

Why eat flowers? *Symphonia globulifera* flowers provide a fatty resource for red-tailed monkeys

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Abstract – Flowers are ubiquitous in primate environments, yet their nutritional advantages are underexamined. *Symphonia globulifera* is a widely distributed tree exploited by a variety of animals in Africa and the Americas. We collected *S. globulifera* flower samples consumed by red-tailed monkeys (*Cercopithecus ascanius*) and compared them nutritionally to flower samples from other plant species in Kibale National Park, Uganda. Flowers were assayed for three fiber fractions (NDF, ADF, lignin), fat, crude protein, acid detergent insoluble nitrogen (ADIN), ash, and soluble sugars. We estimated available protein, total nonstructural carbohydrates (TNC), and metabolizable energy (ME). We calculated the mean and standard deviation for all nutrient categories and applied nutritional geometry to illustrate the balance among the energetic gains from available protein, fat, fiber, and TNC across flower species. Our results suggest that *S. globulifera* flowers provide an unusually high fat resource (14.82% ± 1.41%) relative to other flowers (1.38% ± 5.79%) and other foods exploited in the same habitat.

Keywords – florivory, metabolizable energy, nutritional ecology, nutritional geometry, *Symphonia globulifera*.

Introduction

Florivory occurs ubiquitously among primates, having been documented in 165 primate species, yet comprises less than 10% of the annual food intake in most taxa (Heymann, 2011) contributing to why its nutritional benefits are poorly understood. Coevolutionary interactions between flowering plants and primates

contributed to the adaptive radiation of primates (Sussman, 1991) and are facilitated by their high frequencies of arboreal locomotion (Heymann, 2011). Indeed, it has been proposed that protein acquisition via red leaves in Afro-Eurasian primates and red figs in Central and South American primates was a driving feature in the evolution of trichromatic vision (Valenta and Melin, 2012). Food resource (hereafter

resource) selection models have been applied to investigate why primates select certain foods for consumption and are primarily based on acquiring certain nutrients while minimizing others (see Felton et al., 2009). Animal foraging is often adjusted to meet specific nutritional goals based on fluctuating nutritional needs in tandem with food nutrient content and food availability (Lambert and Rothman, 2015). Liebig's *Law of the Minimum* posits growth is determined by the scarcest resource even when other essential nutrients are abundant, known as limiting factors (Salisbury, 1991). Specific macronutrients are known to be limiting factors in environments depending on the nutritional variability of that environment; for example, protein has been shown to be a limiting factor for frugivorous primates (Ganzhorn et al., 2009). Detecting nutritionally limiting factors can reveal mechanisms of resource limitation and has implications for primate conservation and health (Hanya and Chapman, 2013). Evaluating macronutrient balance in foods helps characterize specific constraints influencing food selectivity.

Symphonia globulifera (Clusiaceae) is a medium to tall sized (~30 m) evergreen tree and aerial roots associated with wetter environments (Bittrich and Amaral, 1996; Dick et al., 2003). *S. globulifera* is used by people to treat a variety of medical conditions (reviewed in Fromentin et al., 2015) including coughs, fever, jaundice, and intestinal parasites in Uganda (Ssegawa and Kasenene, 2007); scabies in Gabon (Akendengué and Louis, 1994); parasites in Cameroon (Lenta et al., 2007); skin disease, diabetes, and malaria in Nigeria (Ajibesin et al., 2008); body pain and skin conditions in Panama (Gupta et al., 2005); and is ranked among the most important medicinal plants by indigenous peoples of Brazil (Prance et al., 1987). The root bark displays strong antiparasitic properties that may aid in the development of new antimalarial drugs (Marti et al., 2010). The ethnopharmacological significance of *S. globulifera* has been substantiated by the phytochemical identification of various secondary metabolites validating its antiparasitic and antimicrobial uses (Fromentin et al., 2015).

Monkeys are attracted to flowering *S. globulifera* by its vibrant red floral displays (Gautier-Hion et al., 1985). Madagascar is the geographic origin of the genus and the island is home to 16 endemic *Symphonia* species (Germeraad et al., 1968). However, only *S. globulifera* is found outside of Madagascar, with a wide distribution throughout tropical Africa and the neotropics (Bittrich and Amaral, 1996; Dick et al., 2003). Flower morphology and physiology are consistent with a "bird pollination syndrome" in that trees exhibit diurnal flowering, produce relatively large quantities of dilute nectar, are odorless, and pollinated primarily by hummingbirds (Bittrich and Amaral, 1996) and perching birds (Gill Jr et al., 1998). Axillary inflorescences contain between 1-17 flowers, with 1-3 flowers at anthesis at a time (Gill Jr et al., 1998). Flowers stay fully open for one day and petals begin to wither thereafter. A large tree generates between 100 to 200 new blooms every day during peak flowering (Bittrich and Amaral, 1996). Previous nutritional analyses of *S. globulifera* have found that flowers and nectar are high in hexose sugars (i.e., glucose plus fructose) (Gill Jr et al., 1998), thus offering a plentiful albeit patchy high-energy resource when seasonally available (Porter, 2001).

Plant foragers can positively or negatively influence plant reproductive success through florivory (Chapman et al., 2013). Frugivorous-faunivorous primates often consume nectar and other flower parts more frequently than whole flowers (Heymann, 2011). Several neotropical primate species have been documented feeding specifically on the nectar of *S. globulifera* including spider monkeys (*Ateles geoffroyi*) (Riba-Hernández and Stoner, 2005), brown capuchins (*Cebus apella*), woolly monkeys (*Lagothrix lagotricha*) (Peres, 1994), tamarins (*Saguinus fuscicollis*, *Saguinus mystax*) (Garber, 1988), and squirrel monkeys (*Saimiri sciureus*) (Lima and Ferrari, 2003). *S. globulifera* flowers and nectar are also consumed by red-tailed monkeys (*Cercopithecus ascanius*) (Struhsaker, 2017; Bryer, 2020), red colobus (*Piliocolobus badius*) (Dominy and Lucas, 2001), grey-cheeked mangabeys (*Lophocebus albigena*) (Rothman, unpubl. data), and blue

monkeys (*Cercopithecus mitis*) (Kaplin et al., 1998; Bryer, 2020) in East Africa.

Exploring the nutritive advantages of flowers and their parts (buds, stalks, nectar, oil) offers insight into the nutritional choices made by primates. Our study examines the benefits of florivory by addressing the following questions: what is the nutritional significance of *S. globulifera* flowers in the diet of primates, and how does the nutrient composition of this flower compare to other flowers and major food categories?

Material and methods

STUDY SITE AND SPECIES

This study was conducted at the Kanyawara site, in Kibale National Park, western Uganda (0°13-0°41N and 30°19-30°32E), a 795 km² mid-altitude (1500 m) evergreen forest, with bimodal rains and high interannual rainfall variability (Chapman et al., 2018). Red-tailed monkeys (*C. ascanius*) are common at this site, with a mean group size of 19.18-23.30 and primarily occupy old-growth forests and areas experiencing mild anthropogenic disturbance (i.e., lightly logged), with their abundance decreasing in heavily logged areas (Chapman et al., 2021). *S. globulifera* flowers (N = 63) were collected from May-July, 2017 coinciding with the dry period of longest duration annually.

OBSERVATIONAL DATA

MAHB and three field assistants estimated nutritional intake of adult female redtail monkeys (Bryer, 2020) by conducting continuous focal follows (aiming for full-day focal follows from 7:00 to 19:00) of adult females in three groups (N = 8 focal females per group) from May 2015 to January 2017 (20 months). Feeding was defined as beginning with ingestion of a food item into the mouth and ending when the female stopped chewing and switched to another activity. Plant species and part were recorded along with a count of the number of items eaten.

Plant collection and handling

We collected whole, freshly fallen flowers of *S. globulifera* (N = 63 samples; N = 7 trees) from the base of focal trees in spring 2017 (fig. 1). We placed flowers into inert plastic bags and immediately transported them to the field station for desiccation using methods described in Rothman et al. (2012). Each individual sample comprised multiple flowers weighing 20 g dry weight, each from a single focal tree.

Additionally, *S. globulifera* flower part samples (N = 1 flower; N = 1 flower stalk) and samples (N = 36) from twelve other flower species consumed by red-tailed monkeys in 2015-2017 were collected by MAHB and a field team; these included: *Erythrina abyssinica*, *Funtumia africana*, *Hoslundia opposita*, *Lantana camara*, *Maesa lanceolata*, *Millettia dura*, *Piper capense*, *Psychotria* sp., *Randia* sp., *Strychnos mitis*, *Tabernaemontana pachysiphon*, and *Urera cameroonensis* (see Bryer 2020 for details). Samples were dried in the field. Dried samples were ground in a Wiley Mill with 1 mm screen (Thomas Scientific) and then exported to Hunter College of the City University of New York's Nutritional Ecology Laboratory where a portion of the field dried samples were re-dried at 105°C to calculate % dry matter.

CHEMICAL ANALYSES, NUTRIENT CALCULATIONS, AND STATISTICAL ANALYSIS

Flower samples were analyzed for crude fat by boiling samples in petroleum ether at 90°C for 120 min in an XT15 Fat Analyzer (ANKOM, Macedon, NY, USA). We conducted sequential fiber analyses through neutral detergent fiber (NDF) with α -amylase and acid detergent fiber (ADF) using an A200 fiber analyzer (ANKOM, Macedon, NY, USA) and 72% sulfuric acid treatment for lignin (ADL) (Van Soest, 1963; Goering and Van Soest, 1970; Van Soest et al., 1991). Total nitrogen (N) was estimated via combustion (AOAC, 1995) using a Leco TruSpec (Leco, St. Joseph, MI, USA) and crude protein (CP) was calculated by multiplying nitrogen by 6.25 (Maynard and Loosli, 1969; Robbins, 1993). We analyzed available protein through subtraction of [Acid Detergent



Figure 1. Floral display of *Symphonia globulifera*.

Insoluble Nitrogen (ADIN)*6.25] from crude protein values (Licitra et al., 1996; Rothman et al., 2008). Ash was measured by burning the sample in a muffle furnace at 550°C. Simple sugars were analyzed with the phenol-sulfuric acid assay (Dubois et al., 1956; Hall et al., 1999) with a sucrose standard. Total nonstructural carbohydrates (TNC) were estimated as:

$$\text{TNC} = 100 - ((\text{Fat} - 1) + \text{AP} + \text{Ash} + \text{NDF}).$$

Metabolizable energy (ME) for intake from plants was estimated following Conklin and Wrangham (1994); (Conklin-Brittain et al., 2006; Rothman et al., 2012) as:

$$\begin{aligned} \text{Energy(kcal)} &= [(\text{NDF intake} \times 3) \\ &\quad \times \text{NDF digestion coefficient}] \\ &\quad + (\text{AP intake} \times 4) \\ &\quad + ((\text{Fat intake} - 1) \times 9) \\ &\quad + (\text{TNC intake} \times 4). \end{aligned}$$

ME for intake from insects was estimated as:

$$(\text{AP intake} \times 4) + ((\text{Fat intake} - 1) \times 9)$$

$$+ (\text{TNC intake} \times 4).$$

ME for plant composition was estimated as:

$$\begin{aligned} &\text{NDF composition} \times 3 \\ &\text{AP composition} \times 4 \\ &(\text{Fat composition} - 1) \times 9 \\ &\text{TNC composition} \times 4. \end{aligned}$$

ME for insect composition was estimated as:

$$\begin{aligned} &\text{AP composition} \times 4 \\ &(\text{Fat composition} - 1) \times 9 \\ &\text{TNC composition} \times 4. \end{aligned}$$

Results are presented on a dry matter basis to control for the effect of variable water content. We calculated the mean and standard deviation for each nutrient category across all 64 samples.

THE RIGHT-ANGLED MIXTURE TRIANGLE

Right-angled mixture triangles (RMTs) are two-dimensional representations of three-component mixtures (e.g., individual foods, observed diets) that provide a proportions-based approach rooted in nutritional geometry shown

to be highly effective in illustrating field-based research (Raubenheimer, 2011; Raubenheimer et al., 2015). For example, three components in the standard two-dimensional Euclidean plot are represented by the X , Y , and Z axes, where Z is the implicit axis ($= 100\% - y\text{-value} - x\text{-value}$), consequently causing the focal axes (X and Y) to be constrained along the line intersecting the point ($100 - Z\%$) on each axis (Raubenheimer, 2011). In our case, these mixtures are identified as the macronutrient composition multiplied by Atwater factors to show the energy value of *S. globulifera* compared to other resources expressed as the three-term-ratios:

$$\% \text{ Available Protein: } \% \text{ Fat: } \% \text{ NDF}$$

$$\% \text{ Available Protein: } \% \text{ TNC} + \text{ Fat: } \% \text{ NDF.}$$

Results

Fat composition was highest in *S. globulifera* flowers and flower stalks in comparison to flowers, flower stalks, and flower buds from all twelve other plant species consumed by red-tailed monkeys (table 1). Flowers of any species accounted for 5.0% of daily kcal intake and represent 3.6% of the time spent feeding over the 20 months and two flowering events, which demonstrates flowers are a relatively rare though potentially energetically valuable resource (fig. 2).

Right-angled mixture triangles indicate that *S. globulifera* flower nutritional composition is uniquely high in fat content compared to samples ($N = 36$) from the other flower species consumed by red-tailed monkeys (fig. 3) and other principal resources (ripe fruit $N = 89$; unripe fruit $N = 104$; insects $N = 6$; young leaves $N = 308$) that are low fat (fig. 4). A minority of fruit parts consumed by red-tailed monkeys contain more fat than *S. globulifera* flowers: these species of fruits include *Celtis gompophylla* (referred to in previous literature as *Celtis durandii*) ripe fruit and unripe fruit, which is known to be a fatty fruit species in primate diets in Kibale (Worman and Chapman, 2005); *Erythrococca* sp. ripe fruit; *Macaranga* sp. seeds of ripe fruit; *Lindackeria* sp. seeds of ripe fruit; and *Maesa lanceolata* unripe fruit. The sum of TNC + fat is more dispersed along

the y -axis with less distinction between *S. globulifera* and other flower species (fig. 5) than when fat is considered independently (fig. 3). The flower portion of the plant is unique in this fat content, as indicated by the lower fat content of the *S. globulifera* flower stalks compared to flowers (table 1). Collectively, our results suggest *S. globulifera* is an infrequently exploited resource yet provides an unusually high source of fat and thus energetic payoff.

Discussion

We determined the macronutrient concentrations of *S. globulifera*, a resource exploited irregularly by red-tailed monkeys (fig. 2) and found these flowers had a high fat composition compared to all other flower species (fig. 3). The high fat content resembled some insects (specifically caterpillars) and was heavily clustered in high fat compared to other food categories with more variable fat content (e.g., ripe, and unripe fruit) (fig. 4). We found *S. globulifera* was lower in sugars than expected (fig. 5, table 1) in contrast to high hexoses reported by Gill Jr et al. (1998). This suggests that primates could be targeting *S. globulifera* more for its fat content opposed to TNC or other nutrient combinations. Fat serves as an available energy store for primates (Thompson, 2013), with the caloric value of high fat foods surpassing that of protein, carbohydrates, and energetic returns from fiber (NRC, 2003). Flowers were exploited less often than other food categories (fig. 2) yet provided more energy in the form of fat than anticipated for an intermittent resource. Fatty acids are composed of long-chain hydrocarbons acting as essential dietary components for primates since no biochemical pathways produce these molecules (White, 2009). Essential fatty acids prevent and mitigate common diseases, notably coronary heart disease, and aid in critical cellular functions by serving as the structural components in the phospholipid membranes of tissues, particularly the brain and eyes (Connor, 2000).

Fruits can contain higher lipid content than other plant tissues and have been shown to provide the majority of essential fatty acids intake (44.8%). The diet of red-tailed monkeys is low

Table 1. Macronutrient concentrations in flower parts consumed by red-tailed monkeys in Kibale National Park, Uganda.

Plant Species	Plant Part [†]	Mean \pm SD*								
		NDF	ADF	Lignin	Fat	Crude Protein	AP	Ash	TNC	Soluble sugars
<i>Symphonia globulifera</i> (N = 64)	FL	50.31 ± 6.95	44.12 ± 6.97	27.87 ± 5.62	14.82 ± 1.42	8.81 ± 0.79	1.44 ± 0.58	4.06 ± 1.91	22.07 ± 8.86	7.00 ± 3.29
<i>Symphonia globulifera</i> (N = 1)	FLS	52.44	46.06	31.30	9.65	8.57	0.90	4.72	33.29	n/a
<i>Erythrina abyssinica</i> (N = 1)	FL	49.31	36.06	20.46	2.99	32.15	25.32	10.11	13.26	n/a
<i>Funtumia africana</i> (N = 1)	FL	26.51	20.26	8.80	5.33	11.44	4.38	7.27	57.50	15.62
<i>Hoslundia opposita</i> (N = 3)	FL	43.16 ± 4.44	32.09 ± 5.18	17.36 ± 4.06	4.51 ± 1.20	20.61 ± 1.78	11.07 ± 2.77	10.78 ± 1.23	31.48 ± 1.36	6.40 [‡]
<i>Lantana camara</i> (N = 9)	FL	41.44 ± 7.74	31.76 ± 6.13	19.05 ± 5.52	2.78 ± 0.38	16.05 ± 1.64	8.58 ± 1.67	9.45 ± 1.51	38.75 ± 7.49	17.60 [‡]
<i>Maesa lanceolata</i> (N = 1)	FL	41.20	33.58	19.30	5.44	15.70	10.44	7.54	36.38	n/a
<i>Millettia dura</i> (N = 2)	FL	43.22 ± 0.31	29.94 ± 3.31	11.00 ± 1.06	2.09 ± 0.25	31.41 ± 4.92	27.02 ± 4.26	10.61 ± 0.51	18.22 ± 3.80	n/a
<i>Millettia dura</i> (N = 1)	FB	21.83	13.76	1.57	2.43	48.50	46.20	8.14	22.40	n/a
<i>Piper capense</i> (N = 7)	FL	32.26 ± 11.73	21.30 ± 3.63	9.91 ± 4.30	3.67 ± 0.97	27.09 ± 3.77	23.85 ± 4.72	17.48 ± 10.95	23.73 ± 10.21	4.65 [‡]
<i>Psychotria</i> sp. (N = 1)	FL	46.86	38.30	25.21	1.76	20.15	11.58	10.85	29.96	4.32
<i>Randia</i> sp. (N = 1)	FL	30.78	22.97	7.27	4.30	26.82	21.19	12.06	32.67	n/a
<i>Randia</i> sp. (N = 1)	FB	35.31	30.78	19.86	2.41	30.91	22.76	8.70	31.82	6.86
<i>Strychnos mitis</i> (N = 1)	FL	35.56	22.36	12.25	1.38	14.34	10.55	9.42	44.09	n/a
<i>Tabernaemontana pachysiphon</i> (N = 1)	FL	26.16	20.25	4.59	5.79	20.02	17.96	7.58	43.51	8.52
<i>Tabernaemontana pachysiphon</i> (N = 4)	FLS	35.19 ± 5.10	27.26 ± 3.60	9.05 ± 3.03	6.21 ± 0.79	21.12 ± 2.23	17.37 ± 1.20	10.72 ± 2.14	31.51 ± 7.83	n/a
<i>Urera cameroonensis</i> (N = 2)	FL	54.73 ± 1.12	44.30 ± 2.68	32.53 ± 0.90	2.01 ± 0.44	25.32 ± 3.65	14.49 ± 0.51	13.87 ± 3.49	15.90 ± 1.43	2.86 [‡]

NDF = neutral detergent fiber; ADF = acid detergent fiber; AP = available protein; TNC = total nonstructural carbohydrates.

*Reported as % dry mass.

[†] Flowers were classified by their parts: flower buds (FB), flowers (FL), and flower stalks (FLS).

[‡] N = 1 for soluble sugars only.

in fat, with the average daily fat intake 10% of metabolizable energy, though daily intake of fat varies widely (Bryer, 2020). Red-tailed monkeys obtain the most fat from resources such as *Celtis gomphophylla* unripe and ripe

fruit, and some insects (Bryer, 2020). Sympatric grey-cheeked mangabeys were observed feeding on *S. globulifera* flowers on one day out of >100 full day follows, likely indicating this species does not serve any sustainable

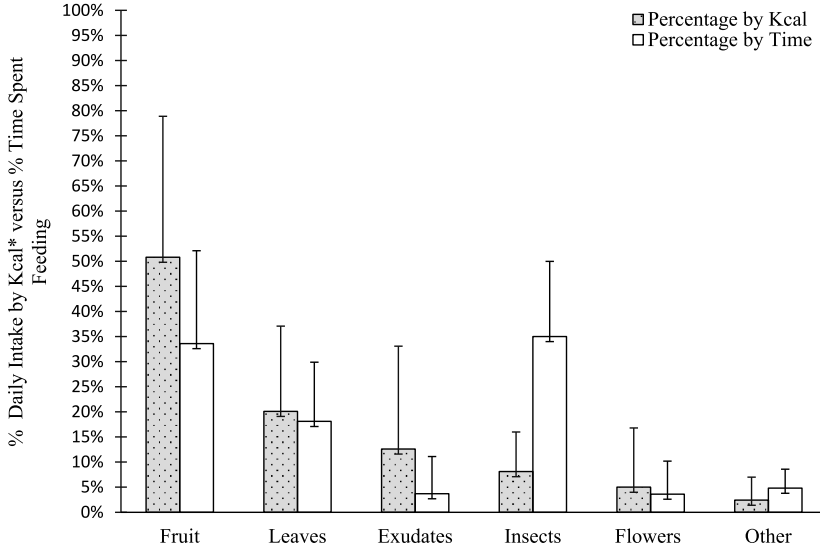


Figure 2. Mean daily resource intake by food category across three red-tailed monkey groups in Kibale National Park, Uganda. *Kcal = kilocalories. Error bars represent standard deviation.

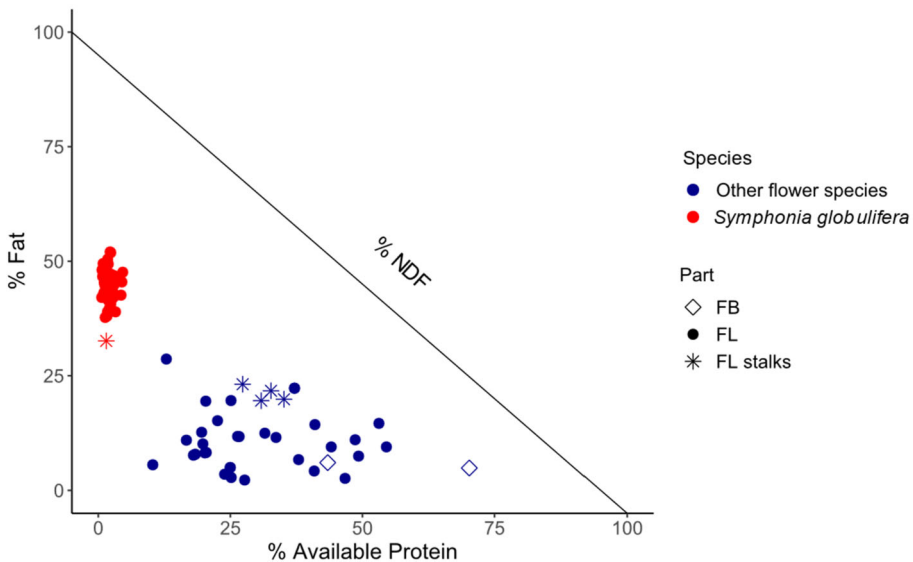


Figure 3. Right-angled mixture triangle representing the macronutrient composition (as ME) of *Symphonia globulifera* flowers expressed as % available protein, % fat, % NDF relative to other flower species consumed by red-tailed monkeys in Kibale National Park, Uganda. ME = metabolizable energy; NDF = neutral detergent fiber. Flowers were classified by their parts: flower buds (FB), flowers (FL), and flower stalks (FL stalks).

nutritional importance in their diet (Rothman, unpubl. data).

The anthers of *S. globulifera* flowers contain a unique oily fluid originating from the tapetum composed exclusively of an unsaturated fatty acid, ester methyl nervonate (15-Tetracosenoic

acid methyl ester), in which pollen grains are suspended (Bittrich et al., 2013). The presence of methyl nervonate as a naturally occurring plant substance is highly unusual, with identification occurring only in several other species and its chemical properties unknown

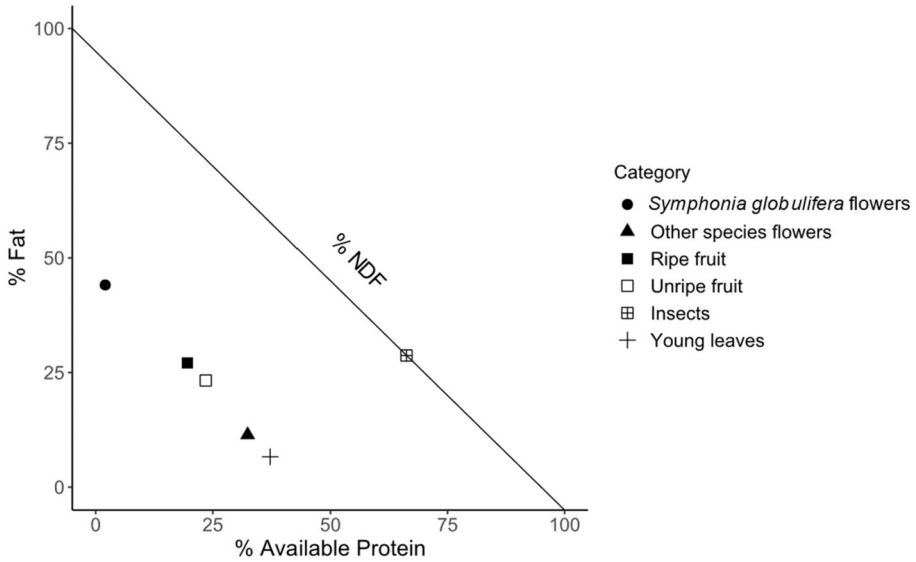


Figure 4. Right-angled mixture triangle representing the macronutrient composition (as ME) of *Symphonia globulifera* flowers expressed as % available protein, % fat, % NDF relative to mean values of other major food types consumed by red-tailed monkeys in Kibale National Park, Uganda. ME = metabolizable energy; NDF = neutral detergent fiber.

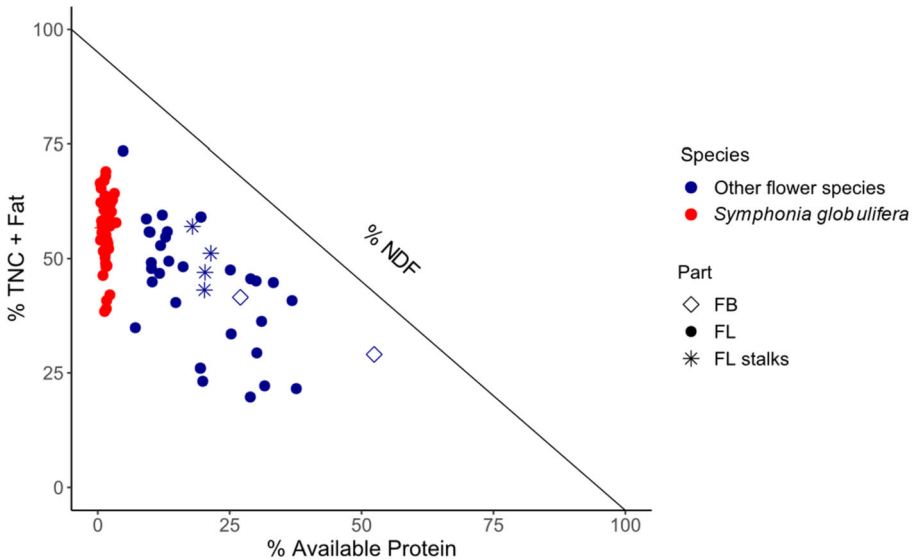


Figure 5. Right-angled mixture triangle representing the macronutrient composition (as ME) of *Symphonia globulifera* flowers expressed as % available protein, % TNC + fat, % NDF relative to other flower species consumed by red-tailed monkeys in Kibale National Park, Uganda. The species of flower with higher TNC + fat proportion than the highest TNC + fat *Symphonia globulifera* is *Funtumia africana* (this is driven by TNC). ME = metabolizable energy; TNC = total nonstructural carbohydrates; NDF = neutral detergent fiber. Flowers were classified by their parts: flower buds (FB), flowers (FL), and flower stalks (FL stalks).



Figure 6. Red-tailed monkeys exploiting *Symphonia globulifera* in Kibale National Park, Uganda.

(see Bittrich et al., 2013). The quantity of nectar secreted by a single flower under normal conditions averages $775 \mu\text{l}$ during one day (Bittrich and Amaral, 1996). Though the oil is adapted to carry pollen grain, this oil-pollen mixture does not attract pollinators, such as bees or birds for reasons that remain unclear (Bittrich et al., 2013). *C. ascanius* consume flower anthers in general, which comprise up to 2.3% of their diet (Struhsaker, 2017) and engage in the behaviour of drinking and licking the inside of the flower while holding the flower cupped in their hands, followed by discarding/dropping the flower that may indicate *S. globulifera* anther oil exploitation as well as nectar consumption (Bryer, 2020), yet its dietary importance is unknown. Female red-tailed monkeys spent 1.55-7.65% of their daily feeding time exploiting *S. globulifera* liquid (nectar and/or anther oil) exclusively, which contributed 0.11-1.08% of daily dry matter intake (Bryer, 2020). If *C. ascanius* were consuming *S. globulifera* anther oil, and not nectar, it contributed based on the assumption of majority fat content and minority pollen content, an average of 18% daily fat intake during only 4% daily feeding time (Bryer, 2020). These distinctions may indicate differences in

the nutritive benefits derived from liquid versus the flower.

The exploitation of fatty *S. globulifera* flowers by monkeys likely represents the interruption of a pollination mutualism with birds. Several studies have shown that birds, in preparation for migration, preferentially accumulate different macronutrient reserves, namely adipose fat, in some cases increasing their fat reserves by 50% in preparation for migration (Pierce and McWilliams, 2005). Because the timing of annual flowering of *S. globulifera* in Kibale (Valenta, unpubl. data) coincides with the spring migration (late April through early June) (Saino et al., 2007), and floral morphology and tree focal observations indicate the importance of birds as pollinators (Valenta, unpub. data; Bittrich and Amaral, 1996), it is likely that the high fat content in *S. globulifera* flowers represents a nutritious reward for birds in exchange for pollination services. While the vibrant pink, red, and yellow floral displays of *S. globulifera* likely evolved to signal nutrient availability to avian mutualists; catarrhine primates, possess trichromatic color vision – thus, these floral displays would appear as vibrantly to Afro-Eurasian monkeys as they appear to humans (Jacobs and Deegan, 1999) (fig. 6). It

may be that catarrhine primates are consuming fat-rich flowers, without in turn providing beneficial pollination services.

In sum, *S. globulifera* is a high-fat resource exploited by red-tailed monkeys in an otherwise fat scarce diet. This is noteworthy since flowers are not characteristically considered a substantial fat resource for primates and highlights the potential nutritional importance of florivory as an intrinsic foraging strategy.

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Statement of ethics

This study protocol was reviewed and approved by the Uganda Wildlife Authority and the Uganda National Council for Science and Technology.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Author contributions

ACR wrote the manuscript and assisted with analysis. MAHB contributed data, assisted with

analysis, and writing of the manuscript. JMR conducted assays and contributed reagents and materials. CAC, JMR, ON, and KV contributed to project design, data collection, and write-up.

Data availability statement

Resource intake data supporting fig. 2 and macronutrient content of flower species supporting figs 3-5 and table 1 are publicly available in MAHB's dissertation. Raw data available on request.

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