

The challenge of interpreting primate diets: mangabey foraging on *Blighia unijugata* fruit in relation to changing nutrient content

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Abstract

Primates often make foraging selections that are not apparent. For example, they may eagerly consume a particular plant part and species in some instances, but reject it at other times. *Blighia unijugata* (Baker) fruit is one of the most frequently eaten foods of mangabeys (*Lophocebus albigena*) in Lwamunda Forest Reserve, Uganda; however, its use varies strikingly depending on the fruit's developmental stage. We conducted feeding observations to investigate the nutritional criteria that mangabeys may have used for the consumption of specific fruit parts by conducting analysis of fruit parts eaten and rejected at different developmental stages. When seeds had low condensed tannins, mangabeys ate them, but seeds were rejected when tannin levels increased. In the first five stages of fruit development, tannin levels in arils declined and the frequency of consumption of the aril increased. Although fat content in seeds increased with maturity, it did not appear to influence seed consumption, but fat content was related to frequency of consumption of the aril. Considering that primates are often making food selections among many species/part combinations, our results illustrate the value of using nutritional analyses to understand foraging decisions. Furthermore, they demonstrate how very specific trade-offs between consumption of critical nutrients and antifeedants can drive which foods and parts are eaten.

Key words: diet choice, food selection, forest restoration, macronutrients, nutritional ecology, tannins

Résumé

Les primates font souvent des choix alimentaires qui ne sont pas apparents. Par exemple, ils peuvent consommer avidement une partie particulière d'une plante à un certain moment et la rejeter à d'autres. Le fruit de *Blighia unijugata* (Baker) est un des aliments le plus souvent consommés par les mangabeys (*Lophocebus albigena*) dans la Réserve forestière de Lwamunda, en Ouganda. Cependant, sa consommation varie fortement selon le stade de développement des fruits. Nous avons observé les mangabeys en train de manger pour chercher les critères nutritionnels que ces singes pourraient utiliser pour l'ingestion de parties spécifiques des fruits en réalisant une analyse des parties de fruits consommées et rejetées à différents stades de développement. Lorsque les graines avaient une faible concentration en tanins, les mangabeys les mangeaient, mais ils les rejetaient lorsque le taux de tanins augmentait. Au cours des cinq premiers stades de développement des fruits, le taux de tanins dans les sarcotests diminuait et la fréquence de leur consommation augmentait, mais le contenu en graisse était lié à la fréquence de la consommation de sarcotests. Vu que les primates sélectionnent souvent leur nourriture parmi de nombreuses combinaisons d'espèces et de parties de fruits, nos résultats montrent qu'il est important de faire des analyses nutritionnelles pour bien comprendre les décisions en matière d'alimentation. De plus, ils illustrent comment des compromis très spécifiques entre consommation de nutriments critiques et éléments anti-appétence peuvent déterminer quelles nourritures et quelles parties sont consommées.

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Introduction

Tropical frugivores and folivores are often described to make unusual food choices. For example, gorillas (*Gorilla beringei*) eat rotten wood (Rothman, van Soest & Pell, 2006; Harcourt & Stewart, 2007), elephants (*Loxodonta africana*) eat soil from termite mounds (Ruggiero & Fay, 1994; Holdo & McDowell, 2004; Rode *et al.*, 2006b), red colobus (*Procolobus rufomitratus*) eat the very fibrous last centimeter of the petioles on *Markhamia lutea* (K. Schum.) leaves (Baranga, 1983; Rode *et al.*, 2003; Ryan, Chapman & Rothman, 2012), and the frugivore community in one African forest eats the fruits of *Celtis durandii* (Engl.) only during a very small time period, even though they are available over longer periods (Worman & Chapman, 2005). However, upon careful evaluation, nutritional explanations for unusual foraging behavior often become apparent – gorillas, elephant, and red colobus are selecting foods high in sodium and the frugivores that eat *C. durandii* cue in on changes in fruit fat content that are not apparent by assessing fruit color, size, or morphology.

Considering that many tropical frugivores and folivores are making selections from hundreds of plant species and thus thousands of species/part combinations, understanding the dietary choices of tropical animals is challenging. For example, in 26 vegetation plots totally 2.4 ha of forest in a 10 km² area of Kibale National Park, Uganda there are more than 60 tree species (Chapman *et al.*, 1997, 2010; Isabirye-Basuta & Lwanga, 2008). If one only considers the most basic plant parts (leaf buds, young leaves, mature leaves, leaf petioles, ripe fruit, unripe fruit, bark, and flowers), an animal with a home range of this size would have to select among approximately 480 different foods; each with changing phenological states. Furthermore, items that appear to be of one consistent type to a human observer (e.g., ripe fruit) often vary dramatically in chemical constituents (Worman & Chapman, 2005) and there can be significant temporal and spatial differences in the quality of the same food item over small scales (Chapman *et al.*, 2003; Houle, Chapman & Vickery, 2007; Rothman *et al.*, 2008; Rothman, Chapman & van Soest, 2012).

Despite the difficulty of understanding dietary selections, such a comprehension is very important for the construction of informed conservation plans. In an ideal situation, conservation plans are built on general principles (e.g., this

class of animal can be protected following this general strategy). This is important because there can be differences in the composition of the forest over small spatial and temporal scales (Chapman *et al.*, 1997; Isabirye-Basuta & Lwanga, 2008), yet most detailed dietary studies are collected at one particular location over a short time (i.e., 1 year or less). If we understand what critical nutrients and antifeedants drive food consumption, it becomes feasible to construct conservation plans for specific animals that relate plant chemistry to food consumption especially when they are associated at the genus or family level [i.e., protect trees in the Fabaceae family as they often have high-protein levels, because protein to fiber levels have been shown to correlate with the biomass of arboreal folivores (Davies, 1994; Oates *et al.*, 1990; Waterman & Kool, 1994; Chapman *et al.*, 2004)]. Such tree species (Fabaceae for folivores - Omeja *et al.*, 2011; food trees of frugivores - Felton *et al.*, 2010; Ficus - Felton *et al.*, 2013) can be promoted in restoration programs or avoided in logging operations.

Here, we determine factors influencing the selection of parts of the fruits of one frequently consumed food, *Blighia unijugata* (Sapindaceae), in the diet of grey-cheeked mangabeys (*Lophocebus albigena*) in Lwamunda Forest Reserve, Uganda in relation to macronutrients and condensed tannin. We focused on tannins as an antifeedants, because they bind protein, reduce the digestibility and nutritional quality of foods (Robbins *et al.*, 1987; Rothman, Dusingberre & Pell, 2009b; Rothman, Chapman & van Soest, 2012), and nitrogen (a major component of protein) is limiting in many environments (White, 1993).

Blighia unijugata grows in open habitats including woodlands, forest edges, and along river banks. The Lwamunda Forest Reserve is mainly riverine forest, thus it is commonly found along the river, but it is also found at the forest edges. It is a small- to medium-sized tree and grows to a height of 15–30 m depending on locality; the tree bole is often quite short, usually straight, and can be up to ~200 cm in diameter. It has a bi-annual fruiting period and when in fruit it contributes ~10% of the mangabey diet in the Lwamunda Forest. *B. unijugata* is important in the diet of mangabeys (Olupot, Waser & Chapman, 1998; Baranga, 2004; Wiczekowski & Kinnaird, 2008), black and white colobus - *Colobus guereza* (Rode *et al.*, 2003), red colobus - *Procolobus rufomitratus* (Rode *et al.*, 2003; Ryan, Chapman & Rothman, 2012) (the colobines eat the aril along with the seed), chimpanzees - *Pan troglodytes* (Krief, Hladik & Haxaire, 2005), blue

monkeys - *Cercopithecus mitis* (Butynski, 1990), and redtail monkeys - *C. ascanius* (Stickler, 2004; Rode *et al.*, 2006a). Furthermore, humans have been described to eat the related *B. sapida* (K.D. Koenig) (Hassall & Reyle, 1955; Feng & Patrick, 1958; Brown *et al.*, 1991; Abolaji, Adebayo & Odesanmi, 2007). Unfortunately, no previous study reporting the eating of *B. sapida* fruit by primates indicated the fruit part being consumed.

Methods

We studied the mangabeys in Lwamunda Forest Reserve, Uganda (67 km²-0° 15'N and 0° 23'N longitude 32° 30' E and 32° 43' E; 1200 elevation; 80 km SW of the larger Mbira Forest Reserve) from June 2004 to March 2007 for 5 consecutive days a month. The animals were well habituated prior to our study because of previous and continuous research in the area (Chalmers, 1968; Spuhler & Jorde, 1975; Waser, 1975; Baldwin, Teleki & Kavanagh, 1976). The area receives 1200–1500 mm annually and the rains are typically distributed between two distinct wet seasons; April–May and October–November (Howard, 1991). Lwamunda Forest Reserve is a riverine forest surrounded by flat-topped hills with steep slopes. In 1993, when efforts were made to prohibit human encroachment of the Lake Victoria Basin forest reserves, Lwamunda was not included in prohibition strategy and therefore it is severely degraded as a result of illegal pit sawing; consequently, food options for the threatened mangabey populations are limited. Generally, forest reserves in Uganda are not well protected because of the open-access policy and poorly structured land tenure system (Naughton, Alix-Garcia & Chapman, 2011).

To determine the feeding habits of the mangabeys, we focused on a group of 14 individuals (four adult males, two sub-adult males, four adult females, two sub-adult females, and two infants) and conducted systematic 5-min scan sampling (Altmann, 1974) of all group members from 6 am to 12 pm, and then from 4 pm to 7 pm on weekdays and 7 am to 1 pm on Saturdays, which was supplemented with ad libitum observations of the exact parts of the fruits eaten. A total of 1200 h of observations were made of the mangabeys. Notes on food remains under trees where mangabeys had fed were carefully taken.

We collected a 50 g sample of fruit at each development stage and the sample was analyzed at the Animal Science Laboratory, Makerere University, Uganda. Two samples of each plant part/stage were collected and they were

analyzed in triplicate. Mass and size measurements were taken before splitting the fruit to access the seed and aril and analysis was made only on the seeds and aril, because mangabeys rarely ate other fruit parts. Given the small mass of the aril, samples were taken from multiple trees and pooled for analysis; samples were all collected on the same day and sufficient trees and fruit were used until the 50 g amount was obtained (the number of trees collected from varied depending on availability, Table 1). The seed and aril were oven-dried at 60°C to a constant weight and then ground using a Cyclotech 1093 (Foss, Inc., Hillerød, Denmark) Model 4 mill, or a mortar and pestle. The powdered sample was packed in a vinyl bag, labeled, and stored in plastic containers at room temperature until analyses. The Kjeldahl method (AOAC, 1990; Rothman, Chapman & van Soest, 2012) was used to quantify crude protein; standard methods were used to determine crude fiber (AOAC, 1990), while Harris's (1970) soxhlet method for ether extract was used to determine lipid content, and soluble carbohydrates (sugar) were determined using the anthrone method (Loewus, 1952). Tannins were estimated using the Price and Butler method (Price & Butler, 1977), with quebracho as a standard. Although we acknowledge the problems using quebracho as a standard (Rothman *et al.*, 2009a), because we are comparing the same species and part, it is appropriate to compare the absorbance values of *B. unijugata* to determine the magnitude of change. As the aril on the seed is very small, we only measured its fat and tannin content.

Partial correlation analysis was used to explore the relationship between tannin concentration and the rest of the proximate composition variables in *B. unijugata* seeds,

Table 1 The number of *Blighia unijugata* arils that were collected to make up 50 g used in the nutritional analysis for each of the developmental stages of this fruit, which is an important food for the mangabeys (*Lophocebus albigena*) sampled in Lwamunda Forest Reserve, Uganda

Stage of fruit development	Mean wt (g) & SD	No. arils in 50 g	No. of fruits contributing to 50 g
1	0.01 ± 0.00	5000	1667
2	0.03 ± 0.00	1667	556
3	0.10 ± 0.01	500	167
4	0.15 ± 0.01	334	111
5	0.22 ± 0.01	227	76
6	0.26 ± 0.01	192	64

while controlling for development stage. The r reported in the text is the effect of the variable being discussed, while statistically controlling for the effects of the other variables being considered. To test whether antifeedants explain fruit part selection by mangabeys, we used a logistical regression with the response variable fruit part eaten or avoided and the tannin level as a predictor.

Results

Blighia unijugata fruit exhibited six developmental stages (Fig. 1a–f) and the foraging effort devoted to the different stages varied (Table 2). With respect to stage 1 fruits, mangabeys ate the barely formed green seeds and ignored the green aril. Prior to this stage, fruits were not eaten; they were green and when plucked they exuded sticky sap that may deter consumers. At stage 2, the fruit had been on the tree for approximately 3 months. During periods of general food scarcity, mangabeys consumed fairly young *B. unijugata* fruit at stages 1 and 2 fruits. Stage 3 fruits were about 4-month old and the aril was bright orange, but it was not eaten by mangabeys. At stage 4, fruits had been on the tree for approximately 5 months and both the seed and aril appeared mature from the observer's perspective, but only the seeds were eaten by mangabeys and the aril was discarded. Stage 5 fruits were between 6 and 7 months of age and while mangabeys attempted to bite through it, the pericarp was too fibrous to be easily punctured, thus fruit was not eaten at this stage. At stage 6, fruits were crimson red and had been developing on the tree for approximately 8 months. The pericarp naturally split open allowing easy seed removal. None of the fruit shells found underneath the trees at this stage contained an aril, implying they had been eaten. At stage 6, fruits were eaten by many birds, particularly turacos (great blue turacos - *Corythaeola cristata* and Ross's turacos *Musophaga rossae*), and other primates, particularly the redbellied monkey (*Cercopithecus ascanius*).

When all the major *B. unijugata* seed components were analyzed at all development stages (Table 3, Fig. 2), a linear increase was described for all components. However, the gradient was more pronounced in sugar, protein, and fiber, than in fat for the first four stages. Regardless of the development stage, protein constituted more of the seed, followed by sugar, then fiber, and finally lipid. The tannin level in the seed increased gradually from stages 1 to 4 and then increased rapidly between stages 4 and 5 and remained high in stage 6. The relatively high levels of

tannins may be one of the factors that influenced the choice of developmental stage eaten by mangabeys because they ate the seeds from stages 1–4, but avoided seeds in stages 5 and 6.

There were strong positive partial correlations between tannin and fat content ($r = 0.72$, $P < 0.01$). Tannins were negatively correlated with fiber ($r = -0.76$, $P < 0.001$) and with crude protein ($r = -0.71$, $P < 0.01$). No correlation existed between tannin concentration and sugar content ($r = -0.35$, $P > 0.05$). An inspection of zero-order correlation suggested that controlling for the seed development stages had very strong effects on the strength of the relationship between tannin levels and crude protein, fiber, sugar, and fat.

The level of tannins appears to influence the likelihood of mangabeys eating either aril or seed depending on developmental stage. The tannin concentration in the edible parts of the fruits was about 1.783 times less than the concentration in the inedible parts ($\chi^2 = 27.0$, $P < 0.001$). In contrast, aril tannin concentration in the inedible stages was 1.48 times higher than it was in the edible portions. Further research should consider other metabolites, as these may play roles in the parts eaten at different developmental stages.

The fat content of the *B. unijugata* aril increased with development stage. The increase was gradual from stages 1 to 4, and then there was a dramatic increase in the last two stages. A similar pattern was documented in the seeds, which implies stage 4 was a critical stage influencing animal handling patterns. Contrary to the trend observed in seeds, the tannin levels in arils decreased as the fruit matured (Fig. 3). The low levels documented for stage 6 may have facilitated frugivores dispersing the seeds.

Discussion

Mangabey consumption of *B. unijugata* fruit parts appears to be influenced by nutrient and antifeedant content. Considering that seed fat, sugar, and protein increased with fruit maturity, mangabeys would have been expected to eat seeds up to maturity because of their high nutrient content. However, they stopped eating seeds at stage 4, which we speculate was a result of the increase in tannins. We did not, however, measure starch content in the fruits and it was likely higher in the younger fruits because fat, sugar, and protein are all increased. Because starch is an easily digestible carbohydrate, it also may have had an influence on mangabey fruit part consumption.

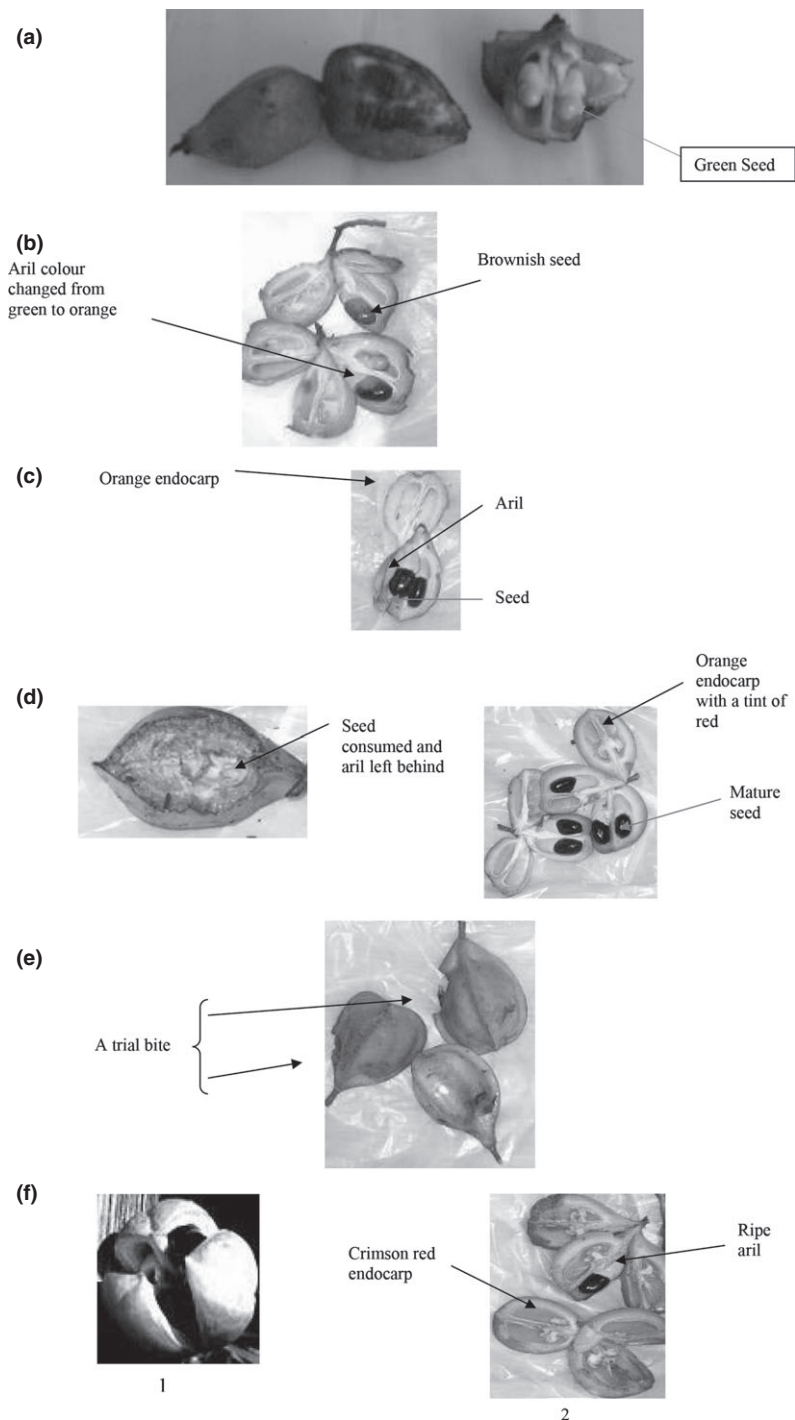


Fig 1 The stages of development of *Blighia unijugata*, an important food for the mangabeys (*Lophocebus albigena*) sampled in Lwamunda Forest Reserve, Uganda. (a) The first stage of fruit showing the outer bright reddish orange color '1' and bitten fruit '2' to access the green seed '3.' Seeds weighed 0.15 g. The green colored aril was not available for consumption by mangabeys. (b) The second development stage showing the brown tinted seed with orange colored aril and still unripe that is inedible to mangabey. The seed weighed 0.21 g. (c) The third development stage showing brown colored seed and orange aril which is still inedible. The seeds weighed 0.25 g. (d) The fourth development stage showing dark brown colored seed, endocarp with a tint of red and bright orange aril which still remains inedible. The seed weighed on average 0.27 g. (e) The fifth stage of development stage of fruits that mangabeys have bitten. The seed weighed 0.31 g. (f) In the sixth development stage, the fruits split open and the aril was available for consumption by mangabeys. The seeds weighed 0.35 g

If the mangabeys were consuming the part of the fruits based on a trade-off between tannin and fat, one would predict animals start consuming arils just before stage 3 as indicated by the intercept that was similar to tannin level

in seed (Fig. 3). However, mangabeys waited to consume arils until stage 6, suggesting that other nutrients/antifeedants within the aril influenced consumption. The likelihood of the aril being eaten in either case tended to

Table 2 The foraging effort devoted to eating in the different developmental stages of *Blighia unijugata* made by the mangabeys (*Lophocebus albigena*) of Lwamunda Forest Reserve, Uganda. The foraging effort was calculated from the number of feeding records based on systematic scan sampling of each stage of development for 4 months this species was available. Then divided by the total feeding scores involving all foods available for that month and then expressed as percentage. The figures in Table 3 are the averages for respective stages during 4 months

Developmental Stage	Foraging Effort	Foraging Effort	Foraging Effort
	Aril	Seed	Other
1	0	10.84	0.2
2	0	15.12	0
3	0	9.86	0
4	0	3.28	0
5	0	0	0
6	8.71	0	0

increase with increasing stages of ripening, as tannin levels declined. Generally, the tannin levels were lower in aril than in seeds.

It was also possible for mangabeys to consume arils just before stage 3, but they did not. We speculate that this is due to the avoidance of toxic hypoglycin A, since the aril of *B. sapida* is known to contain hypoglycin A before maturity (Ayodele, Ajayi & Adewuyi, 2008). Brown *et al.* (1991)

reported that the level of hypoglycin A declined from 1000 ppm to undetectable (<0.1 ppm) as the fruit matured. At all stages, the seed contained appreciable hypoglycin A, ~1000 ppm, as such unopened or partially opened fruit were not consumed. The levels of hypoglycin A may explain why mangabeys ate stage 4 of seed, but did not eat stage 3 arils. Alternatively, mangabeys may not have eaten arils because of low fat content in the stages before maturity (Herrera, 1982).

Theoretically, many macronutrients increase in seeds as they mature to facilitate seed germination and subsequent growth (Richards, 1996; Zanne, Chapman & Kitajima, 2005; Chapman *et al.*, 2008). In contrast, as the seed matures, the secondary compounds increase to potentially inhibit animals from consuming and destroying the seed. Here, we speculate that mangabeys may have avoided tannins by consuming the seeds prior to development. In contrast to the seed, fleshy pericarps and arils attract seed dispersers that move seeds away from the parent tree, providing vital disperser services (Chapman, 1989; Russo & Chapman, 2011). Thus, it confirms hypothesis that we documented that secondary compounds in the arils declined with maturity. Ripe aril is brightly colored, soft, with high levels of lipid, but low tannins, desirable characteristics for seed-dispersing birds and mammals (Howe & Smallwood, 1982; Stiles, 1982; Fischer & Chapman, 1993). Although the ripe arils of *B. unijugata*

Table 3 Variation in chemical composition of *B. unijugata* seeds (a) and arils (b) from stages 1–6 as a percentage of dry matter. Two samples of each plant part/stage were collected and they were analyzed in triplicate

Development stage	Sugar		Fiber		Fat		Protein		Tannin	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
a) Seed										
1	3.03	0.049	3.21	0.147	0.64	0.037	7.41	0.216	1.237	0.161
2	6.36	0.030	5.22	0.112	1.29	0.029	9.63	0.075	2.760	0.162
3	9.74	0.198	9.43	0.223	2.65	0.065	12.89	0.173	3.734	0.037
4	12.22	0.163	11.27	0.140	3.41	0.100	15.33	0.167	4.130	0.100
5	15.09	0.082	12.30	0.170	4.99	0.105	16.42	0.253	7.016	0.051
6	15.87	0.152	12.99	0.046	7.08	0.077	17.94	0.210	8.873	0.083
b) Aril										
1	6.177	1.561	9.143	0.419	1.970	0.024	9.297	0.118	7.006	0.115
2	6.493	0.017	3.668	0.027	3.111	0.089	9.417	0.038	6.016	0.052
3	7.064	0.291	3.707	0.119	5.583	0.103	5.513	0/071	4.130	0.100
4	9.739	0.507	4.595	0.107	8.314	0.133	2.981	0.010	3.734	0.037
5	13.574	0.703	4.528	0.143	16.530	0.130	3.611	0.215	2.760	0.162
6	13.928	0.185	5.511	0.072	25.017	0.237	4.593	0.103	1.237	0.161

Fig 2 Macro-nutrient trends in *B. unijugata* seed based on six developmental stages. All variables are expressed as a % of the total dry weight, with the exception of tannins that are expressed as Quebracho units

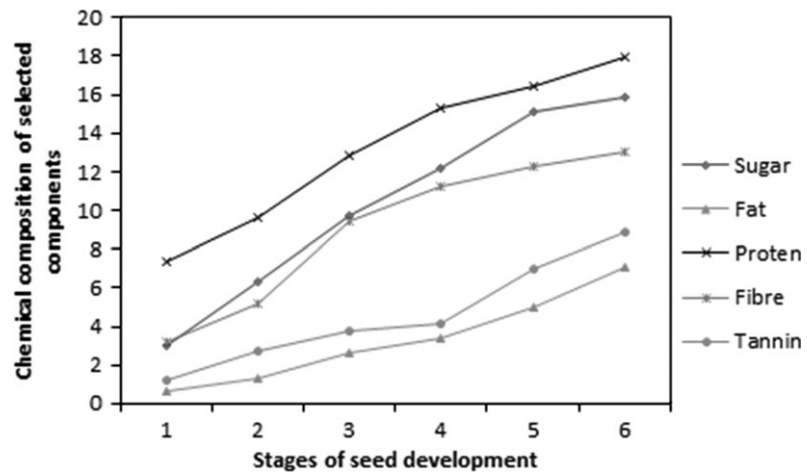
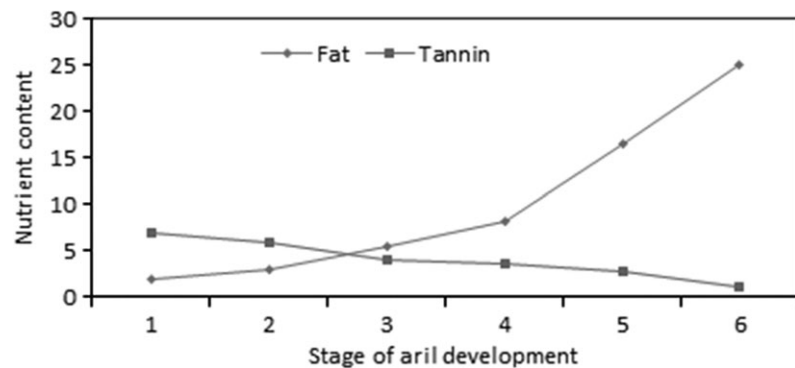


Fig 3 Levels of fat and tannin content in *B. unijugata* aril along developmental stages. Fat is presented as a % of the total dry weight, while tannins are expressed as Quebracho units



fruit appeared to be the most preferred fruit part, during periods of food scarcity mangabeys ate seeds up to stage 4 (Homewood, 1978).

Our results re-enforce the notion that it is inappropriate to consider diet simply in terms of plant parts (e.g., fruit, leaves), but rather it is important to consider the nutritional value of specific food items (McNaughton, 1988; Janson & Chapman, 1999; Rothman *et al.*, 2009a; Chapman, Rothman & Lambert, 2012). For example, a food (i.e., item) that is typically thought to have high protein levels (e.g., young leaves) may have less protein than a plant part typically considered to be low in protein (e.g., fruit). To advance the field and gain a better understanding of diet selection and foraging strategies, it will be useful to analyze food items from the species of interest and, if possible, the actual plant from which the animal fed. With the development of near-infrared reflectance spectroscopy methods for field work, this is now possible and relatively easily accessible (Rothman *et al.*, 2009a).

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References

- ABOLAJI, O.A., ADEBAYO, A.H. & ODESANMI, O.S. (2007) Nutritional qualities of three medicinal plant parts (*Xylopiya aethiopica*, *Blighia sapida* and *Parinari polyandra*) commonly used by pregnant women in the western part of Nigeria. *Pak. J. Nutr.* 6, 665–668.
- ALTMANN, J. (1974) Observational study of behavior: sampling methods. *Behaviour* 48, 227–268.
- AOAC (1990) *Official Methods of Analysis*. Association of Official Analytical Chemists, Arlington, VA.

- AYODELE, R.O., AJAYI, I.A. & ADEWUYI, A. (2008) Nutritional elements, antibacterial activity and cytotoxicity of the leaf, root and stem bark of *Blighia unijugata* Baker (Sapindaceae). *Medicinal Aromatic Plant Sci. Biotech.* **2**, 137–140.
- BALDWIN, L.A., TELEKI, G. & KAVANAGH, M. (1976) Field research on colobus, guenon, mangabey and patas monkeys: a historical, geographical and bibliographical listing. *Primates* **17**, 233–251.
- BARANGA, D. (1983) Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology* **64**, 668–673.
- BARANGA, D. (2004) Forest fragmentation and primate survival status in non-reserve forests of the Kampala area, Uganda. *Afr. J. Ecol.* **42**, 70–77.
- BROWN, M., BATES, R.P., MCGOWAN, C. & CORNELL, J.A. (1991) Influence of fruit maturity on the hypoglycin A level in ackee (*Blighia sapida*). *J. Food Saf.* **12**, 167–177.
- BUTYNSKI, T.M. (1990) Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density sub-populations. *Ecol. Monogr.* **60**, 1–26.
- CHALMERS, N.R. (1968) The visual and vocal communication of free living mangabeys in Uganda. *Folia Primatol.* **9**, 258–280.
- CHAPMAN, C.A. (1989) Primate seed dispersal: the fate of dispersed seeds. *Biotropica* **21**, 148–154.
- CHAPMAN, C. A., ROTHMAN, J. M. & LAMBERT, J. E. (2012) Food selection in primates. In: *The Evolution of Primate Societies* (Eds. J. MITANI, J. CALL, P. KAPPELER, R. PALOMBIT and J. SILK). Chicago University Press, Chicago.
- CHAPMAN, C.A., CHAPMAN, L.J., WRANGHAM, R.W., ISABIRYE-BASUTA, G. & BEN-DAVID, K. (1997) Spatial and temporal variability in the structure of a tropical forest. *Afr. J. Ecol.* **35**, 287–302.
- CHAPMAN, C.A., CHAPMAN, L.J., RODE, K.D., HAUCK, E.M. & McDOWELL, L.R. (2003) Variation in the nutritional value of primate foods: among trees, time periods, and areas. *Int. J. Primatol.* **24**, 317–333.
- CHAPMAN, C.A., CHAPMAN, L.J., NAUGHTON-TREVES, L., LAWES, M.J. & McDOWELL, L.R. (2004) Predicting folivorous primate abundance: validation of a nutritional model. *Am. J. Primatol.* **62**, 55–69.
- CHAPMAN, C.A., KITAJIMA, K., ZANNE, A.E., KAUFMAN, L.S. & LAWES, M.J. (2008) A 10-yr evaluation of the functional basis for regeneration habitat preference of trees in an African evergreen forest. *For. Ecol. Manage.* **225**, 3790–3796.
- CHAPMAN, C.A., CHAPMAN, L.J., JACOB, A.L., ROTHMAN, J.M., OMEJA, P.A., REYNA-HURTADO, R., HARTTER, J. & LAWES, M.J. (2010) Tropical tree community shifts: Implications for wildlife conservation. *Biol. Conserv.* **143**, 366–374.
- DAVIES, A. G. (1994) Colobine populations. In: *Colobine Monkeys. Their Ecology, Behaviour and Evolution* (Eds. A. G. DAVIES and J. F. OATES). Cambridge University Press, Cambridge.
- FELTON, A.M., FELTON, A., FOLEY, W.J. & LINDENMAYER, D.B. (2010) The role of timber tree species in the nutritional ecology of spider monkeys in a certified logging concession, Bolivia. *For. Ecol. Manage.* **259**, 1642–1649.
- FELTON, A.M., FELTON, A., RUMIZ, D.I., PENNA-CLAROS, M., VILLAROELO, N., CHAPMAN, C.A. & LINDENMAYER, D.B. (2013) Commercial harvesting of *Ficus* timber – An emerging threat to frugivorous wildlife and sustainable forestry. *Biol. Conserv.* **159**, 96–100.
- FENG, P.C. & PATRICK, S.J. (1958) Studies of the action of hypoglycin-a, an hypoglycaemic substance. *Br. J. Pharmacol. Chemother.* **13**, 125–130.
- FISCHER, K.E. & CHAPMAN, C.A. (1993) Frugivores and fruit syndromes - differences in patterns at the genus and species level. *Oikos* **66**, 472–482.
- HARCOURT, A.H. & STEWART, K.J. (2007) *Gorilla Society: Conflict, Compromise, and Cooperation Between the Sexes*. University of Chicago Press, Chicago.
- HARRIS, L. E. (1970) *Nutrition Research Techniques for Domestic and Wild Animals*. Animal Science Department Utah State University, Logan, Utah, USA.
- HASSALL, C.H. & REYLE, K. (1955) Hypoglycin A and B, two biologically active polypeptides from *Blighia sapida*. *Biochem. J.* **60**, 334–339.
- HERRERA, C.M. (1982) Seasonal variations in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* **63**, 772–785.
- HOLDO, R.M. & McDOWELL, L.R. (2004) Termite mounds as nutrient rich food patches for elephants. *Biotropica* **36**, 231–239.
- HOMEWOOD, K.M. (1978) Feeding strategy of the Tana mangabey (*Cercocebus galeritus galeritus*) (Mammalia: Primates). *J. Zool.* **186**, 375–391.
- HOULE, A., CHAPMAN, C.A. & VICKERY, W.L. (2007) Intra-tree variation in fruit production and implication for primate foraging. *Int. J. Primatol.* **28**, 1197–1271.
- HOWARD, P.C. (1991) *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland, Switzerland.
- HOWE, H.F. & SMALLWOOD, J. (1982) Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* **13**, 201–228.
- ISABIRYE-BASUTA, G.M. & LWANGA, J.S. (2008) Primate populations and their interactions with changing habitats. *Int. J. Primatol.* **29**, 35–48.
- JANSON, C. H. & CHAPMAN, C. A. (1999) Resources and the determination of primate community structure. In: *Primate Communities* (Eds. J. G. FLEAGLE, C. H. JANSON and K. E. REED). Cambridge University Press, Cambridge.
- KRIEF, S., HLADIK, C.M. & HAXAIRE, C. (2005) Ethnomedicinal and bioactive properties of plants ingested by wild chimpanzees in Uganda. *J. Ethnopharmacol.* **101**, 1–15.
- LOEWUS, F.A. (1952) Improvement in anthrone method for determination of carbohydrates. *Anal. Chem.* **24**, 219.
- MCNAUGHTON, S.J. (1988) Mineral nutrition and spatial concentrations of African ungulates. *Nature* **334**, 343–345.
- NAUGHTON, L., ALIX-GARCIA, J. & CHAPMAN, C.A. (2011) A decade of forest loss and economic growth around Kibale National Park, Uganda: lessons for poverty reduction and biodiversity conservation. *Proc. Natl Acad. Sci. USA* **108**, 13919–13924.
- OATES, J.F., WHITESIDES, G.H., DAVIES, A.G., WATERMAN, P.G., GREEN, S.M., DASILVA, G. L. & MOLE, S. (1990) Determinants of variation in tropical forest primate biomass: new evidence from West Africa. *Ecology* **71**, 328–343.

- OLUPOT, W., WASER, P.M. & CHAPMAN, C.A. (1998) Fruit finding by mangabeys (*Lophocebus albigena*): are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *Int. J. Primatol.* **19**, 339–353.
- OMEJA, P.A., CHAPMAN, C.A., OBUA, J., LWANGA, J.S., JACOB, A.L., WANYAMA, F. & MUGENYI, R. (2011) Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation. *For. Ecol. Manage.* **261**, 703–709.
- PRICE, M.L. & BUTLER, L.G. (1977) Rapid visual estimation and spectrophotometric determination of tannin content of sorghum grain. *J. Agric. Food Chem.* **25**, 1268–1273.
- RICHARDS, P.W. (1996) *The Tropical Rain Forest*. Cambridge University Press, Cambridge.
- ROBBINS, C.T., HANLEY, T.A., HAGERMAN, A.E., HJELJORD, O., BAKER, D.L., SCHWARTZ, C.C. & MAUTZ, W.W. (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* **68**, 98–107.
- 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. *Int. J. Primatol.* **24**, 541–573.
- RODE, K.D., CHAPMAN, C.A., McDOWELL, L.R. & STICKLER, C. (2006a) Nutritional correlates of population density across habitats and logging intensities in redbell monkeys (*Cercopithecus ascanius*). *Biotropica* **38**, 625–634.
- RODE, K.D., CHIYO, P.I., CHAPMAN, C.A. & McDOWELL, L.R. (2006b) Nutritional ecology of elephants in Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *J. Trop. Ecol.* **22**, 441–449.
- ROTHMAN, J.M., CHAPMAN, C.A. & VAN SOEST, P.J. (2012) Methods in primate nutritional ecology: a user's guide. *Int. J. Primatol.* **33**, 542–566.
- ROTHMAN, J.M., DUSINBERRE, K. & PELL, A.N. (2009b) Condensed tannins in the diets of primates: a matter of methods? *Am. J. Primatol.* **71**, 70–76.
- ROTHMAN, J.M., VAN SOEST, P.J. & PELL, A.N. (2006) Decaying wood is a sodium source for mountain gorillas. *Biol. Lett.* **2**, 321–324.
- ROTHMAN, J.M., DIERENFELD, E.S., HINTZ, H.F. & PELL, A.N. (2008) Nutritional quality of gorilla diets: consequences of age, sex and season. *Oecologia* **155**, 111–122.
- ROTHMAN, J.M., CHAPMAN, C.A., HANSEN, J.L., CHERNEY, D.J. & PELL, A. N. (2009a) Rapid assessment of the nutritional value of mountain gorilla foods: applying near-infrared reflectance spectroscopy to primatology. *Int. J. Primatol.* **30**, 729–742.
- RUGGIERO, R.G. & FAY, J.M. (1994) Utilization of termitarium soils by elephants and its ecological implications. *Afr. J. Ecol.* **32**, 222–232.
- RUSO, S. S. & CHAPMAN, C. A. (2011) Primate seed dispersal: linking behavioural ecology and forest community structure. In: *Primates in Perspective* (Eds. C. J. CAMPBELL, A. F. FUENTES, J. C. MACKINNON, M. PANGER and S. BEARDER). Oxford University Press, Oxford.
- RYAN, A.M., CHAPMAN, C.A. & ROTHMAN, J.M. (2012) How do differences in species and part consumption affect diet nutrient concentrations? A test with red colobus monkeys in Kibale National Park, Uganda. *Afr. J. Ecol.* **51**, 1–10.
- SPIHLER, J.N. & JORDE, L.B. (1975) Primate phylogeny, ecology and social behaviour. *J. Anthropol. Res.* **31**, 376–405.
- STICKLER, C.M. (2004) *The Effects of Logging on Primate-Habitat Interactions: A Case Study of Redtail Monkeys (Cercopithecus Ascanius) in Kibale National Park, Uganda*. M.Sc Thesis, University of Florida, Gainesville, Florida.
- STILES, E.W. (1982) Fruit flags: hypotheses. *Am. Nat.* **120**, 500–509.
- WASER, P.M. (1975) Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). *East African Wildlife J.* **13**, 249–264.
- WATERMAN, P. G. & KOOL, K. M. (1994) Colobine food selection and plant chemistry. In: *Colobine Monkeys: Their Ecology, Behaviour, and Evolution* (Eds. A. G. DAVIES and J. F. OATES). Cambridge University Press, Cambridge.
- WHITE, T.C.R. (1993) *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer-Verlag, Berlin.
- WIECZKOWSKI, J. & KINNAIRD, M. (2008) Shifting forest composition and primate diets: a 13-year comparison of the Tana river mangabey and its habitat. *Am. J. Primatol.* **70**, 339–348.
- WORMAN, C.O. & CHAPMAN, C.A. (2005) Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *J. Trop. Ecol.* **21**, 689–697.
- ZANNE, A.E., CHAPMAN, C.A. & KITAJIMA, K. (2005) Evolutionary and ecological correlates of early seedling morphology in East African trees and shrubs. *Am. J. Bot.* **92**, 972–978.

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