

## RESEARCH ARTICLE

Macronutrient Balancing Affects Patch Departure by Guerezas  
(*Colobus guereza*)CALEY A. JOHNSON<sup>1,2\*</sup>, DAVID RAUBENHEIMER<sup>3</sup>, COLIN A. CHAPMAN<sup>4,5</sup>, KAIA J. TOMBAK<sup>6</sup>, ANDREA J. REID<sup>7</sup>,  
AND JESSICA M. ROTHMAN<sup>1,2,8</sup><sup>1</sup>Department of Anthropology, The Graduate Center, City University of New York, New York City, New York<sup>2</sup>New York Consortium in Evolutionary Primatology (NYCEP), American Museum of Natural History, New York City, New York<sup>3</sup>Charles Perkins Centre, Faculty of Veterinary Science and School of Biological Sciences, The University of Sydney, Sydney, New South Wales, Australia<sup>4</sup>Department of Anthropology & McGill School of Environment, McGill University, Montreal, Quebec, Canada<sup>5</sup>Wildlife Conservation Society, Bronx, New York<sup>6</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey<sup>7</sup>Department of Biology, Carleton University, Ottawa, Ontario, Canada<sup>8</sup>Department of Anthropology, Hunter College of the City University of New York, New York City, New York

Foraging strategies are central in shaping social structure and grouping patterns in primates. We address *Colobus guereza* foraging strategies by investigating their patch departure decisions in relation to diet composition and nutrition. We examine whether guerezas are constrained in their intake of food in patches and thereby forage according to a fixed amount strategy that dictates patch departure. Additionally, we assess whether guereza employ a fixed time strategy or attempt to balance nutrients when foraging. We measured food patch occupancy time, intake rates, and analyzed foods for macronutrients, fiber, and condensed tannins. We determined that guerezas do not employ a fixed time foraging strategy; patch residence time varied widely between 1 and 290 min. They also did not depart patches or stop eating when they reached a specific intake of dry mass, macronutrients, or condensed tannins. However, guerezas maintained a macronutrient balance when feeding across patches, and the balance of protein to non-protein energy (fats and carbohydrates) in patches is the best indicator of time adult guerezas spent feeding in patches. Previous studies have shown that the protein-to-fiber ratio is important in predicting food selection for folivores and their biomass; however, we found that guerezas did not maximize protein and minimize fiber intake while foraging in patches, nor did they stay longer in patches with the highest ratio of protein to fiber concentrations. This study raises questions about the nutritional and social implications of patch depletion as a foraging strategy in folivorous monkeys where food limitation predicts competitive and social regimes. *Am. J. Primatol.* 9999:1-9, 2015.

© 2015 Wiley Periodicals, Inc.

**Key words:** guereza; nutrient balancing; patch departure; nutritional geometry

## INTRODUCTION

Theory about food patch use by animals in ecological literature can be divided into questions of how animals choose food patches and when animals should depart from a patch [Green, 1984; Owen-Smith et al., 2010; Plante et al., 2014; Searle et al., 2005; Stephens and Krebs, 1986]; the latter of which is examined in this paper. The simple idea that foragers should remain longer in patches with more food is the starting point for patch departure theory. The marginal value theorem (MVT) predicts that when food distribution is patchy in a habitat, a forager capable of patch depletion will feed in a patch until its quality drops to a level equal to the average

Contract grant sponsor: Hunter College of CUNY NSF BCS; contract grant number: 0922709; contract grant sponsor: Canada Research Chairs Program; contract grant sponsor: Natural Science and Engineering Research Council of Canada; contract grant sponsor: National Geographic Society; contract grant sponsor: National Science Foundation; contract grant number: CNH 1114977; contract grant sponsor: National Institutes of Health; contract grant number: TW009237; contract grant sponsor: UK Economic and Social Research Council

\*Correspondence to: Caley Johnson, Department of Anthropology, The Graduate Center, City University of New York, 365 5th Ave, New York, NY 10016. E-mail: caleyajohnson@gmail.com

Received 19 March 2015; revised 4 October 2015; revision accepted 10 October 2015

DOI: 10.1002/ajp.22495  
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

quality of all patches in the habitat [Charnov, 1976]. At this point, the optimal decision is to move on to feed from patches more favorable than the habitat as a whole, while minimizing travel and other costs. The assumptions of this model are that the animal has information on the value of the current foraging patch and the average value of alternative patches in the environment. Additions to patch use theory include attempts to quantify departure through consideration of factors such as currency, e.g., energy and protein [Altmann, 1998; Grether et al., 1992; Mattson, 1980; Plante et al., 2014; Sayers et al., 2010; Schoener, 1971], toxins and predators [Freeland & Janzen, 1974; Stein & Magnuson, 1976; Verdolin, 2006], digestive limitation [Illius et al., 2002; Jeschke et al., 2002; Verlinden & Wiley, 1989], and social influence [Kazahari & Agetsuma, 2008; Vogel, 2005].

Optimal foraging theory and patch use have been examined in several wild primates [Altmann, 1998; Grether et al., 1992; Kazahari & Agetsuma, 2008; Marshall et al., 2013; Plante et al., 2014; Sayers et al., 2010; Suarez, 2014; Vogel, 2005]. Possible evidence of energy as currency in patch use and selection has been observed in gibbons (*Hylobates lar*, *H. syndactylus*) and langurs (*Semnopithecus entellus*) [Grether et al., 1992; Sayers et al., 2010]. Presence of preferred food items (i.e., fruit vs. leaves) has been found to positively affect the time that black howler monkeys (*Alouatta pigra*) spend in patches [Plante et al., 2014]. Social factors, such as the number of co-feeders positively affect patch use in Japanese macaques (*Macaca fuscata*) [Kazahari & Agetsuma, 2008] and red colobus (*Procolobus rufo-mitratus*) [Snaith & Chapman 2005], whereas aggression and rank differences affect energy intake in patches by capuchin monkeys (*Cebus capucinus*) [Vogel, 2005]. Additionally, testing the MVT parameter of prescience of food resources, wild baboons (*Papio ursinus*) and spider monkeys (*Ateles* spp.) have been shown to utilize previous experiences to optimize patch departure and patch choice [Chapman, 1988; Marshall et al., 2013; Suarez, 2014].

Many studies of patch decisions in herbivores have been unsuccessful in quantifying patch departure using MVT, suggesting that alternative approaches should be explored [see Searle et al., 2005 for review]. MVT may be particularly limited in situations where an animal does not deplete a food patch as shown by a linear function in feeding gain during patch use [Searle et al., 2005]. For example, this may occur if an animal is physiologically constrained through a fixed gut capacity, or capacity to ingest nutrients or toxins [Chapman & Chapman, 2002; Hirakawa, 1997; Verlinden & Wiley, 1989]; if foraging is influenced by a time constraint [e.g., marine mammals; Rosen et al., 2007], or if individuals seek to gain a specific balance of nutrients in patches [Hengeveld et al., 2009; Simpson et al., 2004]. Folivorous mammals,

particularly foregut fermenters, such as guereza monkeys (*Colobus guereza*), may be especially susceptible to feeding constraints due to their slow gut passage and complex gut structure that may limit fibrous material from passing quickly through the gut [Chivers, 1994; Clauss et al., 2008; Kay & Davies, 1994; Stevens & Hume, 1995]. Thus, although colobines can probably gain more energy from fiber than hindgut fermenters [Edwards & Ullrey, 1999], their fecal particle size is small compared to other primates suggesting that colobines spend more time chewing their food, or possess digestive features that stop large pieces of fiber from passing through the gut [Matsuda et al., 2014]. By contrast, other herbivores like giant pandas (*Ailuropoda melanoleuca*) have a rapid transit rate and pass large particles using a different strategy that allows them to eat less digestible foods [Fritz et al., 2009].

A study by Tombak et al. [2012] suggested that guerezas do not deplete food patches. The authors observed the feeding behavior of adult guerezas in Kibale National Park, Uganda, quantifying feeding gain (measured as bites/minute) and effort (measured as distance moved) during food patch (tree) occupancy. If depletion is occurring, a negative relationship should exist between patch size or number of individuals feeding in a patch, and time individuals spend feeding. In their study, the time guerezas spent in a patch was not a function of patch size or number of individuals feeding. Additionally, guerezas showed a constant feeding gain in patches and a decrease in feeding effort as foraging persisted, suggesting satiation rather than patch depletion. Guerezas had a lower feeding rate when eating mature leaves, which may be more structural and most likely harder to digest than young leaves [Oates, 1994], possibly reflecting a physiological constraint in fiber digestion.

Guerezas in Kibale National Park, Uganda, are highly folivorous, with a diet consisting predominantly of young leaves [Harris & Chapman, 2007; Oates, 1977; Wasserman & Chapman, 2003]. There is some evidence that guerezas select foods that are high in protein and low in fiber, and that the protein to fiber content of mature leaves from the most abundant tree species in Kibale is correlated with guereza biomass [Chapman and Chapman, 2002; Chapman et al., 2004; Wasserman & Chapman, 2003]. Although guerezas have not shown evidence of patch depletion, they may still be food limited during periods of food scarcity and may experience physiological and behavioral effects of food paucity. During a period of severe food scarcity, Kibale guereza responded behaviorally by diversifying their diet and increasing their daily path length, the percentage of time spent feeding and the number of patches visited per day [Harris et al., 2010]. In the context of extreme food limitation it is not known whether guereza would deplete food patches [Tombak et al., 2012].

The objective of our study was to examine the patch departure rule employed by guerezas. If guereza patch departure is constrained by food intake, we expect monkeys to employ a “fixed-amount strategy,” whereby foragers will leave a patch when they reach a preset mass of food [Brown, 1989; Brown & Morgan, 1995]. Similar to this fixed amount strategy, guerezas may follow a fixed-energy gain, fixed protein, or fixed toxin strategy whereby they will stop feeding in a patch when a fixed mass of nutrients or toxins (e.g., tannins) is reached. Guerezas may be constrained by tannin intake as tannins reduce diet quality by binding and precipitating protein, reducing fiber digestion, and inhibiting growth of gut microbes [Foley & Moore, 2005; McSweeney et al., 2001]. Presence of tannins has been found to negatively affect food choice in Kibale guerezas [Oates et al., 1977].

Several recent studies have shown that wild animals balance multiple nutrients while foraging [Felton et al., 2009a; Johnson et al., 2013; Nie et al., 2014; Rothman et al., 2011; Rothman, 2015; Raubenheimer et al., 2015; Simpson & Raubenheimer, 2012]. Patch departure decisions may be dictated by maintaining a balanced intake of nutrients rather than obtaining, or avoiding any single nutrient or toxin [Hengeveld et al., 2009; Simpson et al., 2004]. If guerezas maintain a balance of nutrients when foraging, we expect individuals to consume a similar ratio of nutrients across patches. Additionally, we expect individuals to spend more time feeding in patches that have a better balance of nutrients, and would leave those patches that do not sooner.

In addition to testing whether guereza departure decisions are constrained by feeding thresholds or nutrient balancing, we also examined if they employ a “fixed time strategy.” A fixed time strategy may be employed if a forager is unable to assess patch resource density [Iwasa et al., 1981] or by animals that have temporal foraging constraints. Foragers may then leave patches after a constant period of time to minimize costs. Terrestrial foragers, such as some birds and rodents, have been found to employ a fixed time strategy where they lack sensory abilities to assess patch density, or where disparity in patch density is below a perceptible threshold [Kotler & Brown, 1999; Valone & Brown, 1989].

We examined whether guereza employ a fixed amount, fixed time or nutrient balancing departure strategy in their patch use through behavioral observations of individuals. By intensively studying food use and limitation in folivorous primates, we may reveal why differences in social grouping occur despite socioecological theory that predicts similar grouping patterns and social behavior based on a diet of leaves [Snaith and Chapman, 2007; Tombak et al., 2012; van Schaik, 1989; Wrangham, 1980]. Although MVT has improved our understanding of animal foraging, it has often failed to quantitatively predict

herbivore patch departure decisions, which has led to a call for alternative approaches [Searle et al., 2005]. Through consideration of digestive constraints and amounts-based nutritional data in a natural foraging environment, this study will consider strategies beyond MVT and may provide a more predictive framework for patch departure.

## METHODS

### Subjects and Focal Sampling

We performed this study in Kibale National Park, Uganda (0.13–0.41°N; 30.19–30.32°E), between October 2008 and May 2010, using focal sampling on adult guerezas in three groups—Basaija ( $n = 7$  individuals), Kasembo ( $n = 6$ ), and Zikuru ( $n = 11$ ). Guerezas are medium sized (males = 9.1 kg, females = 7.8 kg), arboreal, diurnal primates that are distributed across sub-Saharan Africa, and eat mainly leaves [Oates, 1994]. Focals were sequential and chosen opportunistically, beginning when an individual entered a tree (feeding patch) and ending when the individual departed the patch [Astrom et al., 1990]. During patch occupancy, we recorded tree species, total occupancy time, and the time individuals fed or performed non-feeding behaviors. We included a measure of time spent feeding in patches relative to other activities, as the total patch occupancy time may be influenced by behaviors besides feeding (e.g., grooming, resting). We recorded all food items consumed (e.g., young leaves, flowers) and estimated feeding rate (g/min) by counting the number plant parts eaten during patch occupancy.

### Food Collection and Nutritional Analyses

We collected food items from the same tree as the feeding event as soon as the focal ended and processed foods in the same way the guerezas processed them. Food items were weighed to estimate wet mass intake [Rothman et al., 2012]. We dried samples (<40°C out of sunlight) and milled samples in the field. Samples were then exported to the Nutritional Ecology Laboratory at Hunter College in New York, where we analyzed samples with near-infrared reflectance spectroscopy (NIRS) [Foley et al., 1998, Rothman et al., 2009a] and wet-chemistry for nutrient composition. We measured hemicellulose, cellulose, and lignin via neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) [Goering & Van Soest, 1970; Van Soest et al., 1991]. We measured crude and available protein through combustion (Dumas method) [AOAC, 1990] and subtraction of acid detergent insoluble nitrogen [Licitra et al., 1996; Rothman et al., 2008a, 2012]. We measured crude fat using ether extract, and ash through combustion

[Rothman et al., 2012]. Total non-structural carbohydrates (TNC) were measured by difference, subtracting the contributions of NDF, crude protein, fat, and ash from the total plant mass [Rothman et al., 2012]. We estimated metabolizable energy [Conklin-Brittain et al., 2006] taking into account fiber digestibility by using lignin as a fecal marker [Rothman et al., 2008b]. We also measured condensed tannins (CT) by estimating their quantity via sephadex separation [Rothman et al., 2009b].

## Data Analyses

### *Fixed-amount and fixed-time strategy*

To observe the departure strategies of guerezas we summed the total wet and dry mass of consumed food, and the total mass intake of macronutrients and condensed tannins. To determine if intake or time spent in patches was consistent, we calculated the coefficient of variation for intakes in each focal patch, patch occupancy time, and feeding time. The coefficient of variation (CV) is a measure of dispersion that is calculated as the standard deviation divided by the mean. We define a CV value close to or greater than one as reflecting a wide and non-constant range of values. If guerezas are employing a fixed-intake strategy, we expect to see a constant mass of nutrients or non-nutrients maintained across focals, reflected in a CV value close to zero across patches. Therefore, when guerezas reach this fixed amount, we expect them to stop feeding, or depart patches at possibly varying amounts of time. If guerezas are employing a fixed time strategy, we expect the CV value for feeding time in patches, or patch occupancy time, to be low showing guerezas consistently abandon patches after a set amount of time.

### *Physiological threshold*

We also used linear regression to compare the nutrient, fiber, and tannin composition of foods eaten in each patch with total occupancy time, time spent feeding in a patch, and percentage of time spent feeding relative to other activities. If guerezas are constrained physiologically by intake, we expect nutrient, fiber, or tannin composition of foods to have a negative relationship with measures of patch occupancy time. From these regressions we observed the coefficient of determination ( $R^2$ ) to assess the strength of the relationship between food composition and time spent in a patch.

### *Nutrient balancing*

To address how nutrient balancing relates to patch departure decisions, we looked at the ratios of macronutrients, tannin, and fiber ingested by guerezas, and compared this to time individuals occupied food patches. We employed nutritional geometry, using linear regression to see whether nutrient

balances were maintained across focals [Simpson and Raubenheimer, 2012]. To visualize the relationship between food macronutrient composition and patch residence time, we used thin plate splines to construct a residence time response surface superimposed on the compositions of right-angled mixture triangles (RMTs). We plotted RMTs to observe the relative contribution of available protein, carbohydrates (non-structural carbohydrates and digestible fiber, i.e., fermentable fiber), and fat to metabolizable energy in patch foods [Raubenheimer, 2011; Raubenheimer et al., 2015]. The relationships were statistically tested using generalized additive models (GAM). Statistical analyses were performed using R statistical software.

The research complied with protocols approved by the Hunter College and McGill University Institutional Animal Care Committee. The research adhered to the legal requirements of Uganda (Uganda Wildlife Authority and Uganda National Council of Science and Technology), in which the research was conducted, and the research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of non-human primates.

## RESULTS

A total of 1,225 focals were collected on patch occupancy over 312 hrs involving 48 tree species and 465 patches. The most commonly occupied tree species was *Celtis durandii* (42% of focals) and the most common food part consumed was young leaves (79% of focals).

### **Fixed-Amount and Fixed-Time Strategy**

Total food mass, nutrient, and tannin intakes were non-normally distributed, highly skewed (skewness >3.71, SE=0.07), and varied widely between focals, as did patch occupancy time and time spent feeding in patches. Guerezas consumed between <1 and 462g total wet weight mass (median = 198.40 g, CV = 1.17), <1–104 g total dry weight mass (median = 8.48 g, CV = 1.60), <1–44 g NDF (median = 3.59 g, CV = 1.82), <1–24 g ADF (median = 2.13 g, CV = 1.99), <1–12 g lignin (median = 0.95 g, CV = 2.34), <1–5 g fat (median = 0.21 g, CV = 1.66), <1–29 g available protein (median = 1.84 g, CV = 1.59), <1–25 g TNC (median = 1.50 g, CV = 1.62), <4–1247 kJ metabolizable energy (median = 93.38 kJ, CV = 1.53) in each patch. In 37% of focals, guerezas consumed foods containing condensed tannins with intakes ranging between <1–5 g (median = 0.09 g, CV = 2.39). Time spent in patches ranged from 1 to 290 mins (median = 9.87 mins, CV = 1.10). Time spent feeding in patches ranged from <1 to 75 mins (median = 5.03 mins, CV = 2.76).

## Physiological Threshold

We did not find strong evidence of a relationship between digestive constraints and patch departure. The composition of foods consumed in focals showed very weak correlation with time in patches. The NDF, ADF, ADL, fat, protein, TNC, CT, and metabolizable energy (ME) content all showed coefficient of determination ( $R^2$ ) values  $<0.01$  when regressed against time spent in patch and time spent feeding in patch. Although the correlation between some singular items (i.e., NDF, TNC, ME) and time was statistically significant ( $P < 0.05$ ), we consider the relationships biologically spurious due to the small amount of variance explained.

## Nutrient Balancing

We found that the diet of guerezas was tightly balanced with respect to the non-protein energy (nPE) (fats, non-structural carbohydrates, and digestible fiber) to available protein (P) ratio across patches; an outcome that was achieved by eating more dry matter in patches that had a balance close to  $nPE/P = 1.55$  ( $R^2 = 0.80$ ) (Fig. 1). Generalized additive models (GAM) showed that the time guereza spent in patches was significantly related to the interactive effects of nPE and P (edf = 1.86,  $F = 10.45$ ,  $P < 0.001$ ), and not individual macronutrients. This result shows that patch residence time is a function of macronutrient balance, as shown in Figure 2. Guerezas spent more time feeding in patches that have a balance close to  $nPE/P = 1.55$ ,

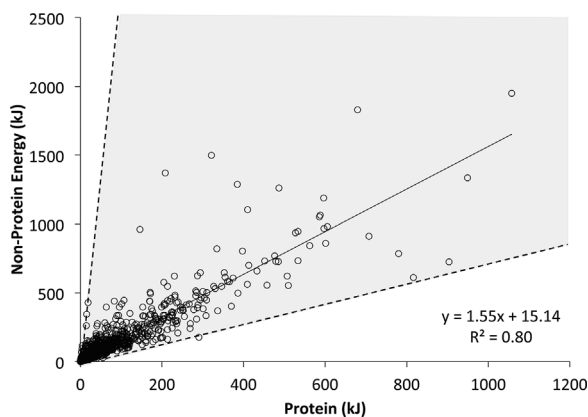


Fig. 1. Macronutrient balance gained during patch occupancy by guerezas. X-axis = protein intake (P) (kJ), Y-axis = non-protein energy intake from total non-structural carbohydrates, digestible fiber and fat (nPE) (kJ). Black circles = protein and non-protein energy gained by individuals during 1225 focals. Dashed rails show the balance of the most nutritionally extreme patch foods. Grey area demarcates the bounds of “nutritional space” of all potential macronutrient balances available to guereza from foods in the study. Guereza maintained a balance of  $nPE/P = 1.55$ , reflected in the slope of the solid line, by consuming more food in patches with a balance close to 1.55 nPE/P.

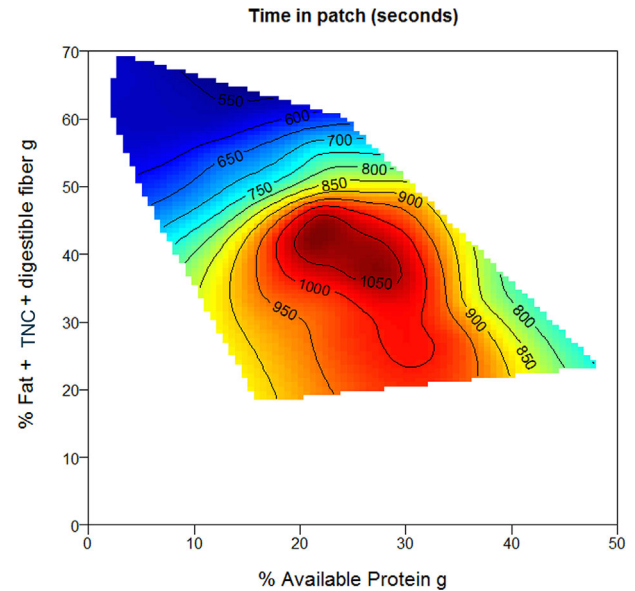


Fig. 2. Response surface showing time spent feeding in patches by individual guereza versus macronutrient concentrations and balance of food in patch (g/100 g). X-axis = available protein, Y-axis = non-protein energetic components (TNC + fat + digestible fiber). The balance and concentrations of protein and non-protein macronutrients in patch foods significantly predicted the time guereza individuals spent in patches. The greatest occupancy occurred in patches with a balance of 1.55 nPE/P shown by hot spot (edf = 1.86,  $F = 10.45$ ,  $P < 0.001$ ).

and they fed less frequently and for less time in patches that differ from this balance.

By using right-angled mixture triangles (RMTs), we found guerezas fed in patches with a consistent contribution of digestible fiber to metabolizable energy, a less consistent protein contribution, and a variable contribution from non-structural carbohydrates to (Fig. 3). Fat contributed little to the nutrient balance as it was low ( $<5\%$ ) in the majority of food types. We combined fat with the more abundant and variable macronutrients in the RMTs to account for all components of metabolizable energy and to parse the more notable roles other macronutrients played in balancing.

## DISCUSSION

As folivores and foregut fermenters, we hypothesized that guerezas would have digestive limitations due to constrained gut passage that prevent them from depleting patches [Chivers, 1994; Kay & Davies, 1994; Stevens & Hume, 1995; Tombak et al., 2012]. However, we did not find evidence of constraint relating to a fixed-amount patch departure. Guerezas did not reach a similar mass intake of food bulk or of any nutrient or non-nutrient item before patch departure. We found no evidence for constraint in the relationship between single nutrient or non-nutrient food composition and time spent feeding in patches. Additionally, guerezas left patches after

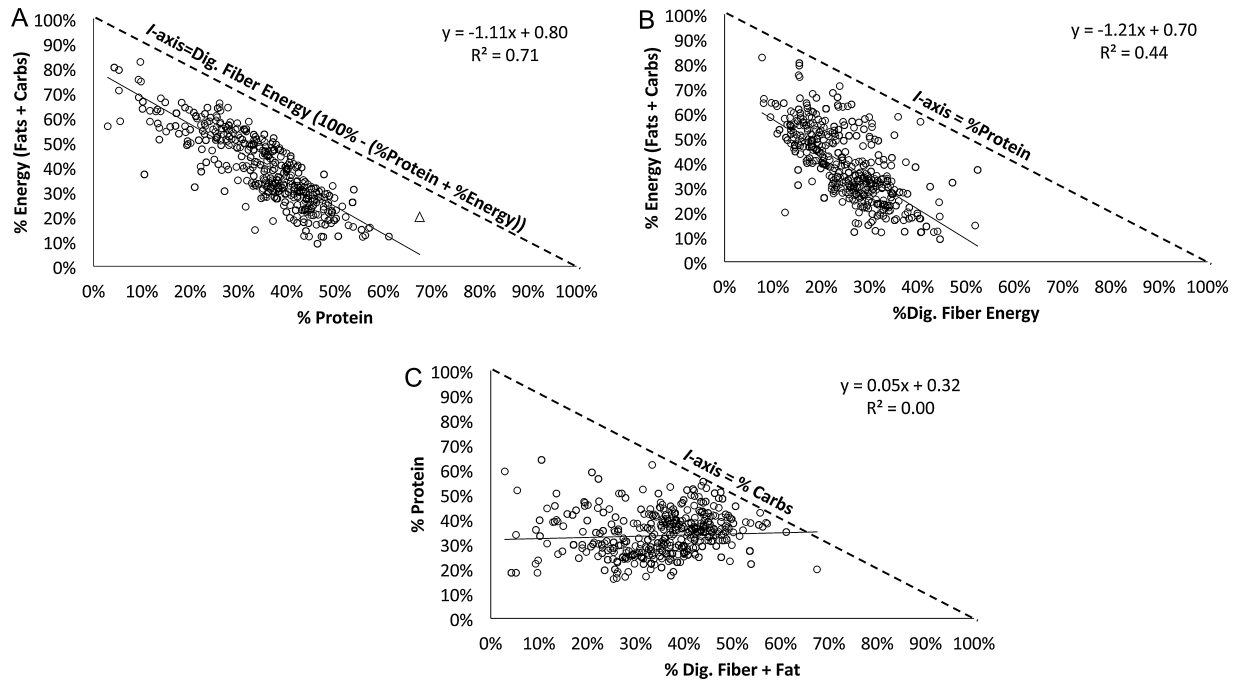


Fig. 3. **A:** Right-Angled Mixture Triangle (RMT) showing the relative components of metabolizable energy (ME). X-axis = % ME from protein. Y-axis = % ME from fats and total non-structural carbohydrates (“Carbs”), I-axis (implicit-axis) = % ME from digestible fiber. Circles = contributions of nutrients to ME for foods from 1225 focals. Each point represents an energy mixture, e.g., the triangle represents a food with ME contributions of 70% protein, 20% fats + carbs, 10% digestible fiber, totaling 100%. The foods guerezas consumed have a similar balance of digestible fiber compared to other macronutrients shown in the slope of the solid line =  $-1.11x$ , falling parallel to the implicit axis with an  $R^2$  value = 0.71. **B:** X-axis = % ME from digestible fiber. Y-axis = % ME from fats and total non-structural carbohydrates. I-axis = % ME from protein. The foods guerezas consumed also have a similar balance of protein shown in the slope of the solid line falling parallel to the implicit axis, but a less conserved balance than digestible fiber shown in a smaller  $R^2$  value. **C:** X-axis = % ME from digestible fiber + fat. Y-axis = % of ME from protein. I-axis = % ME from total non-structural carbohydrates. TNC is variable across patch focals shown in large spread of values, slope near zero, and small  $R^2$  value.

varying amounts of time and thus, there is no evidence for a fixed-time strategy.

We found support that nutrient balancing affects patch departure decisions. Nutrient balancing is employed by a variety of taxa, including several primate species [Felton et al., 2009a; Johnson et al., 2013; Rothman et al., 2011; Simpson & Raubenheimer, 2012]. Guerezas fed more frequently, ate more food, and spent more time in patches with a balance of non-protein energy (fats, non-structural carbohydrates, digestible fiber) (nPE) to protein (P) of 1.55, despite a selection of foods with varying nutrient compositions (Fig 1). As the nPE:P balance of foods differed from a ratio of 1.55, the monkeys departed patches more quickly (Fig. 2). Additionally, guereza foods showed a consistent contribution to metabolizable energy (ME) from digestible fiber, a less consistent protein contribution, and a large fluctuation of ME from non-structural carbohydrates (Fig. 3). The large fluctuation of energy from non-structural carbohydrates between patch foods suggest that guerezas exploit this form of energy in the form of leaves where possible. While we did not test how an individual would maintain nutrient balance when visiting multiple consecutive patches, or across

multiple day follows, we suggest individuals would employ a similar pattern as indicated by within-patch feeding and maintain a balance close to 1.55 nPE/P.

The macronutrient balance maintained by guerezas accords with other data on balancing and adds to a building picture of the role of nutrient balancing in ecological niche separation that is not necessarily based on plant parts or canopy level. When compared to other dietary geometric studies in primates, guerezas displayed the lowest non-protein energy to protein balance at 1.55:1 nPE/P across patch feeding. This is likely because as folivores, they incorporate a large amount of leaves in their diet, with leaves tending to be higher in protein than fruits, or a diet of mixed food types [Harris et al., 2010; Janson et al., 1999; Milton, 1981]. Primates that incorporate more fruit or diverse food types, such as mountain gorillas (*Gorilla beringei*), which are seasonally frugivorous/folivorous maintain seasonal balances of 3:1 and 2:1 nPE/P [Rothman et al., 2011]. Omnivorous baboons (*Papio hamadryas ursinus*,  $n = 1$ ) followed across multiple days maintained a balance of 5:1 nPE/P [Johnson et al., 2013], and frugivorous spider monkeys (*Ateles chamek*) maintain a balance of 8:1 nPE/P [Felton et al., 2009b].

Many hypothesize that folivorous primates choose leafy foods based on a high protein: fiber content and that the average protein: fiber ratio of mature leaves in a habitat can predict folivore monkey biomass [Chapman et al., 2002; Davies et al., 1988; Fashing, 2007; Ganzhorn, 1992; Oates et al., 1990; Wasserman & Chapman, 2003]. Previous studies of guerezas concluded that they select foods in an attempt to maximize protein and/or minimize fiber intake [Fashing, 2007; Wasserman & Chapman, 2003]. We found no support for this hypothesis in relation to patch feeding. Rather than spending more time feeding in patches with foods containing a high protein: fiber ratio, the guerezas in our study spent more time and ate more in patches with a particular macronutrient balance of energy to protein. Further, the foods eaten by guerezas in patches showed a consistent balance of digestible fiber to protein. This adds to growing evidence that questions the generality or causal mechanism behind the protein: fiber model [Chapman et al., 2014; Gogarten et al., 2012; Wallis et al., 2012].

Guerezas may alternate between complementary nutrient patches to maintain a nutrient balance, leaving before patches are depleted. If this is the case, they may be less limited by food resources than the sympatric and patch-depleting red colobus monkey [Harris et al., 2010; Snaith & Chapman, 2005]. Differences in resource limitation and within group food competition [Harris et al., 2010; Snaith & Chapman, 2005; Tombak et al., 2012] among folivores may explain differences between these two colobines in social behavior and grouping patterns. If guerezas are in fact less food limited than red colobus, it still remains unclear why they are not free to form larger groups than red colobus monkeys in Kibale [Snaith & Chapman, 2007; Tombak et al., 2012], which raises questions concerning varying nutritional goals between the species and how these goals influence patch depletion and food competition. Our intensive nutritional observations quantified patch departure rules, suggesting that guerezas spend more time feeding in patches that have a specific nutrient balance. This study treated group members as individual units and did not take into account social effects on patch residency, which is an avenue for future research. Additionally, with future use of all-day individual follows we can more specifically predict patch departure rules by taking into account intake from previous patches.

## ACKNOWLEDGMENTS

The Uganda Wildlife Authority and the Uganda National Council for Science of Technology gave us permission to conduct this research. We thank Moses Musana, James Magaro, Peter Iumba, Richard Mutageki and Hillary Musinguzi for their assistance in the field. Finally, we thank Dawn Frasch, Jenny

Paltan and the Rothman Nutritional Ecology Lab for assistance with sample processing. All research performed in this study complied with animal care regulations and national laws.

## REFERENCES

- Altmann SA. 1998. Foraging for survival: yearling baboons in Africa. Chicago, IL: University of Chicago Press. p 608.
- AOAC. 1990. Official methods of analysis. Arlington, VA: Association of Official Analytical Chemists. p 74.
- Astrom M, Lundberg P, Danell K. 1990. Partial prey consumption by browsers: trees as patches. *The Journal of Animal Ecology* 59:287–300.
- Brown JS. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. *Ecological Monographs* 59:1–20.
- Brown JS, Morgan RA. 1995. Effects of foraging behavior and spatial scale on diet selectivity: a test with fox squirrels. *Oikos* 54:33–43.
- Chapman CA. 1988. Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behavioral Ecology* 105:99–116.
- Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 133:861–875.
- Chapman CA, Chapman LJ, Bjornndal KA, Onderdonk DA. 2002. Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology* 23:283–310.
- Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR. 2004. Predicting folivorous primate abundance: validation of a nutritional model. *American Journal of Primatology* 62:55–69.
- Chapman CA, Snaith TV, Gogarten JF. 2014. In: Yamagiwa J, Karczmarski L, editors. How ecological conditions affect the abundance and social organization of folivorous monkeys. *Primates and Cetaceans. Japan: Springer*. p 3–23.
- Charnov EL. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129–136.
- Chivers DJ. 1994. Functional anatomy of the gastrointestinal tract. In: Davies AG, Oates JF, editors. *Colobine monkeys*. Cambridge: Cambridge University Press. p 205–226.
- Clauss M, Streich WJ, Nunn CL, et al. 2008. The influence of natural diet composition, food intake level, and body size on ingesta passage in primates. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 150:274–281.
- Conklin-Brittain NL, Knott CD, Wrangham RW. 2006. Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In: Hohmann G, Robbins MM, Boesch C, editors. *Feeding Ecology in Apes and Other Primates: Ecological, physical and behavioral aspects*. Cambridge: Cambridge University Press. p 445–571.
- Davies AG, Bennet EL, Waterman PG. 1988. Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society of London* 34:33–56.
- Edwards MS, Ullrey DE. 1999. Effect of dietary fiber concentration on apparent digestibility and digesta passage in non-human primates. II. Hindgut and foregut fermenting folivores *Zoo Biology* 18:537–549.
- Fashing JP. 2007. African colobine monkeys: patterns of between-group interaction. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. *Primates in perspective*. Oxford: Oxford University Press. p 201–224.

- Felton AM, Felton A, Raubenheimer D, et al. 2009. Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioural Ecology* 20:685–690.
- Felton AM, Felton A, Wood JT, et al. 2009. Nutritional ecology of *Ateles chamek* in lowland Bolivia: how macronutrient balancing influences food choices. *International Journal of Primatology* 30:675–696.
- Foley WJ, McIlwee A, Lawler I, et al. 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* 116:293–305.
- Foley WJ, Moore BD. 2005. Plant secondary metabolites and vertebrate herbivores—from physiological regulation to ecosystem function. *Current Opinion in Plant Biology* 8:430–435.
- Freeland WJ, Janzen DH. 1974. Strategies in herbivory by mammals—role of plant secondary compounds. *American Naturalist* 108:269–289.
- Fritz J, Hummel J, Kienzle E, et al. 2009. Comparative chewing efficiency in mammalian herbivores. *Oikos* 118:1623–1632.
- Ganzhorn JU. 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests: tests of a hypothesis. *Oecologia* 91:540–547.
- Goering HK, Van Soest PJ. 1970. Forage fiber analysis (apparatus, reagents, procedures, and some applications). United States Department of Agriculture. p 1–20.
- Gogarten JF, Guzman M, Chapman CA, et al. 2012. What is the predictive power of the colobine protein-to-fiber model and its conservation value. *Tropical Conservation Science* 5:381–393.
- Green RF. 1984. Stopping rules for optimal foragers. *American Naturalist* 123:30–43.
- Grether GF, Palombit RA, Rodman PS. 1992. Gibbon foraging decisions and the marginal value model. *International Journal of Primatology* 13:1–17.
- Harris T, Chapman C. 2007. Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates* 48:208–221.
- Harris TR, Chapman CA, Monfort SL. 2010. Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. *Behavioral Ecology* 21:46–56.
- Hengeveld GM, van Langevelde F, Groen TA, de Knegt HJ. 2009. Optimal foraging for multiple resources in several food species. *The American Naturalist* 174:102–110.
- Hirakawa H. 1997. Digestion-constrained optimal foraging in generalist mammalian herbivores. *Oikos* 78:37–47.
- Illius A, Tolamp B, Yearsley J. 2002. The evolution of the control of food intake. *Proceedings of the Nutrition Society* 61:465–472.
- Iwasa Y, Higashi M, Yamamura N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist* 117:710–723.
- Janson CH, Chapman CA. 1999. Resources and primate community structure. In: Fleagle JG, Janson C, Reed K, editors. *Primate communities*. Cambridge: Cambridge University Press. p 237–267.
- Jeschke JM, Kopp M, Tollrian R. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* 72:95–112.
- Johnson CA, Raubenheimer D, Rothman JM, Clarke D, Swedell L. 2013. 30 days in the life: daily nutrient balancing in a wild chacma baboon. *PLoS ONE* 8:e70383.
- Kay RF, Davies AG. 1994. Digestive physiology. In: Davies AG, Oates JF, editors. *Colobine monkeys*. Cambridge: Cambridge University Press.
- Kazahari N, Agetsuma N. 2008. Social factors enhancing foraging success of a wild group of Japanese macaques (*Macaca fuscata*) in a patchy food environment. *Behaviour* 145:843–860.
- Kotler BP, Brown JS. 1999. Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. *Journal of Mammalogy* 80:361–374.
- Licitra G, Hernandez TM, Van Soest PJ. 1996. Standardization of procedures for nitrogen fractionation of ruminant feeds. *Animal Feed Science and Technology* 57:347–358.
- Marshall HH, Carter AJ, Ashford A, Rowcliffe JM, Cowlishaw G. 2013. How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions. *Journal of Animal Ecology* 82:894–902.
- Matsuda I, Tuuga A, Hashimoto C, et al. 2014. Faecal particle size in free-ranging primates supports a ‘rumination’ strategy in the proboscis monkey (*Nasalis larvatus*). *Oecologia* 174:1127–1137.
- Mattson WJ. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* 11:119–161.
- McSweeney CS, Palmer B, McNeill DM, Krause DO. 2001. Microbial interactions with tannins: nutritional consequences for ruminants. *Animal Feed Science and Technology* 91:83–93.
- Milton K. 1981. Food choice and digestive strategies of two sympatric primate species. *American Naturalist* 117:496–505.
- Nie Y, Zhang Z, Raubenheimer D, et al. 2014. Obligate herbivory in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry. *Functional Ecology* 29:26–34.
- Oates JF. 1977. The guereza and its food. In: Clutton-Brock TH, editor. *Primate ecology*. New York: Academic Press. p 275–321.
- Oates JF. 1994. The natural history of African colobines. In: Davies AG, Oates JF, editors. *Colobine monkeys: their ecology, behaviour and evolution*. Cambridge: Cambridge University Press. p 432.
- Oates JF, Swain T, Zantovska J. 1977. Secondary compounds and food selection by colobus monkeys. *Biochemical Systematics and Ecology* 5:317–321.
- Oates JF, Whitesides GH, Davies AG, et al. 1990. Determinants of variation in tropical forest biomass: new evidence from West Africa. *Ecology* 71:328–343.
- Owen-Smith N, Fryxell JM, Merrill EH. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2267–2278.
- Plante S, Colchero F, Calmé S. 2014. Foraging strategy of a neotropical primate: how intrinsic and extrinsic factors influence destination and residence time. *Journal of Animal Ecology* 83:116–125.
- Raubenheimer D. 2011. Toward a quantitative nutritional ecology: the right-angled mixture triangle. *Ecological Monographs* 81:407–427.
- Raubenheimer D, Machovsky-Capuska GE, Chapman CA, Rothman JM. 2015. Geometry of nutrition in field studies: an illustration using wild primates. *Oecologia* 177:223–234.
- Rosen DA, Winship AJ, Hoopes LA. 2007. Thermal and digestive constraints to foraging behaviour in marine mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:2151–2168.
- Rothman JM. 2015. Nutritional geometry provides new insights into the interaction between food quality and demography in endangered wildlife. *Functional Ecology* 29:3–4.
- Rothman JM, Chapman CA, Van Soest PJ. 2012. Methods in primate nutritional ecology: a user’s guide. *International Journal of Primatology* 33:542–566.
- Rothman JM, Chapman CA, Pell AN. 2008a. Fiber-bound protein in gorilla diets: implications for estimating the



- intake of dietary protein by primates. *American Journal of Primatology* 70:690–694.
- Rothman JM, Dierenfeld ES, Hintz HF, Pell AN. 2008b. Nutritional quality of gorilla diets: consequences of age, sex and season. *Oecologia* 155:111–122.
- Rothman JM, Chapman CA, Hansen JL, Cherney DJ, Pell AN. 2009a. Rapid assessment of the nutritional value of foods eaten by mountain gorillas: applying near-infrared reflectance spectroscopy to primatology. *International Journal of Primatology* 30:729–742.
- Rothman JM, Dusinger K, Pell AN. 2009b. Condensed tannins in the diets of primates: a matter of methods. *American Journal of Primatology* 71:70–76.
- Rothman JM, Raubenheimer D, Chapman CA. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biology* 7:847–849.
- Sayers K, Norconk MA, Conklin-Brittain NL. 2010. Optimal foraging on the roof of the world: Himalayan langurs and the classical prey model. *American Journal of Physical Anthropology* 141:337–357.
- Schoener TW. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369–404.
- Searle KR, Hobbs NT, Shipley LA. 2005. Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. *Oikos* 111:417–424.
- Simpson SJ, Raubenheimer D. 2012. The nature of nutrition: a unifying framework from animal adaptation to human obesity. Princeton: Princeton University Press. p 239.
- Simpson SJ, Sibley RM, Lee KP, Behmer ST, Raubenheimer D. 2004. Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour* 68:1299–1311.
- Snaith TV, Chapman CA. 2005. Towards an ecological solution to the folivore paradox: patch depletion as an indicator of within-group scramble competition in red colobus monkeys (*Piliocolobus tephrosceles*). *Behavioral Ecology and Sociobiology* 59:185–190.
- Snaith TV, Chapman CA. 2007. Primate group size and socioecological models: do folivores really play by different rules? *Evolutionary Anthropology* 16:94–106.
- Stein RA, Magnuson JJ. 1976. Behavioral response of crayfish to a fish predator. *Ecology* 57:751–761.
- Stephens DW, Krebs JR. 1986. Foraging theory. Princeton: Princeton University Press. p 262.
- Stevens CE, Hume ID. 1995. Comparative physiology of the vertebrate digestive system. Cambridge: Cambridge University Press. p 420.
- Suarez SA. 2014. Ecological factors predictive of wild spider monkey (*Ateles belzebuth*) foraging decisions in Yasuni, Ecuador. *American Journal of Primatology*. 76: 1185–1195.
- Tombak KJ, Reid AJ, Chapman CA, et al. 2012. Patch depletion behavior differs between sympatric folivorous primates. *Primates* 53:57–64.
- Valone TJ, Brown JS. 1989. Measuring patch assessment abilities of desert granivores. *Ecology* 70:1800–1810.
- van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. *Comparative socioecology: the behavioural ecology of humans and other mammals*. Boston: Blackwell Scientific Publications. p 195–218.
- Van Soest PJ, Robertson JB, Lewis BA. 1991. Methods for dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* 74:3583–3597.
- Verdolin JL. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology* 60:457–464.
- Verlinden C, Wiley RH. 1989. The constraints of digestive rate: an alternative model of diet selection. *Evolutionary Ecology* 3:264–272.
- Vogel ER. 2005. Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. *Behavioral Ecology and Sociobiology* 58:333–344.
- Wallis IR, Edwards MJ, Windley H, et al. 2012. Food for folivores: nutritional explanations linking diets to population density. *Oecologia* 169:281–291.
- Wasserman MD, Chapman CA. 2003. Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal of Animal Ecology* 72:650–659.
- Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262–300.