

Macronutrient and Energy Contributions of Insects to the Diet of a Frugivorous Monkey (*Cercopithecus ascanius*)

Margaret A. H. Bryer^{1,2} · Colin A. Chapman^{3,4} ·
David Raubenheimer⁵ · Joanna E. Lambert⁶ ·
Jessica M. Rothman^{1,2,7,8}

Received: 27 December 2014 / Accepted: 23 June 2015 / Published online: 21 August 2015
© Springer Science+Business Media New York 2015

Abstract Most extant primates feed on insects to some degree, yet the nutritional contributions of insects to primate diets are poorly characterized. Like many small-bodied frugivorous primates, redbtail monkeys (*Cercopithecus ascanius*) also eat insects. We quantified the nutritional contributions of insects to the diets of female redbtail monkeys in Kibale National Park, Uganda, from July 2010 to June 2012 through full day follows ($N = 64$) using weight-based estimates of food intake. Female redbtail monkeys targeted insects for 41 % of feeding bouts, plant reproductive parts (including ripe fruits, unripe fruits, flowers, seeds) for 15 % of feeding bouts, and leaves (including young leaves, mature leaves, leaf petioles, leaf buds) for 17 % of feeding bouts. However, females spent just under 10 % of feeding time on insects, in contrast to 42 % on plant reproductive parts and 39 % on leaves. Redtail monkeys fed primarily on

✉ Margaret A. H. Bryer
margaret.bryer@gmail.com

¹ New York Consortium in Evolutionary Primatology, New York, NY, USA

² Department of Anthropology, Graduate Center of the City University of New York, New York, NY 10016, USA

³ Department of Anthropology and McGill School of Environment, McGill University, Montreal H3A 2T7 Quebec, Canada

⁴ Wildlife Conservation Society, Bronx, NY 10460, USA

⁵ Charles Perkins Centre, University of Sydney, Sydney 2006, Australia

⁶ Department of Anthropology, University of Colorado, Boulder, CO 80309, USA

⁷ Department of Anthropology, Hunter College of the City University of New York, New York, NY 10065, USA

⁸ Department of Biology, Graduate Center of the City University of New York, New York, NY 10016, USA

solitary, as opposed to eusocial, insects. Identification of consumed insects is challenging, but of consumed insects that could be identified 74 % were cicadas (order Homoptera), 14 % caterpillars (order Lepidoptera), and 7 % long-horned grasshoppers (order Orthoptera). On a dry matter basis, insects were fairly low in fat (<10 %, except for caterpillars) and high in crude protein content (mean *ca.* 69 %) compared to other foods, and contained low levels of indigestible chitin. Because insects are small, an insect feeding bout is much shorter than a feeding bout on vegetation or fruit. Despite the small proportion of time spent feeding on insects, redbtail monkeys obtained a mean of 24 % of their daily protein intake and 14 % of energy through insectivory, though intake varied widely across females. Our findings demonstrate that female redbtail monkeys gain more nutrients than expected given that they spend <10 % of feeding time ingesting insects. The many primates that complement plant diet items with insects may gain substantial nutrition through minimal feeding time.

Keywords Guenon · Insectivory · Nutrition · Primate ecology

Introduction

Nutrition underlies primate reproductive physiology and behavior, making the understanding of the full repertoire of primate diets essential. For example, female ability to feed on preferred food resources is linked to likelihood of cycling and conception, shorter interbirth intervals, and increased infant survival (Altmann and Alberts 2003; Emery Thompson and Wrangham 2008; Emery Thompson *et al.* 2007). Insects are an important food resource for many living primates (McGrew 2001; O'Malley and Power 2014; Rothman *et al.* 2014). Some small-bodied primates are obligate or frequent insectivores (Dammhahn and Kappeler 2008; Gursky 2000; Harcourt 1986; Nekaris and Rasmussen 2003; Stone 2007), while many other primates practice occasional insectivory that complements diets consisting mostly of plant parts (Altmann 1998; Chapman *et al.* 2002; Fashing *et al.* 2010; Gautier-Hion 1980; Stevenson *et al.* 2000; Veiga and Ferrari 2006). Eusocial insects dominate great ape insectivory, which arguably makes insect feeding energetically worthwhile (Cipolletta *et al.* 2007; O'Malley and Power 2012; Webster *et al.* 2014). However, the nutritional contributions of insects to primate diets are not well understood.

Primates gain protein and energy from insects, though how much of a contribution to the diet insects make is dependent on factors including primate body size, insect availability, and insect type and developmental stage (McGrew 2014; Raubenheimer and Rothman 2013; Redford and Dorea 1984; Rothman *et al.* 2014). Studies of strepsirrhines and monkeys emphasize insect protein as important. Female white-faced capuchins (*Cebus capucinus*) in Costa Rica eat insects that contain more than four times the proportion of protein contained in fruits, flowers, and seeds, “confirming that insects are the food item in the capuchin diet most likely to yield high proportions of protein,” though weight-based intake was not measured (McCabe and Fedigan 2007, p. 846). Some sites show that insectivory is nutritionally valuable to great apes, providing protein and fat as well as micronutrients (Hladik 1977; O'Malley and Power 2014); however, at other sites, macronutrient contributions are negligible (Deblauwe and Janssens 2008; Nishie 2011).

Guenons are among the taxonomic groups that practice occasional insectivory to complement diets dominated by fruit, and, to a lesser extent, leaves (Chapman *et al.* 2002; McGrew 2001). Using a frequency scoring method developed by Rudran (1978), researchers found that most guenons feed on insects for <36 % of their feeding (Butynski 1990; Cords 1986; Gathua 2000; Struhsaker 1978). When percent of feeding time is measured, however, blue monkeys in Malawi devote just 1 % of feeding time to insects (Beeson *et al.* 1996). Based on stomach content analyses of the moustached guenon (*Cercopithecus cephus*), the crowned guenon (*Cercopithecus pogonias*), and the greater spot-nosed monkey (*Cercopithecus nictitans*) in Gabon, insects make up 13 %, 16 %, and 9 % of their diets, respectively. The greater spot-nosed monkey relies more on sedentary faunal prey including larvae, while the crowned guenon relies more on mobile prey including Orthoptera and moths, with the moustached guenon intermediate in its insect capture preferences (Gautier-Hion 1980). However, using observational methods, Tutin and colleagues (1997) found that the same three *Cercopithecus* species at a different site in Gabon eat insects during <10 % of their feeding time.

Minimal research exists on the nutritional contributions of insectivory in the diets of guenons and their close phylogenetic relatives. In Cameroon, patas monkeys (*Erythrocebus patas*) eat insects that are high in crude protein content (30–65 %), ranging widely in lipid content (7–44 %), and medium to high in available energy (3–5 kcal per insect) compared to plant foods in the diet (Nakagawa 2003). Patas monkeys in Kenya gain one-third of their daily energy from ants (Isbell and Young 2007) and adult female patas ingestion of ants may be enough to meet females' daily protein requirements (Isbell *et al.* 2013). The considerable contribution of insects to patas nutritional requirements is surprising given their large body size.

Redtail monkeys (*Cercopithecus ascanius*) eat substantial amounts of insects in some regions: across groups in Kibale, insect consumption as percentage of foods eaten ranges from 15–31 % (Chapman *et al.* 2002; Struhsaker 1978) and, at two sites in Kenya, 25–31 % (Cords 1986; Gathua 2000). Previous research at Kibale has quantified overall macronutrient intake in the redtail monkey diet (Rode *et al.* 2006) and mineral content of caterpillars eaten (Rode *et al.* 2003). Caterpillars contained high levels of copper, iron, and zinc, demonstrating potentially high micronutrient value (Rode *et al.* 2003).

Our goal in this study was to quantify the nutritional composition of insects consumed by redtail monkeys and to investigate the daily macronutrient and energy contributions of insects to redtail monkey diets. Contribution was based on identification of insects ingested, macronutrient composition of identified insects, and weight-based energy and protein contributions relative to other components of the diet in one redtail monkey group in Kibale National Park, Uganda. Given redtail monkey small body size and frequent ingestion of insects, we hypothesized that insects would contribute substantially to the study species' daily protein and energy intake compared to fruits and leaves. We predicted that insects eaten by redtail monkeys would be high in protein compared to fruits and leaves in the diet as found in other primate diets (McGrew 2001; Rothman *et al.* 2014). Fat content of insects varies widely, especially with developmental stage, with most mature morphs low in fat, while larval morphs can reach as high as 80 % fat (O'Malley and Power 2012; Redford and Dorea 1984; Rothman *et al.* 2014). We therefore also predicted that insects eaten at the adult stage would be low in fat compared to fruits and leaves, while larvae eaten would have fat concentrations comparable to fatty fruits. As fat, out of all macronutrients, contributes the most energy per gram (National

Research Council 2003), we predicted that frequent ingestion of larvae would translate into substantial energy gain for redtail monkeys.

Methods

Study Site

The study took place in Kibale National Park, western Uganda (0°13–0°41N and 30°19–30°32E), a 795 km² mid-altitude evergreen forest, near the Kanyawara village, in a 282-ha area with an elevation of 1500 m. Kibale experiences bimodal seasonality, with rainy seasons March–May and September–November; average annual rainfall is 1696 mm (data from 1990–2011: Chapman and Lambert 2000; Stampone *et al.* 2011; Chapman *unpubl. data*). Redtail monkeys are a common species in the area, with a density of *ca.* 184 individuals/km² (Chapman *et al.* 2010). The study group consisted of *ca.* 40 individuals, including adult males, adult females, subadults, juveniles, and infants, and has been habituated since 2008. At the time of the study, we identified the 16 adult females and 5 adult males in this group by tail, facial, nipple, and/or body size characteristics.

Behavioral Data Collection

From July 2010 to June 2012, we followed one redtail monkey group, conducting full-day focal follows of cycling adult females ($N = 16$). M. A. H. Bryer, J. M. Rothman, and/or two field assistants collected data within 5–15 m from the subjects, although proximity to a focal female varied according to canopy height. From 08:00 to 18:30 h, we recorded whether the female was feeding. Feeding was defined as ingestion of a food item into the mouth and ended when the individual stopped chewing and switched to another activity. Searching for food was *not* included in feeding time. We recorded all feeding bouts; a feeding bout consists of the intake of one food item until the focal female moves on to another food item/feeding bout, or until she stops eating and starts another activity. When the focal female was feeding, we recorded the plant species and the part and counted the number of items eaten (count), when that level of detail was visible to the observer. We recorded insect consumption similarly, except we identified insects to the order or listed them as “unidentified.” We tagged feeding trees and collected plant species and parts for all plant items eaten. We collected identified insects for nutritional analysis opportunistically in the undergrowth and/or lower tree strata, as collection of identified insects in the exact location of consumption by monkeys was not possible owing to location in high tree strata and solitary behavior of most insects consumed. We collected fecal samples opportunistically from focal females and placed samples in ethanol for subsequent digestibility analyses. When a focal female was partially visible, we entered “out of sight.” When we did not know where the focal female was because of poor visibility, we entered “lost.”

Nutritional Analysis

We processed foods as the monkey would process them; for example, if a focal female ate ripe fruit seeds, we collected and analyzed only the seeds of the plant (Rothman *et al.* 2012). We weighed plant parts and insects within 1 h of collection, and we

weighed 50 units of each food to calculate a mean unit weight. A unit was defined as the plant part or insect portion eaten (one seed, one ripe fruit's pulp, one grasshopper, etc.). The 235 foods, including 45 plant species, 74 plant parts, 9 insect samples, and other items (including gum), were dried to constant weight and ground in the field with a Wiley Mill (Thomas Scientific). Each insect sample consisted of *ca.* 75 insects combined (mean individual insect weight = 0.26 g) to obtain 20 g for analyses.

Dried and ground foods and fecal samples were exported to Hunter College's Primate Nutritional Ecology Laboratory. We ran all nutritional analyses on leaf samples with near-infrared reflectance spectroscopy (NIRS) (Foley *et al.* 1998; Rothman *et al.* 2009) using a Foss XDS spectrometer (Laurel, MD). We analyzed the rest of the food samples using wet chemistry techniques: We used established methods for analyzing lipid, crude protein (CP), hemicellulose and cellulose (through neutral detergent fiber [NDF] and acid detergent fiber [ADF] assays), lignin (ADL), nonstructural carbohydrates, and metabolizable energy (National Research Council 2001; Rothman *et al.* 2006, 2008b, 2012; Van Soest *et al.* 1991). We measured neutral detergent fiber (NDF with α -amylase), acid detergent fiber (ADF), and acid detergent lignin (ADL) through sequential analysis using an A200 fiber analyzer (ANKOM, Macedon, NY) (Goering and Van Soest 1970; Van Soest *et al.* 1991). We estimated total nitrogen (N) using a Leco TruSpec (Leco, St. Joseph, MI) via combustion (AOAC 1990) and then calculated crude protein (CP) by multiplying nitrogen by 6.25 (Robbins 1993). The 16 g of nitrogen per 100 g protein method of calculating crude protein content is controversial, as some nitrogen is bound to fiber/chitin and therefore indigestible (Conklin-Brittain *et al.* 1999; Rothman *et al.* 2008a, 2012). However, we opted to use this measurement (1) for comparison with other studies and (2) because previous nutritional analyses indicate that insects have low levels of chitin compared to other nutritional components, and therefore crude protein is a good estimate of available protein (Finke 2007). We measured the amount of lipid in the samples using a XT15 Fat Analyzer (ANKOM, Macedon, NY) by boiling samples in petroleum ether at 90°C for 120 min. We measured ash by burning the sample at 550°C. We estimated total nonstructural carbohydrates (TNC) by subtracting NDF, lipid, CP, and ash from 100 %. We analyzed all insect samples for lipid, CP, and chitin (ADF), using the same assays used for plants.

Calculations of Nutrient Intake

We calculated total nonstructural carbohydrate (TNC) by difference: $TNC = [1 - (NDF + CP + lipid + ash)]$ for plant parts (Rothman *et al.* 2012). We calculated metabolizable energy from plants as follows: Digestible energy (kcal) = $[(NDF \times 3) \times NDF \text{ digestion coefficient}] + (CP \times 4) + (lipid \times 9) + (TNC \times 4)$ (Conklin and Wrangham 1994; Conklin-Brittain *et al.* 2006). We calculated the NDF digestion coefficient as per Rothman *et al.* (2008b) with lignin as an internal marker to estimate the percentage of fiber digested. We calculated TNC and energy intake from insects with the same equations, excluding NDF values, as ADF can be used as an estimate of insect chitin (Finke 2007).

Based on amount eaten (unit nutrient mean \times unit count), we calculated intake of macronutrient and energy for each feeding bout. For unidentified insects, we used mean values for identified insect CP, ADF, and lipid. Given that each full-day follow included periods when the focal female was "out of sight" or "lost," we extrapolated wet weight and dry weight intake in these missing times based on known wet weight and dry

weight intake for that day, as well as the percentage of time spent feeding by the focal female when visible on that day. We present standard error (SE) for all values.

We could not always record unit count of plant parts and insects owing to periods of low visibility. For food intake data *without* recorded counts, we used the median unit count for the species and food part eaten, when available. We also recorded intake rates for adult female monkeys in the study group outside of focal day data collection, to better estimate the feeding rates of particular females on particular plant parts and insects.

Data Analysis

We conducted 75 all-day focal follows on 16 adult females, of which 68 were completed all-day follows and 7 were aborted before 15:00 h. Our analyses include completed full-day follows only. Four of the 68 remaining focal days were removed because >40 % of dry matter intake consisted of “unidentified foods” due to bad visibility, resulting in $N = 64$ for analysis. Our analyses here include only adult female feeding events ($N = 4862$) as substantial effort is required to conduct full-day focal follows of redbtail monkey individuals and, for comparative purposes, we wanted a large sample of females.

We analyzed both the percentage of feeding bouts per food type, similar to previous guenon feeding studies that have employed a frequency method (Butynski 1990; Cords 1987; Gathua 2000; Rudran 1978; Struhsaker 1978, 1980), and the percentage of time spent feeding per food type. We argue that time spent feeding is a more useful measure of how redbtail monkeys divide up their feeding time, whereas percentage of feeding bouts, and similar frequency-based methods, overemphasize rarely eaten food items (as previously pointed out by Gathua 2000). Employing scan sampling methods to examine guenon feeding (as done previously by Bryer *et al.* 2013; Isbell 1998; Tashiro 2006) also overemphasizes rarely eaten food items such as insects, and should therefore no longer be used in quantifying feeding.

As our data departed significantly from normality, we conducted nonparametric statistical tests in R with statistical significance set to $P = 0.05$ as follows. We ran Kruskal–Wallis χ^2 to test the following: (1) differences in macronutrient content across insects, plant reproductive parts, and leaves, and differences in insect contribution to (2) daily energy and (3) protein intake across individual female redbtail monkeys. We also ran linear mixed-effects models fit by REML with individual identity as random effect to examine the following: (1) comparison of time spent feeding on insects in rainy versus dry seasons and morning vs. afternoon and (2) comparison of time spent feeding on plant reproductive parts in rainy vs. dry seasons and morning vs. afternoon.

Results

Female redbtail monkeys spent most of their feeding time on plant reproductive parts (including unripe fruits, ripe fruits, seeds, flowers, flower buds), followed by leaves (including young leaves, mature leaves, leaf buds, leaf petioles) and then insects (Homoptera, Orthoptera, Lepidoptera, leaf galls assumed induced by insects, and unidentified insects) (Fig. 1). In terms of proportion of feeding bouts, female redbtail

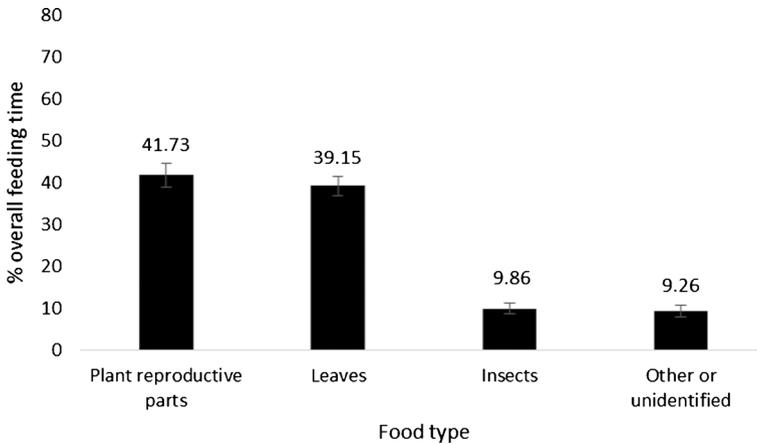


Fig. 1 Percentage of female redtail monkey feeding time devoted to different food types in one group in Kibale National Park, Uganda, July 2010–June 2012. Error bars (SE) show variation across individual females.

monkeys targeted insects for 41 % of feeding bouts, reproductive parts of plants for 15 % of feeding bouts, and leaves for 17 % of feeding bouts. Time spent feeding on insects did not differ between rainy and dry seasons ($\chi^2 = -0.30$, $df = 96$, $P = 0.94$) or between morning and afternoon ($\chi^2 = 5.13$, $df = 96$, $P = 0.27$). In addition, female redtail monkeys spent more time feeding on plant reproductive parts during the rainy season than during the dry season ($\chi^2 = 18.09$, $df = 96$, $P = 0.02$), though the model revealed that there was no effect of time of day ($\chi^2 = 5.72$, $df = 96$, $P = 0.49$) on fruit eating. Of the insects eaten, 44.53 % were identified, of which the majority of feeding bouts targeted cicadas (Homoptera), though females also consumed long-horned grasshoppers (Orthoptera), caterpillars (Lepidoptera), and leaf galls assumed induced by unknown insects (Fig. 2). Of caterpillars consumed, 40.27 % were noctuid moth larvae

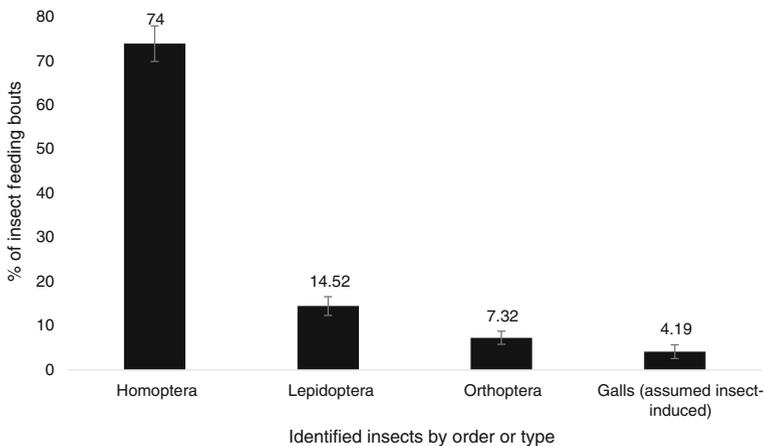


Fig. 2 Percentage of female redtail monkey feeding bouts on identified insects devoted to different insect orders and types in one group in Kibale National Park, Uganda, July 2010–June 2012. Error bars (SE) show variation across individual females.

(order Lepidoptera, family Noctuidae); noctuid or owlet moths are common generalist feeders in Kibale (H. Roininen *pers. commun.*).

We analyzed 235 food samples, which spanned 46 plant species and included 9 insect samples, for their nutritional chemistry. The insect samples consisted of the following: 1 cicada sample (i.e., *ca.* 20 g of desiccated and ground cicadas; order: Homoptera), 2 grasshopper samples (order: Orthoptera), 3 caterpillar samples (order: Lepidoptera), and 3 gall samples (each *ca.* 20 g of desiccated and ground individually-removed *Teclea nobilis* leaf galls believed to be insect-induced). Galls are excluded from the following results (see *A Note About Galls* later), resulting in $N = 6$. Insect samples were high in crude protein (CP) content: Cicadas (Homoptera) contained 77.55 %, long-horned grasshopper sample 1 (Orthoptera) 75.55 %, long-horned grasshopper sample 2 (Orthoptera) 75.90 %, and caterpillars (Lepidoptera) mean CP of 56.67 %. All insect samples were low in indigestible chitin (ADF) compared to other nutritional components: Cicadas (Homoptera) contained 12.60 %, long-horned grasshopper sample 1 (Orthoptera) 8.08 %, long-horned grasshopper sample 2 (Orthoptera) 9.20 %, and caterpillars (Lepidoptera) mean chitin of 7.68 %. All insects were low in fat, with caterpillars highest in fat content: Cicadas (Homoptera) contained 7.02 %, long-horned grasshopper sample 1 (Orthoptera) 10.49 %, long-horned grasshopper sample 2 (Orthoptera) 9.05 %, and caterpillars (Lepidoptera) mean fat of 16.67 % (Fig. 3).

Compared to insects, plant reproductive part and leaf samples ($N = 224$) were lower in protein content (Kruskal–Wallis $\chi^2 = 31.53$, $df = 2$, $P < 0.0001$) and higher in ADF (analogous to chitin) content (Kruskal–Wallis $\chi^2 = 47.77$, $df = 2$, $P < 0.0001$). Though some fruits and leaves, including *Celtis durandii* unripe fruits (mean = 21.15 ± 0.58) and *Celtis africana* leaf buds (mean = 30.76 ± 0.80), have high protein compared to other plant part foods, these high-protein plant parts are still substantially lower in protein than insects. Plant reproductive parts and insects were, unsurprisingly, higher in fat content than leaves (Kruskal–Wallis $\chi^2 = 48.91$, $df = 2$, $P < 0.0001$). Plant reproductive parts and insects were not significantly different in fat content

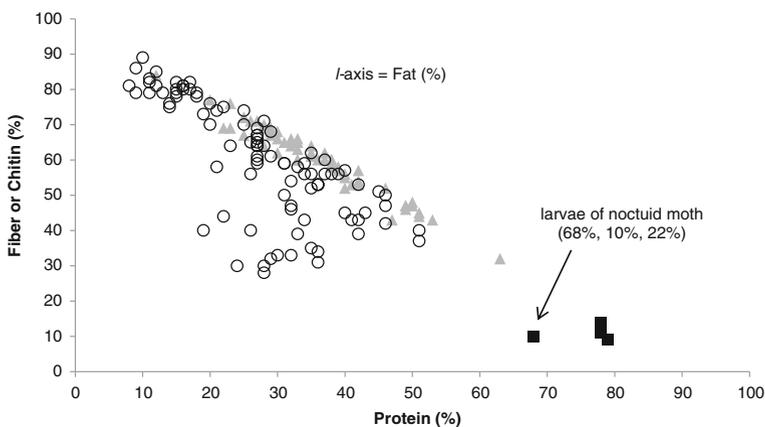


Fig. 3 A right angle mixture triangle illustrating the nutritional composition of plant parts and insects eaten by female redtail monkeys in one group in Kibale National Park, Uganda. Each data point represents one food (species and part in the case of plant foods). The x and y axes represent proportion of crude protein and fiber/chitin content for a given food. The third axis (l -axis) is implicit and represents the proportion of fat in the given food. Circles represent plant reproductive parts, triangles represent leaves, and squares represent insects.

(Wilcoxon rank sum test $W = 79, P = 0.75$), though a larger insect sample size is most likely needed to verify this finding. The plant portion of the redbtail monkey diet is low in fat, with the exception of some ripe fruits such as those of *Celtis durandii* (mean fat content of ripe fruit of *C. durandii* = 29.05 % ± 1.13). Caterpillar fat content (16.67 % ± 0.60) was in fact higher than mean fruit fat content when fruits of *C. durandii* fruit were excluded (6.59 % ± 3.47). Plant reproductive parts (ripe fruit, unripe fruit, flowers, flower buds, seeds) contained means of 16.72 % ± 0.81 CP, 38.55 % ± 1.57 fiber (NDF), and 8.00 % ± 1.98 fat. Leaf parts (young leaves, mature leaves, leaf buds, leaf petioles, leaf stems) contained means of 24.64 % ± 0.85 CP, 45.80 % ± 1.51 fiber (NDF), and 2.64 % ± 0.08 fat (Fig. 3).

Redtail monkeys consumed a mean daily fresh weight of 462.74 g ± 32.62 and mean dry weight of 188.58 g ± 11.71 of all food types per day. Daily mean dry mass (DM) intake consisted of 10.87 % ± 1.33 insects, 36.27 % ± 3.06 leaves, and 44.04 % ± 2.53 fruits. Compared across adult females ($N = 14$, focal females with more than one full-day follow), the mean DM intake of insects was low compared to fruits, leaves, and other items (Fig. 4).

Mean percent contribution of insects (galls excluded) to daily intake of protein was 24.62 % ± 2.07. However, insect protein contribution varied widely across focal females (Fig. 5), ranging overall from 2.53 % to 69.01 % of protein intake. Insect mean daily contribution to protein intake was less than that of leaves (34.44 % ± 2.29) and fruits (31.00 % ± 2.66) (other or unidentified items contributed 10.00 % ± 1.48 mean protein). Mean percent contribution of insects (galls excluded) to daily intake of energy was 14.6 % ± 1.6. However, insect energy contribution varied widely across

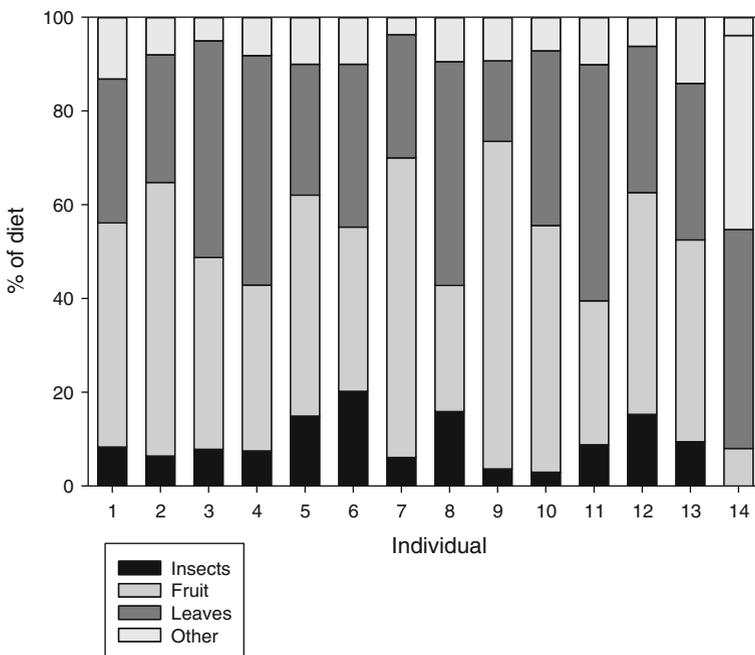


Fig. 4 Mean percent dry matter contribution to daily intake by food type across 14 adult female redbtail monkeys in one group in Kibale National Park, Uganda, July 2010–June 2012.

focal females as well (Fig. 6), ranging from 1.2 % to 57.3 % of energy intake. Mean daily contribution to energy intake from insects (14.61 % \pm 1.61) was far less than fruits (45.07 % \pm 3.09) and leaves (28.16 % \pm 2.22) (other or unidentified items contributed 12.96 % \pm 1.92 to mean daily energy intake). We found no significant differences across individual females in insect contribution to protein (Kruskal–Wallis $\chi^2 = 11.45$, $df = 13$, $P = 0.57$), energy (Kruskal–Wallis $\chi^2 = 12.58$, $df = 13$, $P = 0.48$), or insect dry matter intake (Kruskal–Wallis $\chi^2 = 14.21$, $df = 13$, $P = 0.36$).

Discussion

Protein and Energy Contributions of Insects

Despite redtail monkeys spending a small proportion of their feeding time on insects, weight-based estimates of food intake showed that insects contributed almost one-quarter of the mean daily protein intake of redtail females and 14 % to mean daily energy intake. Though these nutritional contributions from insects are far less than from plant parts, they demonstrate a substantial nutritional payoff for minimal feeding effort. Dry matter intake of insects across females was low (≤ 20 %) compared to dry matter intake of plant reproductive parts and leaves, arguably due to both insect small body size and the dominance of fruits and leaves in the redtail monkey diet. To our knowledge, this study is the first to examine the nutritional composition and contributions to daily intake of energy and protein by insects to the diet of a guenon. Although many of the insects eaten by redtail monkeys have not yet been identified, redtail monkeys appear to focus on solitary, rather than eusocial, insects, which may partially explain the modest protein and energy intake contributions of insects.

In addition to protein and energy gains in a short feeding time, insects may also provide monkeys with micronutrients. We did not measure micronutrients in this study, but redtail monkeys in Kibale eat caterpillars that are higher in copper, zinc, and iron than plant parts eaten, and the majority of foods eaten by monkeys at Kibale are deficient in copper and iron (Rode *et al.* 2003). Furthermore, copper and sodium intake

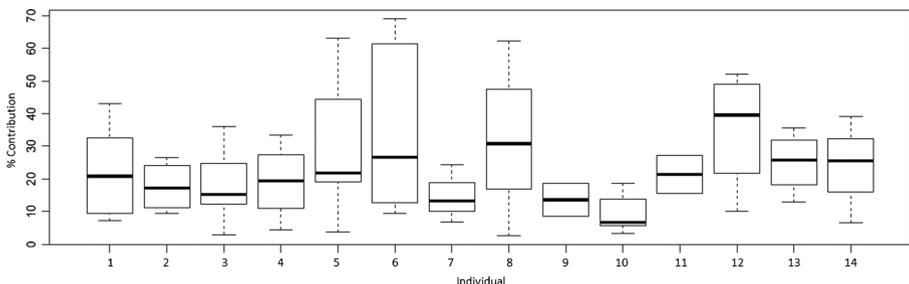


Fig. 5 Insect contribution to daily protein intake across 14 adult female redtail monkeys in one group in Kibale National Park, Uganda, July 2010–June 2012. For each female: the bold line represents the median daily protein contribution (%) from insects based on multiple full-day focal follows; the boxes above and below the bold line represent the upper and lower quartiles of daily protein contribution (%) from insects, respectively; and the top and bottom “whiskers” represent the maximum and minimum daily protein contribution (%) from insects, respectively.

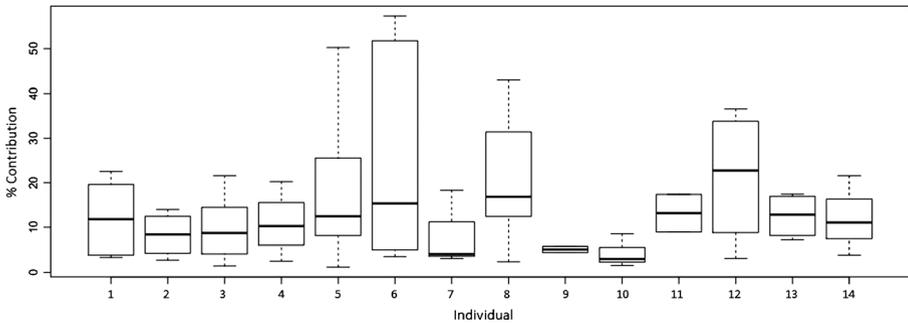


Fig. 6 Insect contribution to daily energy intake across 14 female redtail monkeys in one group in Kibale National Park, Uganda, July 2010–June 2012. For each female: the bold line represents the median daily energy contribution (%) from insects based on multiple full-day focal follows; the boxes above and below the bold line represent the upper and lower quartiles of daily energy contribution (%) from insects, respectively; and the top and bottom “whiskers” represent the maximum and minimum daily energy contribution (%) from insects, respectively.

correlate with redtail monkey density at Kibale, indicative of a fitness effect of mineral intake (Rode *et al.* 2006). Our finding that there is high variability across females in one group in nutritional contributions of insects may reflect underlying behavioral or nutritional mechanisms that have yet to be explored. For example, redtail monkeys may be switching diet items to avoid competition with conspecifics and other sympatric primate species or to avoid plant secondary compounds.

Nutritional Composition of Insects

In terms of nutritional composition, identified insects eaten by female redtail monkeys were higher in protein than fruits, leaves, or other items eaten. Though some fruits and leaves, including unripe fruits of *Celtis durandii* and leaf buds of *Celtis africana*, have high protein compared to other plant part foods, these plant parts are still substantially lower in protein than insects. Chitin content was low in cicadas, grasshoppers, and caterpillars (7.68–12.60 %) compared to other nutritional components of insects. Chitin is the structural carbohydrate in insects that comprises the exoskeleton in arthropods and is found in the mouth area in many invertebrates; it is largely indigestible to primates that do not have the specialized digestive enzyme chitinase (Bukkens 2005). That said, some omnivorous primates (Krykbaev *et al.* 2010; Paoletti *et al.* 2007), not just insectivores (Comelius *et al.* 1976), also have chitinase in their digestive systems. We do not currently know if the redtail digestive tract harbors chitinase, though the redtail monkey has a long retention time for a primate with such a simple stomach and unspecialized gut morphology (Lambert 2002). This extended retention time may indicate additional processing in the gut of more difficult to digest items in a diverse diet.

Fat content was low in cicadas and grasshoppers (7.01–10.49 %) compared to caterpillars (mean = 16.67 %). As caterpillars are butterfly or moth larvae, and larvae are known to have higher fat content than other developmental stages, we predicted this high fat content (Bukkens 2005; Nakagawa 2003). The plant portion of the redtail monkey diet is low in fat, with the exception of some ripe fruits like that of *Celtis durandii*; as <5 % of feeding records from full-day focal follows included ripe or unripe

fruits of *C. durandii*, the nutritional influence of these fruits on the redbtail monkey diet may be small. We predicted that caterpillar high fat content would translate into some insect morphs being an important source of fat, and therefore energy. In the context of ape insectivory, researchers have found that different eusocial insect castes have different nutritional compositions (Hladik 1977; O'Malley and Power 2012, 2014; Redford and Dorea 1984), complicating evaluation of the nutritional contribution of insects to the chimpanzee diet. For example, protein and lipid contents vary between *Macrotermes* alates and soldiers, castes that are both eaten by chimpanzees (Hladik 1977; O'Malley and Power 2012, 2014). Though redbtail monkeys do not appear to target eusocial insects, further insect prey identification is needed and such caste nutritional variation may be relevant.

The fact that <50 % of the eaten insects were identified points to the challenges and need for improved methods in quantifying insectivory in arboreal primates. Most primate insectivory nutrition studies have been conducted with species with more terrestrial locomotor patterns and/or in more open habitats and/or on eusocial insect prey (Isbell *et al.* 2013; O'Malley and Power 2014), making identification of insects consumed easier than in the case of arboreal guenons. Arboreal primate insectivory studies such as that of McCabe and Fedigan (2007) do not mention the percentage of insects identified, though we assume it cannot be 100 % given the habitat and arboreal study species.

A Note About Galls

The high ADF content found in the gall samples (mean = 26.90 %) most likely indicates that some or most of the leaf galls did *not* contain insects, either because the insects vacated the gall or because the gall was induced by fungi or bacteria. As a result, the high “chitin” content of the gall samples instead most likely reflects fiber. When insects induce leaf galls, they multiply and enlarge leaf cells, creating structures in which to place larvae or themselves (Shorthouse and Rohfritsch 1992); if the insect was absent in a gall sample, only leaf cells were analyzed, which, especially if the leaf was mature, could be especially high in fiber. Many primates eat leaf galls, picking them off leaves individually (Goodall 1986; McGrew 2014; Srivastava 1991; Tutin 1999); future studies can better address the nutritional contributions of this unique diet item.

Conclusions and Future Directions

Our study contributes to the improved understanding of the nutrition of primate insectivory, a portion of the primate diet that is understudied and crucial for creating complete diet and nutrition profiles for frugivorous–insectivorous primates. By developing a more complete picture of the nutritional ecology of redbtail monkeys, we form a basis for a better understanding of what underlies this guenon's reproduction and behavior. Future challenges include identifying more of the insects eaten by redbtail monkeys, analyzing them for macronutrients and micronutrients, as well as measuring insect abundance in the area to develop a more complete redbtail monkey insectivory profile. A better understanding of the developmental stages of different insects that

redtail monkeys eat will also be important to examining availability and spatiotemporal variation in nutritional composition. Identifying insect prey in feces through molecular methods (Bohmann *et al.* 2011; Pickett *et al.* 2012; Mallott *et al.* 2015) is also a powerful tool to complement behavioral observation methods of quantifying insectivory. Measuring variation in insectivorous feeding and nutritional contribution across multiple redtail monkey groups may allow us to gain insight into ecological, behavioral, and reproductive drivers of such variation.

Acknowledgments We thank the Uganda Wildlife Authority and the Uganda National Council for Science and Technology for permission to conduct this research. We are grateful to Hillary Musinguzi, Richard Mutegeki, Moses Musana, and Peter Irumba for their help with data collection. Thank you to Joanna Setchell and two anonymous reviewers for providing helpful comments to earlier versions of this manuscript. Thank you to Caley Johnson, Jenny Paltan, and Rebecca DelliCarpini for help with nutritional analyses, and Kristin Sabbi and Santiago Cassaletti for help with statistical analyses. Thank you to Thomas Struhsaker for his advice on observing redtail monkey insectivory. Thank you to Heikki Roininen for providing preliminary identification of some of the insects eaten by redtail monkeys. This research was funded by Hunter College of the City University of New York, The Wieland Fund for Field Anthropology to M. A. H. Bryer; NSF Grant 0922709 to J. M. Rothman, C. A. Chapman, and J. E. Lambert; and Gravida, the National Research Centre for Growth and Development, New Zealand to D. Raubenheimer.

References

- Altmann, S. A. (1998). *Foraging for survival: Yearling baboons in Africa*. Chicago: University of Chicago Press.
- Altmann, J., & Alberts, S. C. (2003). Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, 15(3), 401–409.
- AOAC. (1990). *Official methods of analysis*. Arlington, VA: Association of Official Analytical Chemists.
- Beeson, M., Tame, S., Keeming, E., & Lea, S. (1996). Food habits of guenons (*Cercopithecus* spp.) in Afro-montane forest. *African Journal of Ecology*, 34(2), 202–210.
- Bohmann, K., Monadjem, A., Noer, C. L., Rasmussen, M., Zeale, M. R., Clare, E., Jones, G., Willerslev, E., & Gilbert, M. T. P. (2011). Molecular diet analysis of two African free-tailed bats (Molossididae) using high throughput sequencing. *PLoS One*, 6(6), e21441.
- Bryer, M. A., Chapman, C. A., & Rothman, J. M. (2013). Diet and polyspecific associations affect spatial patterns among redtail monkeys (*Cercopithecus ascanius*). *Behaviour*, 150(3–4), 277–293.
- Bukkens, S. (2005). Insects in the human diet. In M. G. Paoletti (Ed.), *Ecological implications of minilivestock: Potential of insects, rodents, frogs and snails* (pp. 545–577). Enfield, NH: Science Publishers.
- Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-and low-density subpopulations. *Ecological Monographs*, 60(1), 1–26.
- Chapman, C. A., Chapman, L. J., Cords, M., Gathua, A., Gautier-Hion, A., Lambert, J. E., Rode, K., Tutin, C. E. G., & White, L. J. T. (2002). Variation in the diets of *Cercopithecus* species: differences within forests, among forests, and across species. In M. Glenn & M. Cords (Eds.), *The guenons: Diversity and adaptation in African monkeys* (pp. 325–350). New York: Academic/Plenum Publishers.
- Chapman, C. A., & Lambert, J. E. (2000). Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. *American Journal of Physical Anthropology*, 50, 169–185.
- Chapman, C. A., Struhsaker, T. T., Skorupa, J., Snaith, T. V., & Rothman, J. M. (2010). Understanding long-term primate community dynamics: Implications for forest change. *Ecological Applications*, 20, 179–191.
- Cipolletta, C., Spagnoletti, N., Todd, A., Robbins, M. M., Cohen, H., & Pacyna, S. (2007). Termite feeding by *Gorilla gorilla gorilla* at Bai Hokou, Central African Republic. *International Journal of Primatology*, 28(2), 457–476.
- 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.

- Conklin-Brittain, N. L., Dierenfeld, E. S., Wrangham, R. W., Norconk, M., & Silver, S. C. (1999). Chemical protein analysis: A comparison of Kjeldahl crude protein and total ninhydrin protein from wild, tropical vegetation. *Journal of Chemical Ecology*, 25(12), 2601–2622.
- Conklin-Brittain, N., Knott, C., & Wrangham, R. (2006). Energy intake by wild chimpanzees and orangutans: Methodological considerations and a preliminary comparison. In G. Hohman, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates* (pp. 441–471). Cambridge: Cambridge University Press.
- Cords, M. (1986). Interspecific and intraspecific variation in diet of two forest guenons, *Cercopithecus ascanius* and *C. mitis*. *Journal of Animal Ecology*, 55, 811–827.
- Cords, M. (1987). Mixed-species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. *University of California Publications in Zoology*, 117, 1–109.
- Cornelius, C., Dandriofosse, G., & Jeuniaux, C. (1976). Chintinolytic enzymes of the gastric mucosa of *Perodicticus potto* (Primate Prosimian): Purification and enzyme specificity. *International Journal of Biochemistry*, 7, 445–448.
- Dammhahn, M., & Kappeler, P. M. (2008). Comparative feeding ecology of sympatric *Microcebus berthae* and *M. murinus*. *International Journal of Primatology*, 29(6), 1567–1589.
- Deblauwe, I., & Janssens, G. P. (2008). New insights in insect prey choice by chimpanzees and gorillas in southeast Cameroon: The role of nutritional value. *American Journal of Physical Anthropology*, 135(1), 42–55.
- Emery Thompson, M., & Wrangham, R. W. (2008). Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *American Journal of Physical Anthropology*, 135(2), 171–181.
- Emery Thompson, M., Kahlenberg, S. M., Gilby, I. C., & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, 73(3), 501–512.
- Fashing, P. J., Nguyen, N., & Fashing, N. J. (2010). Behavior of geladas and other endemic wildlife during a desert locust outbreak at Guassa, Ethiopia: Ecological and conservation implications. *Primates*, 51(3), 193–197.
- Finke, M. D. (2007). Estimate of chitin in raw whole insects. *Zoo Biology*, 26, 105–115.
- 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, 293–305.
- Gathua, J. M. (2000). *Intraspecific variation in foraging patterns of redtail monkeys (Cercopithecus ascanius) in the Kakamega Forest, Kenya*. Ph.D. dissertation, Columbia University, New York.
- Gautier-Hion, A. (1980). Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *Journal of Animal Ecology*, 49, 237–269.
- Goering, H., & Van Soest, P. (1970). Forage fiber analysis. *United States Department of Agriculture Handbook* 79, 1–20.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University Press.
- Gursky, S. (2000). Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum*. *International Journal of Primatology*, 21(3), 477–495.
- Harcourt, C. (1986). Seasonal variation in the diet of South African galagos. *International Journal of Primatology*, 7(5), 491–506.
- Hladik, C. M. (1977). Chimpanzees of Gabon and chimpanzees of Gombe: Some comparative data on the diet. In *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys, and apes* (pp. 81–501). New York: Academic Press.
- Isbell, L. A. (1998). Diet for a small primate: Insectivory and gummivory in the (large) patas monkey (*Erythrocebus patas pyrrhonotus*). *American Journal of Primatology*, 45(4), 381–398.
- Isbell, L. A., Rothman, J. M., Young, P. J., & Rudolph, K. (2013). Nutritional benefits of *Crematogaster mimosae* ants and *Acacia drepanolobium* gum for patas monkeys and vervets in Laikipia, Kenya. *American Journal of Physical Anthropology*, 150(2), 286–300.
- Isbell, L. A., & Young, T. P. (2007). Interspecific and temporal variation of ant species within *Acacia drepanolobium* ant domatia, a staple food of patas monkeys (*Erythrocebus patas*) in Laikipia, Kenya. *American Journal of Primatology*, 69(12), 1387–1398.
- Krykbaev, R., Fitz, L. J., Reddy, P. S., Winkler, A., Xuan, D., Yang, X., Fleming, M., & Wolf, S. F. (2010). Evolutionary and biochemical differences between human and monkey acidic mammalian chitinases. *Gene*, 452(2), 63–71.

- Lambert, J. E. (2002). Digestive retention times in forest guenons (*Cercopithecus* spp.) with reference to chimpanzees (*Pan troglodytes*). *International Journal of Primatology*, 23(6), 1169–1185.
- Mallott, E. K., Malhi, R. S., & Garber, P. A. (2015). High-throughput sequencing of fecal DNA to identify insects consumed by wild Weddell's saddleback tamarins (*Saguinus weddelli*, Cebidae, Primates) in Bolivia. *American Journal of Physical Anthropology*, 156(3), 474–481.
- McCabe, G. M., & Fedigan, L. M. (2007). Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female *Cebus capucinus* at Santa Rosa, Costa Rica. *International Journal of Primatology*, 28(4), 837–851.
- McGrew, W. C. (2001). The other faunivory: primate insectivory and early human diet. In C. B. Stanford & H. T. Bunn (Eds.), *Meat-eating and human evolution* (pp. 160–178). Oxford: Oxford University Press.
- McGrew, W. C. (2014). The 'other faunivory' revisited: Insectivory in human and non-human primates and the evolution of human diet. *Journal of Human Evolution*, 71, 4–11.
- Nakagawa, N. (2003). Difference in food selection between patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*) in Kala Maloue National Park, Cameroon, in relation to nutrient content. *Primates*, 44(1), 3–11.
- National Research Council. (2001). *Nutrient requirements of dairy cattle*. Washington, DC: National Academies Press.
- National Research Council. (2003). *Nutrient requirements of nonhuman primates*. Washington, DC: National Academies Press.
- Nekaris, K., & Rasmussen, D. T. (2003). Diet and feeding behavior of Mysore slender lorises. *International Journal of Primatology*, 24(1), 33–46.
- Nishie, H. (2011). Natural history of Camponotus ant-fishing by the M group chimpanzees at the Mahale Mountains National Park, Tanzania. *Primates*, 52(4), 329–342.
- O'Malley, R. C., & Power, M. L. (2012). Nutritional composition of actual and potential insect prey for the Kasekela chimpanzees of Gombe National Park, Tanzania. *American Journal of Physical Anthropology*, 149(4), 493–503.
- O'Malley, R. C., & Power, M. L. (2014). The energetic and nutritional yields from insectivory for Kasekela chimpanzees. *Journal of Human Evolution*, 71, 46–58.
- Paoletti, M. G., Norberto, L., Damini, R., & Musumeci, S. (2007). Human gastric juice contains chitinase that can degrade chitin. *Annals of Nutrition and Metabolism*, 51, 244–251.
- Pickett, S. B., Bergery, C. M., & Di Fiore, A. (2012). A metagenomic study of primate insect diet diversity. *American Journal of Primatology*, 74(7), 622–631.
- Raubenheimer, D., & Rothman, J. M. (2013). Nutritional ecology of entomophagy in humans and other primates. *Annual Review of Entomology*, 58, 141–160.
- Redford, K. H., & Dorea, J. G. (1984). The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. *Journal of Zoology (London)*, 203, 385–395.
- Robbins, C. T. (1993). *Wildlife feeding and nutrition*. San Diego: Academic Press.
- Rode, K. D., Chapman, C. A., Chapman, L. J., & McDowell, L. R. (2003). Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. *International Journal of Primatology*, 24(3), 541–573.
- Rode, K. D., Chapman, C. A., McDowell, L. R., & Stickler, C. (2006). Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). *Biotropica*, 38, 625–634.
- Rothman, J. M., Chapman, C. A., Hansen, J. L., Cherney, D. J., & Pell, A. N. (2009). Rapid assessment of the nutritional value of foods eaten by mountain gorillas: Applying near-infrared reflectance spectroscopy to primatology. *International Journal of Primatology*, 30(5), 729–742.
- Rothman, J. M., Chapman, C. A., & Pell, A. N. (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, J. M., Chapman, C. A., & Van Soest, P. J. (2012). Methods in primate nutritional ecology: A user's guide. *International Journal of Primatology*, 33(3), 542–566.
- Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008b). Nutritional quality of gorilla diets: Consequences of age, sex and season. *Oecologia*, 155, 111–122.
- Rothman, J. M., Dierenfeld, E. S., Molina, D. O., Shaw, A. V., Hintz, H. F., & Pell, A. N. (2006). Nutritional chemistry of foods eaten by gorillas in Bwindi Impenetrable National Park, Uganda. *American Journal of Primatology*, 68(7), 675–691.
- Rothman, J. M., Raubenheimer, D., Bryer, M. A. H., Takahashi, M., & Gilbert, C. C. (2014). Nutritional contributions of insects to primate diets: Implications for primate evolution. *Journal of Human Evolution*, 71, 59–69.

- Rudran, R. (1978). Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanii*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology*, 249, 1–83.
- Shorthouse, J. D., & Rohfritsch, O. (1992). *Biology of insect-induced galls*. Oxford: Oxford University Press.
- Srivastava, A. (1991). Insectivory and its significance to langur diets. *Primates*, 32(2), 237–241.
- Stampone, M. D., Hartter, J., Chapman, C. A., & Ryan, S. J. (2011). Trends and variability in localized precipitation around Kibale National Park, Uganda, Africa. *Research Journal of Environmental and Earth Sciences*, 3(1), 14–23.
- Stevenson, P. R., Quiñones, M. J., & Ahumada, J. A. (2000). Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. *Biotropica*, 32(3), 533–544.
- Stone, A. I. (2007). Responses of squirrel monkeys to seasonal changes in food availability in an eastern Amazonian forest. *American Journal of Primatology*, 69(2), 142–157.
- Struhsaker, T. T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In D. J. Chivers & J. Herbert (Eds.), *Recent advances in primatology* (Behaviour, Vol. 1, pp. 225–247). London: Academic Press.
- Struhsaker, T. T. (1980). Comparison of the behaviour and ecology of red colobus and redtail monkeys in the Kibale Forest, Uganda. *African Journal of Ecology*, 18(1), 33–51.
- Tashiro, Y. (2006). Frequent insectivory by two guenons (*Cercopithecus lhoesti* and *Cercopithecus mitis*) in the Kalinzu Forest, Uganda. *Primates*, 47(2), 170–173.
- Tutin, C. E. (1999). Fragmented living: Behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates*, 40(1), 249–265.
- Tutin, C. E., Ham, R. M., White, L. J., & Harrison, M. J. (1997). The primate community of the Lopé Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology*, 42(1), 1–24.
- Van Soest, P., Robertson, J., & Lewis, B. (1991). Methods for dietary fiber, neutral detergent fiber, and non-starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science*, 74, 3583–3597.
- Veiga, L. M., & Ferrari, S. F. (2006). Predation of arthropods by southern bearded sakis (*Chiropotes satanas*) in eastern Brazilian Amazonia. *American Journal of Primatology*, 68(2), 209–215.
- Webster, T. H., McGrew, W. C., Marchant, L. F., Payne, C. L., & Hunt, K. D. (2014). Selective insectivory at Toro-Semliki, Uganda: Comparative analyses suggest no ‘savanna’ chimpanzee pattern. *Journal of Human Evolution*, 71, 20–27.