources of nutrients for FAs during 6 of the 8 sample months (Table III). Nutrient concentrations of figs varied greatly between species and stages of maturity (Table I). Compared with other fruit, figs contained low to medium concentrations of lipids, available protein, and TNC (Table I). However, ripe figs of *Ficus boliviana*, 1 of the 2 most eaten fig species, have a macronutrient balance that resembles the intake trajectories of the spider monkeys (Fig. 3). In contrast, most other ripe fruits had higher TNC or lipid content than these ripe figs (Fig. 3). The mean observed ratio of protein energy to nonprotein energy intake of days when figs were consumed did not differ significantly from the ratio on those days when monkeys did not eat figs ($F=3.62$, df=36, $p=0.07$). This supports the conclusion that the ripe figs of *Ficus boliviana*, 2 other types of figs, and 3 kinds of nonfig fruits are nutritionally balanced for the spider monkeys (shaded section in Fig. 3).

Most (88%) of the unripe figs consumed came from *Ficus boliviana*. These unripe figs had high ratios of protein energy to nonprotein energy (Fig. 3), and had more available protein, lipid, and ash than did the ripe figs of the species (Table I). Although the ripe figs of *Ficus boliviana* contained higher concentrations of crude protein than did the immature figs, the reverse was true for available protein (Table I). Also, spider monkeys ingested both available protein (ANOVA, $F=19.21$, df=32, $p<0.001$) and lipids ($F=4.61$, df=32, $p=0.039$) more efficiently (g nutrient ingested/minute feeding) when eating immature figs versus ripe figs of *Ficus boliviana,* whereas there is no difference in the intake efficiency of TNC ($F=2.74$, df=26, $p=0.11$). Spider monkeys always ate unripe figs in combination with other food types (mean 5.8 other food types ± 0.7 SE, range 1–10). Usually (79% of days), the other food was predominantly ripe fruit, rich in TNC or lipids (mean 55% of DM; SE = 7% SE). In the remaining cases, individuals supplemented their unripe fig consumption with nutritionally balanced foods, such as ripe figs or palm fruit.

Fig. 2 Contributions of different food categories to total nutrient intakes by spider monkeys during 3 phenological periods **(a–c)**, and the associated mean macronutrient intake balance **(d)**. **(a)** Late wet season ($n=5$ focal days). **(b)** Early–mid dry season ($n=19$). **(c)** Late dry–early wet season ($n=26$). For explanations of abbreviations of food categories see Fig. 1 (O = other). **(d)** Mean seasonal intake ratios of available protein versus nonprotein energy that result from changing dietary composition in seasons **a–c**. Vertical bars indicate 95% confidence limits. The unit mega joule (MJ) is used for both axes for the sake of uniformity.
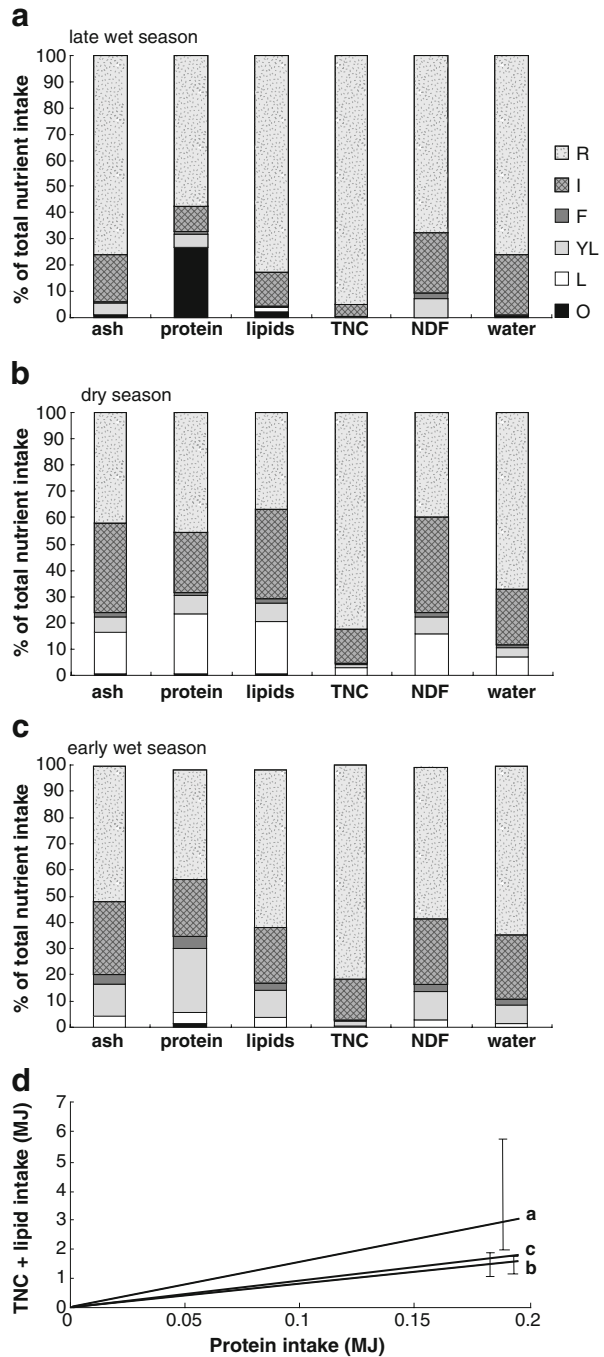
Table III Proportion of seasonal intake of nutrients contributed by the top 10 food species in the diet of *Ateles chamek* during three distinct phenological periods, sorted by percentage of total dry matter ingested

Species	Items	% DM	% Water	% Ash	% CP	% AP	% TNC	% Lipids	% NDF
Late peak season diet: Late wet season (5 FAD; 24/2–6/4; 99% DM intake; 3 spp. excluded)									
Spondias mombin	R	45.8	36.8	44.1	55.2	29.6	47.5	38.3	36.6
Pouteria nemorosa	R (MR+R)	35.0	46.0	31.0	34.6	32.7	37.5	44.0	18.2
Ficus boliviana	I,R	5.5	3.3	10.4	15.8	10.4	1.2	5.8	21.7
Jacaratia spinosa	R	5.2	5.3	3.6	15.0	15.2	6.1	3.0	7.8
Hirtella triandria	R	3.7	3.0	3.6	4.5	2.4	3.9	3.1	3.0
Inga edulis	R	2.2	4.2	0.7	3.3	3.9	2.8	0.6	2.3
Urera baccifera	L	1.5	0.7	4.3	9.6	7.6	0.1	1.5	7.3
Syagrus sancona	F	0.5	0.4	0.7	2.7	1.1	0.3	0.6	2.1
Arboreal termite mound[a]	O	0.4	0.0	1.3	–	37.7[a]	–	2.4	–
Celtis iguanea	R	0.2	0.1	0.2	0.6	0.7	0.3	0.0	0.0
Estimated mean daily intake		273 g	1971 g	15 g	15.6 g	11.5 g	151 g	8.3 g	34
Interday variation (SE)		53.3	343.5	3.4	3.6	4.5	27.8	1.6	10.0
Diet composition (% of tot dwt)				5.5	5.7	4.2	55	3.0	12
Fall-back diet: Early–mid dry season (19 FAD; 10/4–28/6; 97% DM intake; 12 spp. excluded)									
Myrciaria sp.	R,I	30.5	27.2	19.2	20.4	13.5	36.2	7.2	23.9
Ficus boliviana	I,IB,R,YL	25.5	18.6	35.1	39.3	34.3	10.3	37.5	36.5
Heliocarpus americanus	YL,L	8.5	6.0	14.2	28.8	27.2	2.8	18.5	14.3
Jacaratia spinosa	L,R	8.1	11.1	4.7	13.5	21.9	16.6	6.6	4.1
Ficus trigona	R,I	7.7	19.3	8.2	7.9	5.2	5.7	8.2	7.3
Astrocarium murumuru	R	6.3	4.2	4.1	4.0	6.7	11.9	9.7	3.4
Celtis iguanea	R	4.8	4.7	4.1	7.8	15.3	11.2	0.0	0.3
Batocarpus amazonicus	LB+YL	3.2	2.8	4.2	11.0	7.8	1.1	5.4	5.2
Pseudolmedia laevis	FB	1.1	0.9	1.8	2.4	1.8	0.5	1.6	1.5
Spondias mombin	R	1.1	1.2	0.9	0.8	0.7	2.1	1.3	0.3
Estimated mean daily intake		248 g	1309 g	17 g	24.1 g	11.2 g	76 g	5.5 g	96 g

Table III (continued)

Species	Items	% DM	% Water	% Ash	% CP	% AP	% TNC	% Lipids	% NDF
Interday variation (SE)		21.0	145.4	1.6	2.4	1.4	12.7	0.7	8.9
Diet composition (% of tot dwt)				6.9	2.8	4.5	31	2.2	39
Early peak season diet: Late dry–Early wet season (26 FAD; 12/7–15/9; 94% DM intake; 24 spp. excluded)									
Pseudolmedia laevis	R, FB, MR, I, IB, YL	30.2	35.8	21.8	37.7	37.3	54.3	14.6	18.9
Ficus boliviana	LB, IB, R, MR, I	22.7	15.7	35.3	38.6	34.6	11.3	23.7	27.6
Myrciaria sp.	R	14.5	12.0	10.3	9.8	6.8	15.8	3.8	11.3
Guazuma ulmifolia	R	8.6	2.8	4.2	7.7	6.6	6.7	3.7	13.0
Ficus trigona	R, MR, LB, I, IB,YL	8.5	20.0	10.4	9.8	7.2	5.1	8.4	9.1
Dendropanax arboreus	R	3.2	2.7	0.7	3.5	4.3	1.0	25.8	4.5
Terminalia oblonga	YL, L	2.2	1.9	4.3	6.9	7.8	0.5	3.9	3.6
Batocarpus amazonicus	LB+YL	1.7	1.5	2.7	6.0	4.4	0.6	2.5	2.9
Jacaratia spinosa	F, L	1.3	1.6	2.6	5.2	5.7	0.3	2.3	2.0
Melloa quadrivalvis	YL	1.0	0.9	1.3	5.9	11.8	0.2	1.2	1.0
Estimated mean daily intake		272 g	1499 g	16 g	27 g	12 g	90 g	7.3 g	104
Interday variation (SE)		22.0	136.4	1.3	2.3	1.4	16.3	0.7	7.5
Diet composition (% of tot dwt)				5.9	9.9	4.5	33	3.2	38

Estimated mean daily intake of nutrients and nutritional composition (%) of diets for each period is also shown.

In parentheses after season description: FAD = number of full focal animal days included; range of dates of FAD; % of the total dry matter intake of the period represented by the listed items; number of food species recorded for the period that are not listed in this table. Column headings: Items = if multiple types of items are listed for one species, they are listed according to dominance in diet (abbreviations explained in Table 1); %water = proportion of fresh weight; CP = crude protein (tot N×6.25); AP = available protein estimated from in vitro assay (available N×6.25); TNC = total nonstructural carbohydrates (water-soluble carbohydrates + starch); NDF = neutral detergent fiber.

[a] Nutritional data from Dufour (1987). Protein concentration of mound likely overestimated as the original data were analyzed on termite bodies only, excluding mound material.
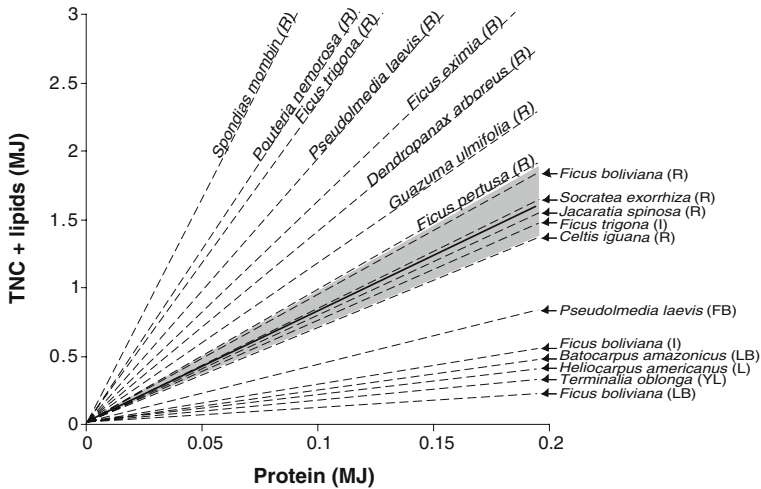
Fig. 3 Ratios of the available protein energy versus nonprotein energy of the 17 most commonly eaten foods (dashed lines), in relation to the mean observed intake ratio across all observation days (solid line, 95% confidence intervals depicted with a shaded area). Each food item is depicted by a dashed line that represents its macronutritional balance in nutritional space and shows the hypothetical intake trajectory of an individual that is restricted to this food item. We include 2 additional species of *Ficus* for comparison. R = ripe fruits; I = immature fruits; L = leaves; YL = young leaves; LB = leaf buds; FB = flower buds.

Daily Tracking Between Feeding Events

By assessing cumulative nutrient intake trajectories across consecutive feeding events, we found that individuals would attain an average balance between available protein and nonprotein energy (TNC+lipids) by maintaining: 1) a straight intake trajectory (13% of days) or 2) zigzagging trajectory (83% of days). The straight intake trajectory (1) was a result of individuals eating nutritionally balanced foods, whereas the zigzagging trajectory (2) was a result of alternating between foods with high or low protein:(TNC+lipid) ratios. Alternatively, they would ingest more nonprotein energy than average by 3) staying on a straight intake trajectory while eating foods extremely rich in TNC and lipids (4% of days). Individuals were more likely to concentrate on nutritionally balanced foods (option 1) when ripe figs were abundant and made up a large part of their diets (Table IV). In contrast, individuals were more likely to mix complementary foods on a daily basis (option 2) when both ripe figs and other ripe fruit were in moderate abundance. Finally, they were more likely to ingest extremely large amounts of nonprotein energy (option 3) when figs were scarce but other ripe fruits were abundant and therefore highly prominent in their diet (Table IV). We assume that spider monkeys consumed surplus energy when using option 3, i.e., more energy than needed to maintain body weight.

During the months when ripe nonfig fruit was abundant (late wet season, $n=3$ monthly phenological surveys; and early wet season, $n=2$), there was a negative hyperbolic relationship between the availability of ripe figs and the mean number of different nonfig fruit types consumed per day ($R^2=0.72$; Fig. 4). During these months, individuals could choose whether to eat a multitude of ripe fruit types, but they did so only when the availability of ripe figs was low (Fig. 4).

Table IV Ecological parameters that differed significantly among 3 different strategies which individuals used to reach their daily nutritional requirements

	A: Straight/ balanced	B: Zigzagging/ balanced	C: Straight/ surplus TNC+L	p-value[b]
Number of days[a]	4	32	2	
Dietary composition				
Mean % of diet consisting of nonfig fruits (±SE)	18 (±11)	45 (±5)	95 and 100	0.007
Mean % of diet consisting of figs (±SE)	80 (±13)	31 (±5)	0	0.005
Habitat-wide food availability				
Availability of ripe figs (score)	31	13	8	0.007
Availability of ripe nonfig fruits (score)	13	25	40	0.049

For a description of how feeding behavior and diet composition in general was influenced by phenological changes, see Felton *et al.* (2008).

A: Individuals followed a straight intake trajectory reaching a balanced end- point in nutritional space (see text for definition) by eating nutritionally balanced foods. B: Individuals reached a balanced end-point in nutritional space by alternating between complementary foods. C: Individuals followed a straight intake trajectory but reached their daily end-point by ingesting a surplus of nonprotein energy (TNC+L).

[a] The analysis uses 38 of the 51 full-day follows, i.e., those with detailed data from every feeding event.

[b] Results from 1-way ANOVA.

Discussion

Spider monkeys ate food items of widely varying macronutrient composition. Despite this variation, individuals often managed to ingest a similar daily balance of available protein and non-nitrogenous energy sources. We consider this mean ratio to be their preferred region in nutritional space, as it appears to be defended by individuals in the face of large variation in diet composition (Simpson and Raubenheimer 1993, 1995). They reached this point in nutritional space either by consuming a small number of nutritionally balanced foods over the course of a day (here: foods that have a ratio of available protein:(TNC+lipids) similar to their
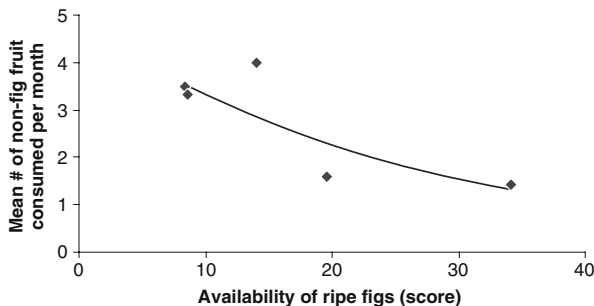
Fig. 4 The hyperbolic relationship between habitat-wide availability of ripe figs and the mean number of nonfig fruit types consumed. We measured availability of fruit in monthly phenological surveys.

observed mean intake), or by alternating between nutritionally complementary foods that contained either high or low ratios. We discuss each of these alternatives in turn.

Consuming nutritionally balanced foods represents the most direct route to a preferred region of nutritional space. Three types of figs were nutritionally balanced, as were food items from 3 other plant species: ripe fruit of the tree *Jacaratia spinosa*, the liana *Celtis iguanea*, and the palm *Socratea exorrhiza* (Fig. 3). Of these plant species, figs played a disproportionately large role in the spider monkey's diet. Spider monkeys spent 45% of their feeding time eating figs that provided them with approximately a third of their total intake of lipids and available protein. Individuals were more likely to follow a straight intake trajectory toward a balanced macronutritional end-point when ripe figs were highly abundant and comprised a large proportion of their diet.

We suggest that there are several reasons why figs played a pivotal role in the diet of these spider monkeys. First, *Ficus boliviana* and *F. trigona* were relatively common in their territory and produced large fruit crops for 8–9 mo of the year (Felton *et al.* 2008). Second, our findings suggest that these figs are balanced nutritionally in relation to the spider monkeys' nutritional target. As such, the nutrient balance of figs may be more indicative of their value than the concentrations of individual macronutrients *per se*, which are generally moderate to low (this study; Conklin and Wrangham 1994; Herbst 1986; Jordano 1983). Our conclusion that figs are nutritionally balanced is not a byproduct of their dominating the diet because the mean observed ratio of protein to nonprotein energy intake across days when figs were consumed did not differ significantly from the ratio on days when monkeys did not eat figs at all. Third, figs contained high concentrations of inorganic material, presumably minerals (ash), and contributed 44% of the monkeys' total intake of inorganic material. Figs are extremely rich sources of available calcium (Duhan *et al.* 1992; O'Brien *et al.* 1998; Ruby *et al.* 2000; Silver *et al.* 2000; Wendeln *et al.* 2000), which is critical for maintenance and reproduction (Robbins 1993). We suggest that all of these factors contributed to figs being the staple food of spider monkeys in La Chonta.

Interestingly, the spider monkeys included a large number of other ripe fruit types in their diet only when ripe figs were scarce, despite the opportunity to do otherwise (Fig. 4). There is a common perception that tropical frugivores regard figs as critical fall-back foods, rather than as preferred foods when other options are available (Milton *et al.* 1982; Shanahan *et al.* 2001). Our results are not congruent with this opinion and indicate that these spider monkeys eat a diverse array of different fruit to endure periods of fig scarcity (Kinnaird and O'Brien 2005). We tentatively suggest that the unusually large size of this spider monkey community —55 individuals, mean for communities of *Ateles* is 31 (Campbell 2008)— is partly attributable to the preponderance of this nutritionally balanced and mineral-rich staple food. This conclusion is relevant to the conservation of spider monkeys in Bolivia because *Ficus boliviana* is commercially harvested for timber in this country.

If nutritionally balanced foods were not sufficiently available for spider monkeys to meet their daily requirements, individuals could reach their preferred region in nutritional space by eating nutritionally imbalanced but complementary foods (Milton 1982). Although this zigzagging feeding strategy was by far the most commonly used (84% of cases), it may have associated costs. Repeated alternation

between foods involves lost feeding time, higher energetic costs of locomotion, and presumably increased risk of predation (Chambers *et al.* 1995; Dunbar 1988). Individuals were more likely to employ this zigzagging strategy when ripe figs and other ripe fruit were of low to moderate availability. For example, monkeys always used the zigzagging strategy during the early–mid dry season when ripe fruit was scarce. Leaves were frequently part of this fall-back diet and individuals would systematically alternate between leaves and the few ripe fruits available. Notably, the presence or absence of leaves and flowers in the diet did not influence the daily protein intake of these monkeys. Researchers often assume that frugivorous primates must eat some leaves to obtain sufficient protein (Chapman and Russo 2007; Lambert 2007; Milton 1981, 1993; Oates 1987; Oftedal 1991; Strier 2007; *cf.* Milton 1999). Our results show that this is not the case for spider monkeys at least on a daily basis, because they consistently reached the protein intake target even when eating only ripe fruit.

During the late wet season when ripe fruits were highly abundant, individuals consumed large amounts of fruit rich in TNC or lipids (energy-dense fruit, e.g., *Spondias mombin* and *Pouteria nemorosa*), resulting in a dramatically higher total energy intake than average (Fig. 2d). We hypothesize that the spider monkeys took advantage of these peak season foods by ingesting surplus energy and storing it as fat in preparation for the impending period of food scarcity when total energy intake halved. This and other ateline species (*Ateles paniscus*: Milton 1998; *Lagothrix lagotricha cana*: Peres 1994; *Ateles chamek*: Wallace 2005) accumulate fat during periods of peak fruit abundance, which is a logical strategy for animals experiencing fluctuating food supply. Seasonal accumulation of fat reserves may be crucial for survival and reproduction in spider monkeys, and we therefore suggest that energy-dense peak-season foods be given appropriate attention in conservation planning (see also Stevenson 2005).

Researchers can use the framework of protein-dominated nutrient balancing to unravel spider monkey food choices that are difficult to explain using traditional schools of thought in nutritional ecology. For example, in contrast to other spider monkey communities studied, the spider monkeys at La Chonta spent much time consuming unripe figs (18% of feeding time, primarily from *Ficus boliviana*) both during periods of abundance and scarcity of ripe figs and other fruit (Felton *et al.* 2008). When ripe figs and other fruits were scarce, the consumption of unripe figs was likely a matter of availability (Norconk *et al.* 1998; Schaefer and Schaefer 2006). Unripe figs were always available in the home range, making them a more reliable food source than ripe figs. The more intriguing issue is why spider monkeys ate unripe figs when ripe figs and other fruits were available.

Ripe-fruit specialists often avoid unripe fruits because they are usually less palatable than ripe fruits (Venu *et al.* 2005), contain less gross energy (Schaefer *et al.* 2003), and often contain toxins or antifeedants (Cipollini and Levey 1997a, b). Some of this may be true for the unripe figs in this study but, importantly, the unripe figs of *Ficus boliviana* provided spider monkeys with more lipids and available protein per minute feeding than did their ripe counterparts. This greater efficiency was partly due to the high concentrations of lipids and available protein, the latter likely enhanced by the inclusion of protein-rich wasp bodies (Herbst 1986). Another reason for the high intake efficiency was the speed at which monkeys could consume

the small unripe figs in their entirety. When eating ripe figs monkeys usually separated the juicy pulp from the husk in a relatively time-consuming manner. Further, our data show that the consumption of unripe figs always occurred in combination with other food types, and usually the alternative foods contained relatively high concentrations of nonprotein energy. Unripe figs thus constituted an easily harvestable, nutritionally rewarding, and continuously available complementary food.

We emphasize that unripe figs contained less crude protein than their ripe counterparts, whereas the reverse was true for available protein. Further, daily intake of crude protein by spider monkeys fluctuated by 75% across all 3 seasons, whereas available protein intake remained steady. Both of these examples provide ample evidence of the importance of estimating nitrogen availability to understand accurately food choice and underlying nutritional goals (Felton *et al.* 2009a).

Conclusions

We highlight 4 important findings from this study: 1) To reach their daily protein target spider monkeys followed 1 of 3 nutrient intake trajectories, the choice of which was influenced by seasonal variation in fruit availability. 2) In contrast to prevailing theory, spider monkeys did not need to supplement their frugivorous diet with leaves to reach their daily protein target. 3) Our data provided an exception to the general rule that figs are a less-preferred food that assists animals in overcoming lean periods. In our study, spider monkeys consumed a diverse array of different fruits to endure periods of fig scarcity. 4) During all seasons, unripe figs were a substantial component of the spider monkeys' diet. We suggest the reason is that unripe figs constituted a nutritionally rewarding food resource, especially in terms of protein and lipids, that was efficiently harvestable and available throughout the entire year.

References

Altmann, S. A. (1998). *Foraging for survival*. Chicago: University of Chicago Press.
ANON. (1995). *Standard practices for infrared multivariate quantitative analysis (designation E1655–00)*. West Conshohocken, PA.: American Society for Testing and Materials.

Beehner, J. C., Onderdonk, D. A., Alberts, S. C., & Altmann, J. (2006). The ecology of conception and pregnancy failure in wild baboons. *Behavioral Ecology, 17*(5), 741–750.

Campbell, C. J. (2008). *Spider monkeys: Behavior, ecology and evolution of the genus Ateles*. Cambridge, UK: Cambridge University Press.

Castellanos, H. G. (1995). *Feeding behaviour of* Ateles belzebuth *E. Geoffroy 1806 (Cebidae: Atelinae) in Tawadu Forest Southern Venezuela.* Ph.D dissertation, The University of Exeter, UK.

Chambers, P. G., Simpson, S. J., & Raubenheimer, D. (1995). Behavioural mechanisms of nutrient balancing in *Locusta migratoria* nymphs. *Animal Behaviour, 50*, 1513–1523.

Chapman, C. A., & Russo, S. E. (2007). Primate seed dispersal: Linking behavioral ecology with forest community structure. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder (Eds.), *Primates in perspective* (pp. 510–524). Oxford: Oxford University Press.

Cipollini, M. L., & Levey, D. J. (1997a). Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. *American Naturalist, 150*(3), 346–372.

Cipollini, M. L., & Levey, D. J. (1997b). Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. *Ecology, 78*(3), 782–798.

Conklin, N. L., & Wrangham, R. W. (1994). The value of figs to a hind-gut fermenting frugivore—a nutritional analysis. *Biochemical Systematics and Ecology, 22*(2), 137–151.

De Gabriel, J. L., Wallis, I. R., Moore, B. D., & Foley, W. J. (2008). A simple, integrative assay to quantify nutritional quality for browsing herbivores. *Oecologia, 156*(1), 107–116.

Dearing, M. D., Foley, W. J., & McLean, S. (2005). The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annual Review of Ecology Evolution and Systematics, 36*, 169–189.

Dew, J. L. (2005). Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*. *International Journal of Primatology, 26*(5), 1107–1135.

Di Fiore, A., & Rodman, P. S. (2001). Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a neotropical terra firma forest. *International Journal of Primatology, 22*(3), 449–480.

Di Fiore, A., Link, A., & Dew, J. L. (2008). Diets of wild spider monkeys. In C. J. Campbell (Ed.), *Spider monkeys: Behavior, ecology and evolution of the genus Ateles* (pp. 81–137). Cambridge, UK: Cambridge University Press.

Dufour, D. L. (1987). Insects as food—a case study from the Northwest Amazon. *American Anthropologist, 89*(2), 383–397.

Duhan, A., Chauhan, B. M., & Punia, D. (1992). Nutritional value of some nonconventional plant foods of India. *Plant Foods for Human Nutrition, 42*(3), 193–200.

Dunbar, R. I. M. (1988). *Primate social systems*. London and Sydney: Croom Helm Ltd.

Felton, A. M., Felton, A., Wood, J. T., & Lindenmayer, D. B. (2008). Diet and feeding ecology of the Peruvian spider monkey (*Ateles chamek*) in a Bolivian semi-humid forest: the importance of *Ficus* as a staple food resource. *International Journal of Primatology, 29*, 379–403.

Felton, A. M., Felton, A., Lindenmayer, D. B., & Foley, W. J. (2009). Nutritional goals of wild primates. *Functional Ecology, 23*(1), 70–78.

Felton, A. M., Felton, A., Raubenheimer, D., Simpson, S. J., Foley, W. J., Wood, J. T., et al. (2009). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology,*. doi:10.1093/beheco/arp021.

Foley, W. J., McIlwee, A., Lawler, I., Aragones, L., Woolnough, A. P., & Berding, N. (1998). Ecological applications of near infrared reflectance spectroscopy a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. *Oecologia, 116*(3), 293–305.

Freeland, W. J., & Janzen, D. H. (1974). Strategies in herbivory by mammals - role of plant secondary compounds. *American Naturalist, 108*(961), 269–289.

Herbst, L. H. (1986). The role of nitrogen from fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. *Biotropica, 18*(1), 39–44.

Jordano, P. (1983). Fig-seed predation and dispersal by birds. *Biotropica, 15*(1), 38–41.

Kinnaird, M. F., & O'Brien, T. G. (2005). Fast foods of the forest: The influence of figs on primates and hornbills across Wallace's line. In J. L. Dew & J. P. Bouble (Eds.), *Tropical fruits and frugivores: The search for strong predictors* (pp. 155–184).

Kinzey, W. G. (1997). Ateles. In W. G. Kinzey (Ed.), *New World primates: Ecology, evolution, and behavior* (pp. 192–199). New York: Aldine de Gruyter.

Lambert, J. E. (2007). Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder (Eds.), *Primates in perspective* (pp. 482–495). Oxford: Oxford University Press.

Mattson, W. J. (1980). Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics, 11*, 119–161.

Milton, K. (1981). Food choice and digestive strategies of two sympatric primate species. *American Naturalist, 117*(4), 496–505.

Milton, K. (1982). Dietary quality and demographic regulation in a howler monkey population. In E. G. Leigh, A. S. Rand & D. M. Windsor (Eds.), *The ecology of a tropical forest: Seasonal rhythms and long-term changes* (pp. 273–289). Washington, DC: Smithsonian Institution Press.

Milton, K. (1993). *Diet and primate evolution* (pp.86–93). Scientific American, Aug.

Milton, K. (1998). Physiological ecology of howlers (*Alouatta*): Energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology, 19*(3), 513–548.

Milton, K. (1999). A hypothesis to explain the role of meat-eating in human evolution. *Evolutionary Anthropology, 8*(1), 11–21.

Milton, K., & Dintzis, F. R. (1981). Nitrogen-to-protein conversion factors for tropical plant-samples. *Biotropica, 13*(3), 177–181.

Milton, K., Windsor, D. M., Morrison, D. W., & Estribi, M. A. (1982). Fruiting phenologies of two Neotropical *Ficus* species. *Ecology, 63*(3), 752–762.

Norconk, M. A., Grafton, B. W., & Conklin-Brittain, N. L. (1998). Seed dispersal by Neotropical seed predators. *American Journal of Primatology, 45*(1), 103–126.

Oates, J. F. (1987). Food distribution and foraging behavior. In B. B. Smuts, D. L. Cheyney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 197–209). Chicago: University of Chicago Press.

O'Brien, T. G., Kinnaird, M., & Dierenfeld, E. S. (1998). What's so special about figs? *Nature, 392*, 668.

Oftedal, O. T. (1991). The nutritional consequences of foraging in primates—the relationship of nutrient intakes to nutrient-requirements. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 334*(1270), 161–170.

Peres, C. A. (1994). Diet and feeding ecology of gray woolly monkeys (*Lagothrix lagotricha cana*) in Central Amazonia—comparisons with other atelines. *International Journal of Primatology, 15*(3), 333–372.

Raubenheimer, D., & Simpson, S. J. (1997). Integrative models of nutrient balancing: Application to insects and vertebrates. *Nutrition Research Reviews, 10*, 151–179.

Raubenheimer, D., & Simpson, S. J. (2004). Organismal stoichiometry: quantifying non-independence among food components. *Ecology, 85*(5), 1203–1216.

Raubenheimer, D., & Simpson, S. J. (2006). The challenge of supplementary feeding: can geometric analysis help save the kakapo? *Notornis, 53*, 100–111.

Robbins, C. T. (1993). *WIldlife feeding and nutrition* (2nd edition ed.): Academic Press.

Robbins, C. T., Fortin, J. K., Rode, K. D., Farley, S. D., Shipley, L. A., & Felicetti, L. A. (2007). Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos, 116*(10), 1675–1682.

Rosenberger, A. L., & Strier, K. B. (1989). Adaptive radiation of the ateline primates. *Journal of Human Evolution, 18*(7), 717–750.

Ruby, J., Nathan, P. T., Balasingh, J., & Kunz, T. H. (2000). Chemical composition of fruits and leaves eaten by short-nosed fruit bat, *Cynopterus sphinx. Journal of Chemical Ecology, 26*(12), 2825–2841.

Ruohonen, K., Simpson, S. J., & Raubenheimer, D. (2007). A new approach to diet optimisation: A re-analysis using European whitefish (*Coregonus lavaretus*). *Aquaculture, 267*(1–4), 147–156.

Schaefer, H. M., & Schaefer, V. (2006). The fruits of selectivity: How birds forage on *Goupia glabra* fruits of different ripeness. *Journal of Ornithology, 147*(4), 638–643.

Schaefer, H. M., Schmidt, V., & Winkler, H. (2003). Testing the defense trade-off hypothesis: How contents of nutrients and secondary compounds affect fruit removal. *Oikos, 102*(2), 318–328.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics, 2*, 369–404.

Shanahan, M., So, S., Compton, S. G., & Corlett, R. (2001). Fig-eating by vertebrate frugivores: A global review. *Biological Reviews, 76*(4), 529–572.

Silver, S. C., Ostro, L. E. T., Yeager, C. P., & Dierenfeld, E. S. (2000). Phytochemical and mineral components of foods consumed by black howler monkeys (*Alouatta pigra*) at two sites in Belize. *Zoo Biology, 19*(2), 95–109.

Simpson, S. J., & Raubenheimer, D. (1993). A multilevel analysis of feeding behavior - the geometry of nutritional decisions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 342*(1302), 381–402.

Simpson, S. J., & Raubenheimer, D. (1995). The geometric analysis of feeding and nutrition—a user's guide. *Journal of Insect Physiology, 41*(7), 545–553.

Simpson, S. J., & Raubenheimer, D. (2001). The geometric analysis of nutrient-allelochemical interactions: a case study using locusts. *Ecology, 82*(2), 422–439.

Simpson, S. J., & Raubenheimer, D. (2005). Obesity: the protein leverage hypothesis. *Obesity Reviews, 6* (2), 133–142.

Stevenson, P. (2005). Potential keystone plant species for the frugivore community at Tinigua Park, Colombia. In J. L. Dew & J. P. Bouble (Eds.), *Tropical fruits and frugivores: The Search for Strong Predictors* (pp. 37–57): Springer.

Strier, K. B. (1992). Atelinae adaptations—behavioral strategies and ecological constraints. *American Journal of Physical Anthropology, 88*(4), 515–524.

Strier, K. B. (2007). *Primate behavioral ecology* (3rd ed.). Columbus, OH: Allyn & Bacon.

Venu, D. K., Munjal, S. V., Waskar, D. P., Patil, S. R., & Kale, A. A. (2005). Biochemical changes during growth and development of fig (*Ficus carica* L.) fruits. *Journal of Food Science and Technology-Mysore, 42*(3), 279–282.

Wallace, R. B. (2005). Seasonal variations in diet and foraging behavior of *Ateles chamek* in a southern Amazonian tropical forest. *International Journal of Primatology, 26*(5), 1053–1075.

Wendeln, M. C., Runkle, J. R., & Kalko, E. K. V. (2000). Nutritional values of 14 fig species and bat feeding preferences in Panama. *Biotropica, 32*(3), 489–501.

White, T. C. R. (1993). *The inadequate environment: Nitrogen and the abundance of animals*. Berlin/Heidelberg/New York: Springer.