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Journal of Tropical Ecology / Volume 30 / Issue 04 / July 2014, pp 273 - 290
DOI: 10.1017/S0266467414000236, Published online: 23 June 2014

Link to this article: http://journals.cambridge.org/abstract_S0266467414000236

How to cite this article:
Aaron M. Lamperti, Aaron R. French, Ellen S. Dierenfeld, Mark K. Fogiel, Kenneth D. Whitney, Donald J. Stauffer, Kimberly M. Holbrook, Britta D. Hardesty, Connie J. Clark, John R. Poulsen, Benjamin C. Wang, Thomas B. Smith and V. Thomas Parker (2014). Diet selection is related to breeding status in two frugivorous hornbill species of Central Africa . Journal of Tropical Ecology, 30, pp 273-290 doi:10.1017/S0266467414000236

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Journal of Tropical Ecology (2014) **30**:273–290. © Cambridge University Press 2014
doi:10.1017/S0266467414000236

Diet selection is related to breeding status in two frugivorous hornbill species of Central Africa

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(*Received 29 June 2013; revised 4 May 2014; accepted 5 May 2014*)

Abstract: Avian diet selection is hypothesized to be sensitive to seasonal changes in breeding status, but few tests exist for frugivorous tropical birds. Frugivorous birds provide an interesting test case because fruits are relatively deficient in minerals critical for reproduction. Here, we quantify annual patterns of fruit availability and diet for two frugivorous hornbill (Bucerotidae) species over a 5.5-y period to test for patterns of diet selection. Data from the lowland tropical rain forest of the Dja Reserve, Cameroon, are used to generate two nutritional indices. One index estimates the nutrient concentration of the diet chosen by *Ceratogymna atrata* and *Bycanistes albotibialis* on a monthly basis using 3165 feeding observations combined with fruit pulp sample data. The second index is an estimate of nutrient concentration of a non-selective or neutral diet across the study area based on tree fruiting phenology, vegetation survey and fruit-pulp sample data. Fifty-nine fruit pulp samples representing 40 species were analysed for 16 nutrient categories to contribute to both indices. Pulp samples accounted for approximately 75% of the observed diets. The results support expected patterns of nutrient selection. The two hornbill species selected a diet rich in calcium during the early breeding season (significantly so for *B. albotibialis* in July and August). Through the brooding and fledging periods, they switched from a calcium-rich diet to one rich in iron and caloric content as well as supplemental protein in the form of invertebrates. Calcium, the calcium to phosphorus ratio and fat concentration were the strongest predictors of breeding success (significant for calcium and Ca : P for *B. albotibialis* in June). We conclude that hornbills actively select fruit based on nutritional concentration and mineral concentration and that the indices developed here are useful for assessing frugivore diet over time.

Key Words: avian, Cameroon, Dja Reserve, frugivory, mineral nutrition, nutrition

INTRODUCTION

In the wild, frugivorous birds experience a constantly changing set of available diet options and a consequent variation in overall nutrient availability. Dietary needs vary with the demands of the breeding season, moulting and for many, migration (Dhondt & Hochachka 2001, García-Navas & Sanz 2011, Herrera 1982, Hobson *et al.* 2011, Karr 1976, Leighton & Leighton 1983, Poulin *et al.* 1992). This study seeks to test the hypothesis that seasonal shifts in avian frugivore diets will track reproductive nutritional needs rather than fruiting patterns. A positive result will imply that avian frugivores are choosing a fruit diet based on nutritional needs rather than simple availability.

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Previous studies have proposed that seasonal shifts in diet of tropical frugivorous birds are related to reproductive activity rather than to fruiting patterns (Kannan & James 1999, Karr 1976, Kinnaird & O'Brien 1999, Poonswad *et al.* 2004, Poulin *et al.* 1992). Data from domestic birds indicate that individuals are capable of modifying their behaviour and diet choices to address changing mineral needs (Robbins 1993). Perhaps the most universal period of high mineral demand for birds is during the breeding season, particularly the time leading up to egg laying. Calcium requirements for egg laying are up to five times that of non-breeding birds. Birds have been known to go to great lengths to meet this requirement, including scavenging for bones and other high-calcium objects (Barclay 1995, Dhondt & Hochachka 2001, Graveland & VanderWal 1996, Nager 2006, Robbins 1993, Tilgar *et al.* 2002).

Tropical avian frugivores may have a hard time meeting their mineral needs since many fruits are quite deficient in individual minerals (Robbins 1993). Thus we might expect to see behavioural responses to periods of mineral stress such as egg laying and moulting. Specifically, one might expect that during the time leading up to egg laying, a diet relatively high in calcium would be selected, perhaps at the expense of other nutrients. After eggs are laid, energetic requirements are high for brooding, so diet selection during this period might be for lipid-rich fruits, i.e. what have been traditionally considered high-quality fruits (Dunn 1980, McKey 1975, Robbins 1993, Sibly *et al.* 2012). When eggs have hatched and chicks are growing, protein becomes an important nutritional component, which may mean a switch to higher-protein fruits and/or more time spent foraging for invertebrates and other high-protein, non-fruit foods (Foeken *et al.* 2008, Kinnaird & O'Brien 1999, Poonswad *et al.* 2004).

Traditionally, studies of avian nutrition have focused on macronutrient analysis and energetics (Herrera 1982, McKey 1975, Robbins 1993, Stiles 1993). Existing studies concerning mineral nutrition tend to be relevant to captive populations and mineral deficiencies (Dierenfeld 1996, Robbins 1993). Little work has been done regarding wild populations, diet selection and mineral nutrition (Barclay 1995, O'Brien *et al.* 1998, Otten *et al.* 2001, Ruby *et al.* 2000, Wendeln *et al.* 2000).

Our objective is to develop a method to quantify the nutritional content of a frugivore diet and to test hypotheses regarding temporal shifts in diet. First we introduce a pair of indices, and make a series of logical assumptions to simplify their calculation for field measurement. Second, we examine the question of whether shifts in diet are related to reproductive activity rather than fruiting patterns. If reproduction drives the diet of frugivorous birds, we expect that a shift in concentration of minerals and other nutrients should be related to periods of reproduction and not seasonal change. We use data for two frugivorous hornbill species, the black-casqued hornbill *Ceratogymna atrata* (Temminck, 1835) and the white-thighed hornbill *Bycanistes albotibialis* (Cabanis & Reichenow, 1877), to illustrate the effectiveness of our indices and to test whether reproduction or seasonal fruit availability drive their diets.

METHODS

Selected diet index

One way to analyse avian diet over time is to measure the total amount of each nutrient consumed during a given period. This method requires data on the mass of each food item eaten and the nutrient concentration of that item during that period. An equation for total intake of each nutrient would be:

$$\sum_i n_{ti} \times m_{ti}$$

where n_{ti} is the fraction of the nutrient in food item i during time t, and m_{ti} is the total dry mass of item i eaten during time t. To calculate m_t would require estimating the foraging efficiency of the birds with respect to each fruiting species, the time the birds spend in mature individuals of each fruiting species and the average dry mass of the fruit of that species. Collection of these data for wild birds, particularly in the tropics, is complicated by the expansive diets of most birds (Kitamura 2011, Poulsen *et al.* 2002, Whitney *et al.* 1998).

To ease data collection, we make a number of assumptions. First, we assume that birds are consuming a calorically adequate diet and thus, that we can represent the nutritional content of the diet on a fractional rather than total basis. Next, we assume that samples of fruit collected near peak ripeness make an acceptable substitute for a series of samples collected over time. Finally, we assume that a simple fraction of feeding observations could serve as a substitute for measurements of foraging efficiency and time spent in fruiting trees.

Incorporating these assumptions into the above equation, we get:

$$N_t = \frac{\sum_i n_i \times p_{it}}{\sum_i p_{it}}$$

where N_t is the fraction of the diet represented by a given nutrient during time t, n_i is the concentration of the nutrient in ripe fruit of species i, and p_{it} is the proportion of the feeding observations represented by that species in that period over all the diet species for which there are nutritional data.

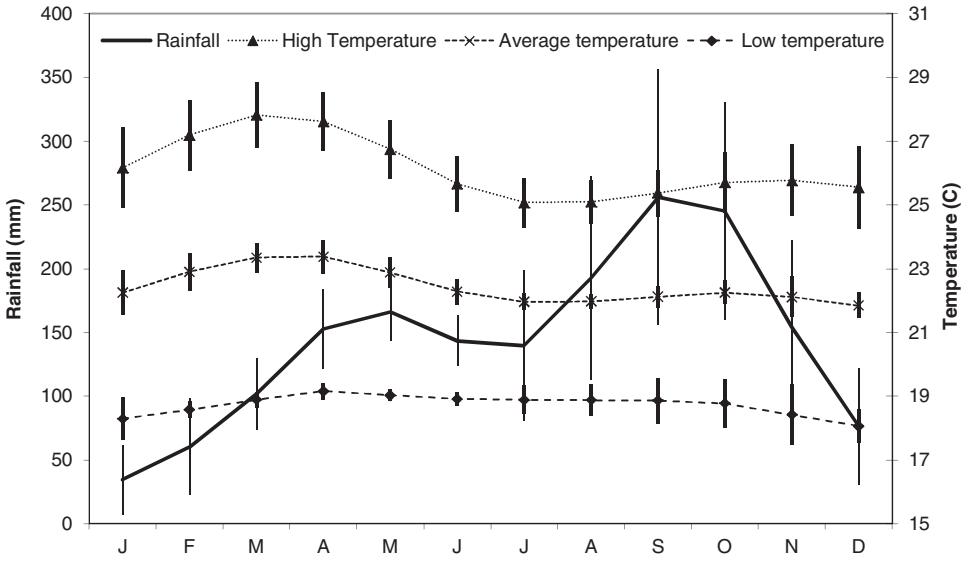

Figure 1. Rainfall and temperature data from the Bouamir Research Station in the Dja reserve, Cameroon. Data were collected from 1994 to 1999. Error bars represent 1 SD, N = 6 for all months.

Neutral diet index

To provide a baseline for comparison with the selected diet, we calculate an index of the nutrient concentrations of the fruit of all species which we know these two hornbill species consume across the study area. This non-selective or neutral diet index allows us to assess whether hornbills are selecting the fruit in their diet based on nutrient concentration rather than simply randomly selecting a diet based on availability.

The neutral diet index begins with an estimate of the total quantity of fruit available from a given set of fruiting species in an area – the Fruit Availability Index (FAI; Fogiel 2007, Holbrook *et al.* 2002, Stauffer & Smith 2004).

$$FAI_t = \sum_i D_i \times P_{ti} \times F_{ti} \times dbh_i$$

where D_i is the density of a given fruiting species in the area, P_{ti} is the average proportion of the canopy of mature individuals in fruit and F_{ti} is the average fraction of fruit which are ripe of those trees with ripe fruit and dbh_i is the average diameter at breast height for the species in the area.

We converted the FAI into a Fruit Nutrition Index or FNI by dividing the FAI for each species *i* by the total FAI for each period *t* to produce a proportion. This fraction was then multiplied by the nutrient concentration of the fruit of species *i*. The resulting values were summed for all diet species and the sum divided by the sum of the proportions of all FAI values for which there were nutritional data.

$$FNI_t = \frac{\sum_i \left(n_i \times \frac{FAI_{ti}}{FAI_t}\right)}{\sum_i \frac{FAI_{ti}}{FAI_t}} = \frac{\sum_i (n_i \times FAI_{ti})}{\sum_i FAI_{ti}}$$

where the sums were taken for those species for which there were both FAI and nutrient data in a given period. The FNI was calculated for each month of the study period where there were data for both fruiting phenology and feeding observations, then a running 3-mo average of both diets was then further averaged by calendar month over the 5-y study period to produce monthly averages. Statistics were calculated using microsoft Excel version 2008 for Macintosh.

Study site and species

Diet observations were made between May 1994 and December 1999 at the Bouamir Research Station (BRS) in the Dja Faunal Reserve in southern Cameroon (3°11′27″N, 12°48′41″E). The Dja is a United Nations-designated biosphere reserve covering about 526 000 ha and is surrounded on three sides by the Dja River, a tributary of the Congo. The area has never been commercially logged. Although legally protected, the area does suffer hunting pressure from villages to the north and west (Muchaal & Ngandjui 1995, 1999). Bouamir is a 25-km^2 study site situated in the approximate centre of the reserve in semi-deciduous tropical rain forest. The study area includes areas of upland forest, *Raphia* swamp and rocky outcrops known as rochers. Annual rainfall is approximately 1600 mm and comes in two wet seasons, with rainfall peaks in late September and mid-May (Fogiel 2007, Lamperti 2004, Poulsen *et al.* 2002, Whitney *et al.* 1996, 1998). Rainfall data were collected daily with a rain gauge placed in the centre of an approximately 0.5-ha clearing at the centre of the BRS (Figure 1).

There are three species of large hornbill (Aves: Bucerotidae) within the Dja Reserve. Two are predominantly frugivorous, the black-casqued hornbill (*Ceratogymna atrata*) and the white-thighed hornbill (*Bycanistes albotibialis*). The third species, the piping hornbill (*C. fistulator sharpii*), is smaller and has a somewhat more general diet (Kemp 2001).

There are approximately 230 tree species within the reserve. *Ceratogymna atrata* and *B. albotibialis* have been observed to eat the fruit of 22% of these species (Poulsen *et al.* 2002, Whitney *et al.* 1998).

The hornbill breeding season runs from early July to mid-October. *Ceratogymna atrata* and *B. albotibialis* begin to court and investigate nesting cavities in July. Females are walled into cavities by early August and eggs are presumably laid soon after. In 1995, pieces of egg shell appeared in traps placed below nest cavities by mid-August likely indicating that chicks were hatching at this time. In 1995, fledging was observed from the end of September to the middle of October (pers obs, Stauffer & Smith 2004).

Vegetation survey

Vegetation data were collected in the study area in 1994. Average dbh and species density (D_i) were estimated from surveys of mature trees (greater than 10 cm dbh) in two belt transects (10×400 m and 10×450 m), 32 40-m^2 plots and three 100-m^2 plots. Plots were randomly placed within the study area (Fogiel 2007). In all, almost 3300 stems were marked with approximately 304 species in 41 families identified (Appendix 1).

Fruiting phenology

Each month between December 1994 and November 1999, we surveyed approximately 450 reproductively mature trees representing over 40 hornbill-diet species for flowering and fruiting phenology. In all, we made nearly 20 000 observations. As trees died or new diet species were added, mature trees were selected with a goal of surveying about 10 trees of each species each month. Selection methods varied by year. For example in 1995, three randomly generated numbers were used to select: (1) Which trail to leave camp on, (2) How far to go down that trail and (3) What compass bearing to take when leaving the trail. Then the first mature tree of the species encountered was added to the list.

Each tree was examined from the ground and given a score from 0 to 4 for each of four categories: (1) fraction of canopy in flower, (2) fraction of canopy in fruit, (3) fraction of flowers in bud and (4) fraction of fruit that were ripe. For flowers and fruit the scores translate as follows: 0 indicates no sign of fruiting or flowering, $1 = 1-25\%$ of the crown in flower or fruit, $2 = 26-50\%$, $3 = 51-75\%$ and $4 = 76-100\%$ (relative to expectations for that species). For flower buds and ripe fruit the same scale was used except the score is relative to the fraction of canopy in flower or fruit, not to the full canopy. So, for example, a score of 3 for flower buds means that between 51% and 75% of the flowering was in bud. We also recorded observations of flowers and fruit on the ground to reinforce our observations from the canopy (Fogiel 2007, Hardesty 1999, Hardesty & Parker 2003, Holbrook & Smith 2000, Lamperti 2004, Whitney *et al.* 1998).

Feeding observations

The diets of *B. albotibialis* and *C. atrata* were quantified in the following manner. A series of six trail loops within the BRS were each walked approximately five times per month for a total distance sampled of approximately 175 km mo^{-1} (Poulsen *et al.* 2001). Trails were walked at a steady pace and species, numbers of individuals, sex and feeding behaviours were recorded for each group of arboreal frugivores encountered. Frugivores were located both visually and by sound and observers left the trail for short distances and times to collect data on groups not visible from the trail. Food species was recorded for each observation of explicit or likely (feeding behaviours and fruit present, but no observed consumption) feeding (Lamperti 2004, Poulsen *et al.* 2002, Whitney & Smith 1998, Whitney *et al.* 1998). Schoener's index was calculated to compare the diets of the two hornbill species (Schoener 1968).

Fruit collection/nutritional analysis

We collected samples of fruit pulp for nutritional analysis in 1995 and 1997. Ripe fruit were collected opportunistically from the canopy of fruiting individuals where possible and from the ground below fruiting individuals when necessary. Fruit pulp was mechanically removed from the seed(s) and placed in 70% ethanol for preservation. Samples of pulp were weighed, dried in a kerosene oven and reweighed to estimate water content.

Samples collected in 1995 were tested for crude protein, dry matter, ash, cell wall constituents (neutral and acid detergent fibre and lignin), water-soluble carbohydrates (or simple saccharides) and assorted minerals (Ca, Cu, Fe, Mg, Mn, Na, P, Zn) at the Department of Nutrition, Wildlife Conservation Society, Bronx, New York. Samples collected in 1997 were analysed for the same components with the addition of crude fat.

Table 1. Fruit tissue samples collected in the Dja reserve in 1995 and 1997. Samples were dried in a kerosene oven to measure water content.

Family	Species	Fruit wet weight (g)(N)	Fruit % water (N)	Year
Anacardiaceae	*Lannea welwitschii*	0.36 (1)		1995
Anisophylleaceae	*Anopyxis klaineana*	4.26 ± 0.82 (8)	64.0 ± 25.9 (8)	1995
Annonaceae	*Cleistopholis glauca*	1.08 ± 0.06 (5)	66.5 ± 2.14 (5)	1995
	Cleistopholis patens	6.03 ± 1.47 (10)	78.3 ± 2.14 (10)	1995
	Enantia chlorantha	1.32 ± 0.68 (21)	57.8 ± 25.5 (21)	1995
	Pachypodanthium staudtii	1.09 ± 0.46 (10)	46.1 ± 33.8 (15)	1995
	Polyalthia suaveolens	1.73 ± 0.31 (8)	74.8 ± 3.79 (8)	1995
	Xylopia aethiopica			1997
	Xylopia rubescens			1995
	Xylopia sp.			1997
	Xylopia staudtii			1997
Apocynaceae	*Rauwolfia macrophylla*			1997
Arecaceae	*Elaeis guineensis*			1997
	Eremospatha macrocarpa	2.87 ± 2.16 (8)	62.8 ± 11.9 (8)	1995
	Lacosperma secundiflorum	1.92 ± 0.26 (10)	66.6 ± 22.3 (11)	1995
	Raphia monbuttorum	15.21 ± 2.92 (2)	56.1 ± 1.48 (2)	1995
Burseraceae	*Canarium schweinfurtii*	4.98 ± 0.37 (10)	51.5 ± 1.71 (10)	1997
	Dacryodes edulis	3.15 ± 1.94 (15)	44.8 ± 19.7 (15)	1995
Combretaceae	*Pteleopsis hylodendron*			1997
Connaraceae	Unknown			1997
Dracaenaceae	*Dracaena arborea*			1997
Euphorbiaceae	*Bridelia* sp.			1995
	Macaranga sp.			1997
	Uapaca paludosa	4.85 ± 1.8 (10)	29.7 ± 31.4 (10)	1995 & 1997
	Uapaca sp.			1997
Meliaceae	*Guarea cedrata*	3.28 ± 2.12 (3)	78.7 ± 5.06 (3)	1995: 1 1997: 2
	Trichilia sp.			1997
	Trichilia sp.			1997
	Trichilia sp.			1997
Moraceae	*Ficus* spp.	0.56 ± 0.13 (20)	74.9 ± 7.70 (20)	1995: 4 1997: 1
	Trilepisium madagascariense			1997
Myristicaceae	*Pycnanthus angolensis*	1.47 ± 1.27 (16)	29.0 ± 22.3 (16)	1995
	Staudtia kamerunensis	0.74 (1)	66.2 (1)	1995
Olacaceae	*Heisteria zimmereri*	0.5 ± 0.12 (15)	18.0 ± 26.4 (15)	1995
	Strombosiopsis tetrandra	10.89 ± 2.22 (12)	88.6 ± 2.79 (12)	1995
Rhamnaceae	*Maesopsis eminii*	1.23 ± 0.24 (10)	76.5 ± 1.33 (10)	1995
Sapindaceae	*Blighia welwitschii*	1.13 ± 0.32 (10)	65.2 ± 3.42 (10)	1995
	Eriocoelum macrocarpum	0.12 ± 0.03 (11)	24.7 ± 21.0 (11)	1995
Sterculiaceae	*Eribroma oblongum*			1997
Ulmaceae	*Celtis tessmannii*			1995

Crude protein was analysed using a macro-Kjeldahl method, which determined CP as total nitrogen × 6.25. Neutral detergent fibre, acid detergent fibre and lignin values were determined using Goering & Van Soest (1970). Water-soluble carbohydrates were analysed by using a modification of Strickland & Parson (1972). Samples were extracted with boiling water for 10 min and then 0.5 ml phenol and 2.5 ml sulphuric acid were added. After 1 h, sample absorption was determined on a Genysis 5 spectrophotometer. Crude fat was measured using a 1045 Tectaor Soxtec system to extract lipid fractions with petroleum ether, following procedures outlined in AOAC for feeds and foods.

Mineral analyses were performed using standard atomic absorption spectrophotometer methods for plants (Perkin Elmer 1982). Duplicate samples were ashed in a muffle furnace at 550 °C overnight, cooled in a desiccator and weighed to determine ash content. They were then dissolved in 20% HCl with heat and then diluted to 25 ml with a 1% lanthanum solution (when necessary samples were further diluted with 0.36 N HCl containing 1% La). Ca, Cu, Fe, Mg, Mn and Zn were individually run on a Perkin Elmer atomic absorption spectrophotometer (Model 3100) with an air acetylene flame and a 0.36 N HCl with 1% La blank. Phosphorus was measured using modified AOAC colorimetric methods (AOAC 1995).

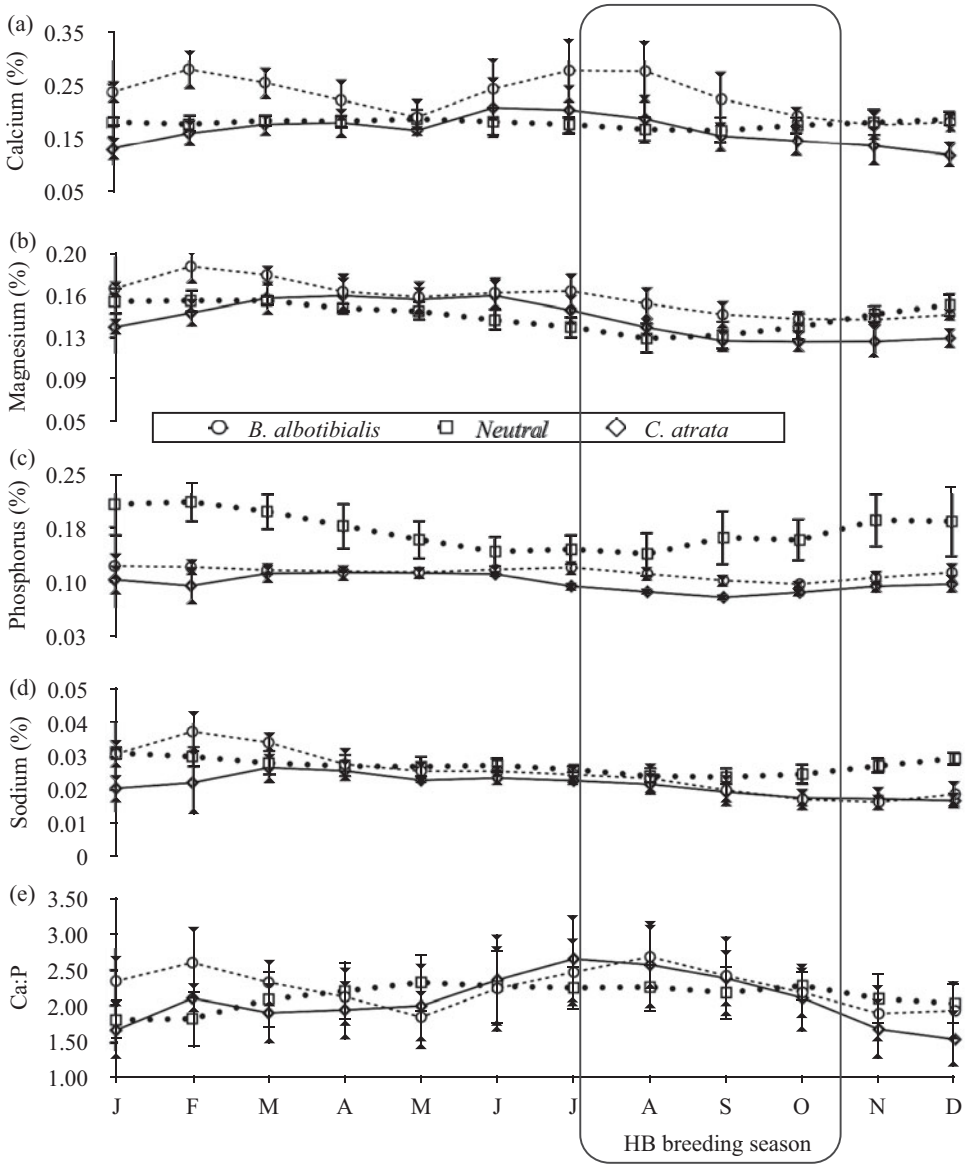

Figure 2. Monthly average concentrations of the macrominerals calcium (a), magnesium (b), phosphorus (c) and sodium (d) along with the calcium to phosphorus ratio (e) in both the selected and neutral diets for *Ceratogymna atrata* and *Bycanistes albotibialis* in the Dja reserve, Cameroon, from 1994 to 1999. Error bars represent 95% confidence intervals; N = 5 for all months and nutrients.

RESULTS

Feeding observations

The number of feeding observations averaged 19.0 (range = 0–91) mo^{-1} (*B. albotibialis*) and 27.7 (0–74) mo^{-1} (*C. atrata*) for the study period. In total we collected 3165 feeding observations over 68 mo (Appendix 2). The hornbills were observed to eat an average of 7.5 (0–16) spp. mo^{-1} (*B. albotibialis*) and 9.8 (0–26) spp. mo^{-1} (*C. atrata*) over the same time period. The diets of the two species were substantially similar, with a diet overlap of 0.65 (Schoener's index) for all feeding observations over the study period. The difference between the diets was primarily due to two species which account for more than half of the difference between the diets: *Maesopsis eminii* and *Pycnanthus angolensis*. *Bycanestes albotibialis* appears to prefer *Maesopsis eminii* while *Ceratogymna atrata* prefers *Pycnanthus angolensis*.

Nutritional analysis

Samples of fruit tissue were collected from 78 trees of 40 species in 1995 and 1997. Some of these collections were combined in the laboratory to create an adequate

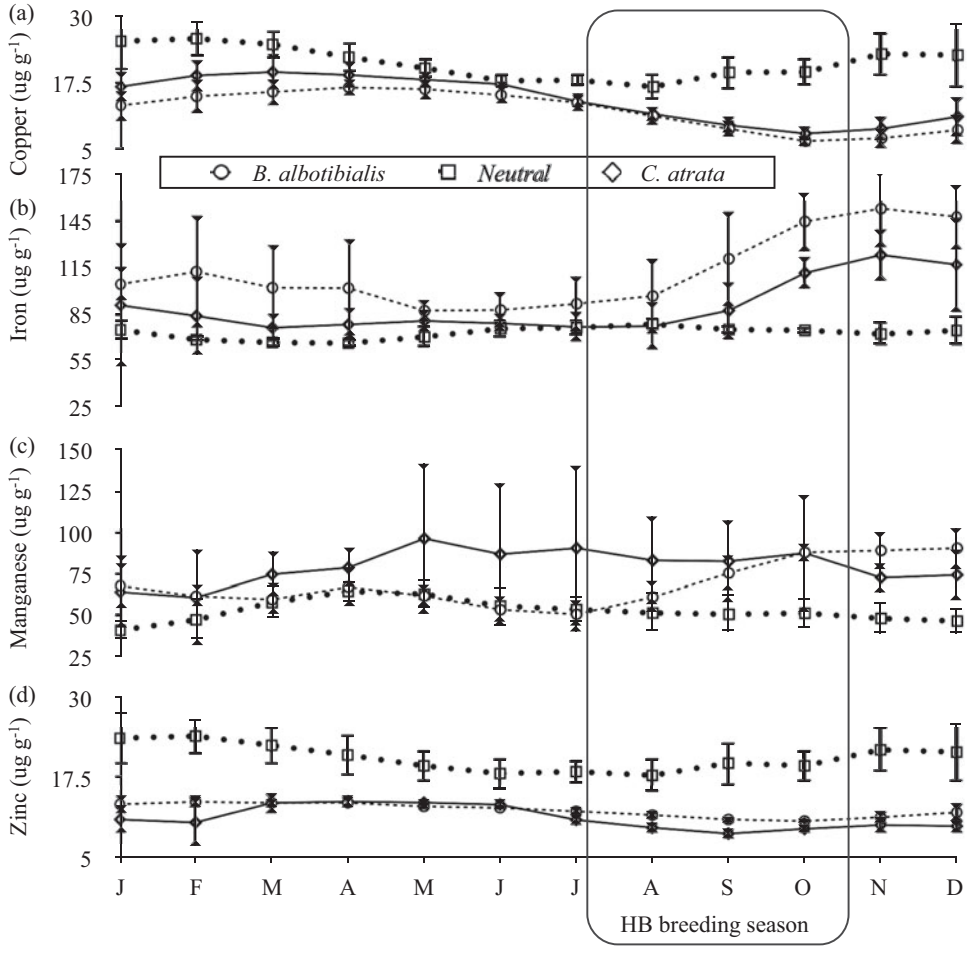

Figure 3. Monthly average concentrations of the microminerals copper (a), iron (b), manganese (c) and zinc (d) in the selected and neutral diets for *Ceratogymna atrata* and *Bycanistes albotibialis* in the Dja reserve, Cameroon, from 1994 to 1999. Error bars represent 95% confidence intervals; N = 5 for all months and nutrients.

sample for analysis. In all, 58 samples were analysed for their nutrient concentrations (Table 1). Together these samples provide nutritional data for 78.3% and 71.7% of the observed diet of *C. atrata* and *B. albotibialis* respectively (Appendix 2).

Monthly selected and neutral diet nutritional content

The nutrient concentrations of both the neutral and the selected diet varied considerably over the 5-y period studied. For the 61 mo for which there are both neutral and selected diet data, the neutral and selected diets were significantly different from each other for all nutrients and for the two hornbill species except for crude protein and lignin for *B. albotibialis* and magnesium and lignin for *C. atrata* ($P < 0.05$, Student's t, $N = 61$, $t = 2.19 - 17.9$).

For calcium and magnesium (Figure 2), iron and manganese (Figure 3), ash (Figure 4) and fat content (Figure 5), there are periods of the year (i.e. 3 mo or more in a row) where the concentration of the selected diet significantly (Student's t, $P < 0.05$, $N = 5$ except December where $N = 6$, $t = 2.8 - 14.6$) exceeds that of the neutral for one or both species. For phosphorus (Figure 2), copper and zinc (Figure 3), neutral detergent fibre (Figure 4) and soluble carbohydrates (Figure 5) the neutral diet concentration is greater than the selected diet concentration for all or most of the year (Student's t, $P < 0.05$, $N = 5$ except December where $N = 6$, $t = 2.88 - 15.4$). The remaining nutrients measured, sodium (Figure 2), copper and zinc (Figure 3), acid detergent fibre and lignin (Figure 4), and crude protein (Figure 5), show relatively little difference between the selected and non-selected diet concentrations over the study period. The fraction of feeding observations that were sightings of feeding on invertebrates also varied considerably over the study period (Figure 6) with peak invertebrate intake roughly coincident with the rainy seasons for both hornbill species.

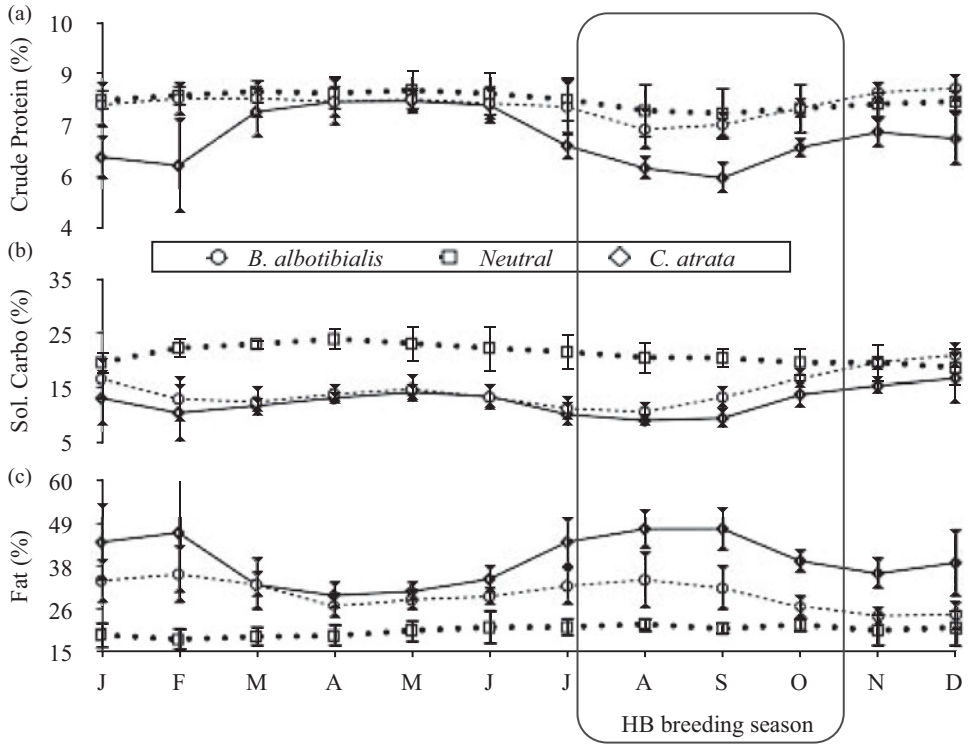

Figure 4. Monthly average concentrations of the cell-wall constituents: neutral detergent fibre (a), acid detergent fibre (b), lignin (c) and ash (d), for both the selected and the neutral diets for *Ceratogymna atrata* and *Bycanistes albotibialis* in the Dja reserve, Cameroon, from 1994 to 1999. Error bars represent 95% confidence intervals; N = 5 for all months and nutrients.

Calcium

If hornbills are selecting their diet for calcium leading up to and during the breeding season, any increase in the calcium concentration of the diet should be apparent by the middle of August. Figure 2 shows that the *B. albotibialis* selected diet contains significantly more calcium than the neutral in July and August (Student's t, $P < 0.05$, $N = 6$, $t = 3.26$ for July and $t = 3.15$ for August). The selected diet calcium for *Ceratogymna atrata* has a similar pattern, rising above the chosen diet for June to August, but not significantly so.

Energy

Once the special need for calcium during egg-laying is over, hornbills should be free to choose a diet appropriate to the next stage of the reproductive process: brooding. Fat represents the majority of the energy in fruit, so we use it here as a proxy for energy (Figure 5). Throughout the year, both species are choosing a diet that is significantly higher in fat than the neutral diet (Student's t, $P < 0.05$, $N = 5$, $t = 2.8-14.6$) except for *B. albotibialis* in December. This preference becomes highly significant for *C. atrata* from July to January (Student's t, $P < 0.01$, $N = 5$ all months except December where $N = 6$, $t = 5.25-14.6$).

Iron

For much of the year, both hornbill species select a diet that is similar in iron to the neutral diet (Figure 3). However starting in September, just as chicks are hatching, there is a rise in iron concentration for both species which becomes significant from August through the end of the year.

Protein

As previously stated, protein is important in the raising of chicks. Figure 5 compares the selected and neutral diet's protein content. From this graph, it appears that hornbills are not generally selecting a high protein fruit diet. The selected diet contains significantly more protein than the neutral only for *B. albotibialis* in November (Student's t, $P < 0.05$, $N = 5$, $t = 3.02$) and December (Student's t, $P < 0.01$, $N = 6$, $t = 5.32$). The overall

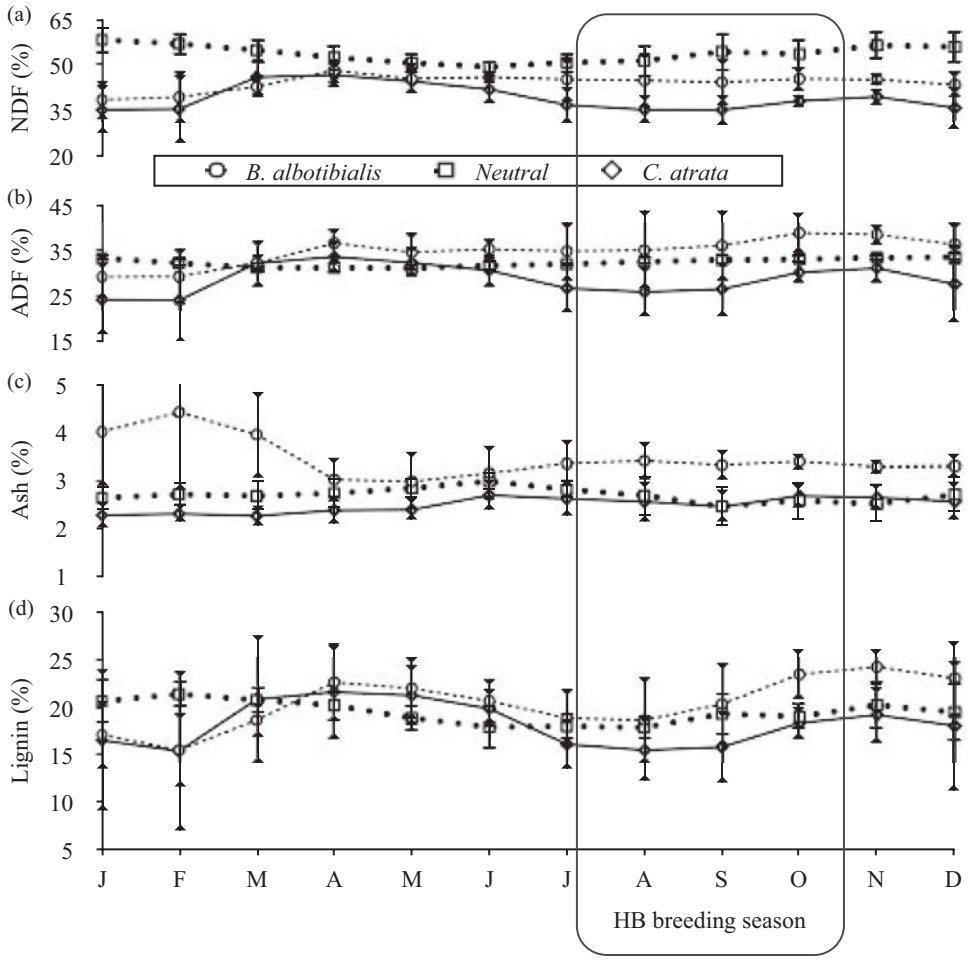

Figure 5. Monthly average concentrations of the macronutrients crude protein (a), soluble carbohydrates (b), and fat (c) for both the selected and the neutral diets of *Ceratogymna atrata* and *Bycanistes albotibialis* in the Dja reserve, Cameroon, from 1994 to 1999. Error bars represent 95% confidence intervals; N = 5 for all months and nutrients.

average protein intake from fruit is 7.1% for *B. albotibialis* and 6.61% for *C. atrata* (Table 2).

However, protein is relatively easily, and commonly, supplemented by the addition of invertebrates to the diet. Although the amount of effort put into observing instances of feeding on invertebrates varied from year to year in this study, making quantitative comparisons difficult, a look at Figure 6 demonstrates a clear pattern. Both hornbill species spend more time foraging for invertebrates during the larger of the two rainy seasons, roughly between August and November. This period is coincident with the period between egg-laying and fledging.

Breeding success

We correlated four nutrient measures in the chosen diet with breeding success calculated as the fraction of nesting starts that fledged at least one chick for June–September, 1994–1997 (Table 3). The number of nesting starts ranged from 0 to 13 for *B. albotibialis* and 0 to 25 for *C. atrata* for the 20–50 cavities monitored. Success ranged from 0 to 54% for *B. albotibialis* and 0 to 67% for *C. atrata*. The measures correlated are calcium, calcium to phosphorus ratio, iron and fat. Calcium ($P < 0.05$, Student's t, $t = 6.19$, $N = 4$) and Ca : P ratio ($P < 0.01$, Student's t, $t = 22.8$, $N = 4$) in June are significantly correlated with breeding success for *B. albotibialis*. Fat is positively correlated with breeding success for both species from June through September, although not significantly so.

DISCUSSION

We developed a pair of indices that use easily collected field data to quantify the nutrient consumption of two hornbill species over several years. By comparing the actual diet of hornbills to a neutral diet reflecting

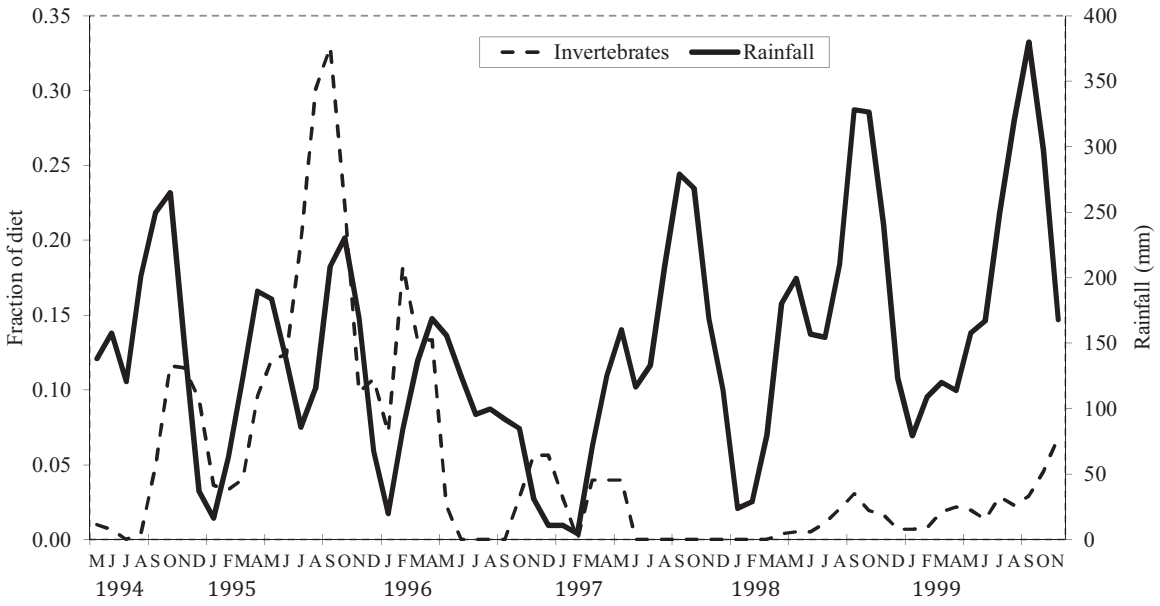

Figure 6. Three-month average fraction of hornbill feeding observations where invertebrates were the food item for the study period (1994 – 1999). Fractions are each month's share of the study year's observations to adjust for varying effort between years. Rainfall (mm) is shown as well to give a sense of the seasonality of invertebrate consumption.

the relative availability of nutrients in the forest, we found that hornbills consume fruit according to the nutritional requirements of breeding, rather than the relative availability of fruit in the forest.

Our indices are based on several assumptions about hornbill diets (e.g. feeding observations reflect the actual mass of fruit consumed by birds), but we are encouraged that the results match expectations based on breeding biology and seasonality. Therefore, while the indices could be rendered more accurate by including additional data, we think they provide a practical way to quantify nutrient consumption of wild animals, and for hornbills, potentially to predict breeding success.

In the Dja, hornbills are actively selecting a diet to meet the mineral and energetic demands of breeding, starting with calcium during egg-laying, and moving to energy, protein and iron for brooding, growth and fledging. However, breeding success was not uniformly high in the Bouamir Research Station in the Dja Reserve between 1994 and 1997 ranging from 0 to 67% for *C. atrata* and 0 to 54% for *B. albotibialis* (Stauffer & Smith 2004). This raises the question of what factors limit breeding success of hornbills in this forest.

Several resources have been reported to limit populations of cavity-nesting birds, including availability of nest cavities, nest predation and nutrient availability (Datta & Rawat 2004, Graveland & Drent 1997, Martin 1987, 1993; Rendell & Robertson 1994). Within our study area, hornbill reproduction does not appear to be limited by lack of nest cavities or predation; rather, nesting success appears to be tied to fruit availability (Stauffer & Smith 2004). At a landscape scale, hornbill densities vary strongly by season and hornbills make large range movements to track fruit resources (Anggraini *et al.* 2000, Holbrook & Smith 2000, Holbrook *et al.* 2002, Kinnaird & O'Brien 2005). Together, this information suggests that hornbills are limited by food resources, not by nesting sites.

This study suggests that hornbills also track resources at a much finer scale, selecting from the food resources available to them at a given site to meet nutritional needs that change through the year. The diet measures that are candidates for predicting breeding success are the ones that the hornbills actively select: diet calcium, iron and fat (energy). In addition it makes sense to look at the diet calcium to phosphorus ratio since it is considered a better indicator of the calcium available for metabolic uptake than calcium alone (McDowell 2003, Robbins 1993). Three of these diet measures appear to be potentially useful as predictors of breeding success in this system. The diet calcium and the calcium to phosphorus ratio are significantly correlated with breeding success for *B. albotibialis* in June. The fat content of the diet is correlated with breeding success throughout the breeding season for both species, although not significantly so (Table 3). These results suggest that breeding success is most dependent on metabolically available calcium and total energetic content.

It is worth noting that hornbills are not actively choosing a diet with a high Ca : P ratio, as they are with

Table 2. Dietary requirements for birds (Murphy 1996) compared with available nutrients (i.e. neutral diet) as well as nutrients provided by the fruit portion of the diets of *Bycanestes albotibialis* and *Ceratogymna atrata* in the Dja reserve between 1995 and 1999. Values are on a dry-mass basis.

Nutrient	Published requirement	Fruit samples Mean (Range) N = 40	Selected diet *B. albotibialis* Mean (Range) N = 68	Selected diet *C. atrata* Mean (Range) N = 68	Neutral diet Mean (Range) N = 61
Macronutrients (% DM)					
Crude Protein	8.0–14.0	7.25 (3.05–19.46)	7.1 (5.73–9.59)	6.61 (3.05–8.95)	7.72 (6.21–9.0)
Soluble carbohydrates		16.3 (0.8–50.58)	13.38 (7.11–21.8)	12.6 (3.75–24.8)	21.2 (12.4–30.1)
Fat		35.1 (0–78.17)	41.24 (29.0–55.4)	39.31 (23.3–72.4)	20.6 (12.8–28.8)
Ash		3.46 (0.6–9.06)	3.44 (1.97–7.54)	2.5 (1.77–3.32)	2.7 (1.76–3.33)
Macrominerals (% DM)					
Calcium	0.44	0.23 (0.01–1.09)	0.23 (0.13–0.4)	0.16 (0.09–0.33)	0.18 (0.12–0.22)
Magnesium	0.15–0.35	0.17 (0.03–0.47)	0.16 (0.13–0.21)	0.14 (0.1–0.19)	0.14 (0.1–0.18)
Sodium	0.12	0.03 (0.004–0.06)	0.02 (0.01–0.05)	0.02 (0–0.03)	0.03 (0.02–0.03)
Phosphorus	0.35	0.11 (0.03–0.4)	0.11 (0.09–0.15)	0.1 (0.06–0.14)	0.17 (0.09–0.27)
Microminerals (mg g^{-1})					
Copper	5	12.9 (0.93–44.9)	12.3 (3.45–19.6)	14.3 (5.08–24.5)	21.44 (12.7–33.7)
Iron	120	123 (24.65–1917)	113 (60.8–202)	90.6 (55.2–171)	72.9 (62.2–88.6)
Manganese	60–70 (egg laying)	120 (4.72–1508)	69.2 (41.0–106)	80.0 (10.6–200)	52.8 (26.4–72.9)
Zinc	25	15.42 (1.3–47.4)	12.4 (10.3–15.3)	11.2 (3.76–15.0)	20.6 (13.7–30.2)
Cell wall constituents (% DM)					
Neutral Detergent Fibre		36.8 (8.88–83.9)	44.2 (24.0–60.0)	39.1 (18.5–54.0)	53.8 (44.1–66.0)
Acid Detergent Fibre		28.71 (3.86–71.1)	35.0 (19.3–49.6)	28.8 (11.7–43.2)	32.4 (29.4–34.9)
Lignin		17.21 (1.05–56.1)	20.5 (8.43–27.6)	18.2 (6.64–31.9)	19.5 (14.7–24.6)

Table 3. Correlations between the calcium, calcium to phosphorus ratio, iron and fat in the neutral diet and hornbill breeding success. Breeding success data are from Stauffer & Smith (2004) and represent data from 1994–1997. Success is calculated as the fraction of nesting starts that fledged at least one chick. Regressions are significant at the 0.05 level (*) and 0.01 (**). N = 4 for all nutrients and months.

	Correlation Coefficient			
Hornbill species	June	July	August	September
Nutrient				
Bycanistes albotibialis				
Calcium	0.975 *	0.464	0.044	− 0.272
Ca : P	0.998 **	0.827	− 0.297	− 0.728
Iron	− 0.119	− 0.051	− 0.495	− 0.422
Fat	0.215	0.405	0.498	0.476
Ceratogymna atrata				
Calcium	0.467	0.077	0.136	− 0.494
Ca : P	− 0.033	− 0.576	0.429	− 0.468
Iron	− 0.192	− 0.616	− 0.827	− 0.904
Fat	0.731	0.768	0.928	0.937

Table 4. Mineral concentrations of fruit samples collected in the Dja Reserve, Cameroon, in 1995 and 1997. Samples were stored in 70% ethanol in the field.

		Ca	Mg	Na	P	Cu	Fe	Mn	Zn
Family	Species (N)	% DM				mg g^{-1}			
Anacardiaceae	*Lannea welwitschii* (1)	0.44	0.18	0.01	0.16	14.0	70.0	12.7	11.1
Anisophylleaceae	*Anopyxis klaineana* (1)	0.19	0.08	0.02	0.09	7.5	74.6	48.5	9.6
Annonaceae	*Cleistopholis glauca* (2)	0.14	0.08	0.04	0.08	8.5	118	61.1	11.7
	Cleistopholis patens (1)	0.34	0.17	0.04	0.09	7.7	50.5	265	16.9
	Enantia chlorantha (3)	0.36	0.28	0.06	0.13	27.2	104	4.7	17.8
	Pachypodanthium staudtii (1)	0.17	0.07	0.02	0.08	7.9	40.5	90.9	8.6
	Polyalthia suaveolens (1)	0.21	0.14	0.01	0.05	13.4	50.6	112	8.6
	Xylopia aethiopica (1)	0.11	0.08	0.03	0.05	22.5	111	61.5	47.4
	Xylopia rubescens (1)	0.12	0.05	0.01	0.05	0.9	133	16.7	8.5
	Xylopia sp. (1)	0.17	0.14	0.02	0.09	13.1	91.0	79.1	29.8
	Xylopia staudtii (1)	0.28	0.07	0.01	0.08	11.7	38.7	79.2	11.0
Apocynaceae	*Rauwolfia macrophylla* (2)	0.30	0.21	0.05	0.13	9.8	99.9	51.6	12.1
Arecaceae	*Elaeis guineensis* (2)	0.12	0.13	0.00	0.05	24.1	136	10.6	3.8
	Eremospatha macrocarpa (1)	0.14	0.11	0.02	0.07	7.5	64.9	138	26.4
	Lacosperma secundiflorum (1)	0.15	0.09	0.03	0.12	9.5	41.0	132	17.6
	Raphia monbuttorum (2)	0.57	0.36	0.02	0.03	5.7	24.7	1,508	10.2
Burseraceae	*Canarium schweinfurthii* (2)	0.26	0.13	0.01	0.05	7.5	61.9	116	9.7
	Canarium schweinfurthii (1)	1.09	0.23	0.05	0.13	23.7	97.8	21.7	24.5
Combretaceae	*Pteleopsis hylodendron* (2)	0.59	0.35	0.03	0.23	20.6	1,917	573	26.3
Connaraceae	Unknown (2)	0.01	0.03	0.03	0.03	7.3	24.7	5.4	1.3
Dracaenaceae	*Dracaena arborea* (1)	0.08	0.10	0.01	0.04	11.3	39.1	23.2	8.2
Euphorbiaceae	*Bridelia* sp. (1)	0.34	0.13	0.01	0.17	8.0	43.0	13.0	16.5
	Macaranga sp. (1)	0.39	0.32	0.05	0.10	16.2	79.6	419	12.7
	Uapaca paludosa (2)	0.12	0.15	0.03	0.05	5.6	117	40.7	7.0
	Uapaca sp. (2)	0.16	0.15	0.03	0.06	7.6	130	9.8	9.4
Meliaceae	*Guarea cedrata* (3)	0.07	0.09	0.02	0.14	12.3	67.3	41.6	11.1
	Trichilia sp. (1)	0.11	0.15	0.02	0.12	9.4	27.0	41.7	5.3
	Trichilia sp. (1)	0.14	0.16	0.03	0.15	15.5	70.4	24.6	23.0
	Trichilia sp. (*welwitschii*?) (1)	0.11	0.25	0.03	0.15	12.5	98.5	17.3	34.1
Moraceae	*Ficus* spp. (5)	0.61	0.23	0.04	0.10	11.3	71.8	43.1	16.9
	Trilepisium madagascariense (1)	0.40	0.21	0.04	0.12	10.3	156	80.7	15.1
Myristicaceae	*Pycnanthus angolensis* (1)	0.03	0.09	0.02	0.06	12.5	42.4	10.6	4.7
	Staudtia kamerunensis (2)	0.11	0.15	0.02	0.13	24.0	61.0	88.6	14.6
Olacaceae	*Heisteria zimmereri* (1)	0.06	0.19	0.02	0.25	13.1	52.7	108	10.0
	Strombosiopsis tetrandra (1)	0.06	0.09	0.03	0.10	9.0	71.3	18.1	17.0
Rhamnaceae	*Maesopsis eminii* (1)	0.13	0.14	0.01	0.10	2.7	199	108	10.0
Sapindaceae	*Blighia welwitschii* (1)	0.18	0.47	0.03	0.18	27.1	71.1	10.5	29.7
	Eriocoelum macrocarpum (1)	0.06	0.13	0.02	0.40	44.9	47.9	25.5	41.9
Sterculiaceae	*Eribroma oblongum* (2)	0.18	0.16	0.02	0.08	2.3	71.7	56.5	7.9
Ulmaceae	*Celtis tessmannii* (1)	0.24	0.31	0.04	0.09	10.1	56.0	222	8.9

calcium alone (Figure 2). This presents some questions for further study: Where there are two independent nutrients that contribute to an animal's health, what behavioural mechanisms exist to optimize both? In this system, what combinations of fruit are leading to a diet with a high Ca : P ratio in some years and not others and thus to greater breeding success? What is the relative importance of each contributor to breeding success?

Figs (*Ficus* spp.) have often been considered to be keystone species in tropical systems (Gautier-Hion & Michaloud 1989, Kinnaird & O'Brien 2005, 2008; Lambert & Marshall 1991, Leighton & Leighton 1983, Shanahan *et al.* 2001, Terborgh 1986). Specifically, they have been found to have high calcium concentration and Ca : P ratios in a number of systems (O'Brien *et al.* 1998, Wendeln *et al.* 2000). In the Dja, the average Ca : P ratio for *Ficus* spp. in our samples is 6.60 (N = 5) and the average for all non-fig samples is 3.03 (N = 56; Table 4). This is similar to the pattern seen in other systems (O'Brien *et al.* 1998). However, *Ficus* spp. make up a small percentage of the feeding observations over the study period (0.88% of the *C. atrata* diet and 5.68% of the *B. albotibialis*; Appendix 2) and those observations are not concentrated in June and July when calcium is peaking in the observed diet. Therefore, while figs do have a disproportionately high Ca : P ratio and hornbills are eating them in the Dja, they are not a keystone calcium source in this system.

Table 5. Macronutrient and cell wall constituent concentrations of fruit samples collected in the Dja Reserve, Cameroon, in 1995 and 1997. Samples were stored in 70% ethanol in the field. CP = Crude Protein, Sol CHO = soluble carbohydrates, NDF = Neutral Detergent Fibre and ADF = Acid Detergent Fibre.

Family	Species (N)	Ash	CP	Sol CHO	NDF	ADF	Lignin	Fat
		% DM						
Anacardiaceae	*Lannea welwitschii* (1)	3.9	6.0	3.1	64.2	51.5	23.1	
Anisophylleaceae	*Anopyxis klaineana* (1)	3.4	6.9	5.5	54.0	46.8	26.8	
Annonaceae	*Cleistopholis glauca* (2)	1.2	5.0	9.7	57.3	40.4	13.0	
	Cleistopholis patens (1)	3.3	6.4	32.0	29.7	25.4	14.2	
	Enantia chlorantha (3)	4.8	12.7	13.0	44.6	32.2	12.6	
	Pachypodanthium staudtii (1)	1.8	5.4	19.8	53.8	45.9	29.0	
	Polyalthia suaveolens (1)	2.5	9.4	28.7	37.2	27.4	15.6	
	Xylopia aethiopica (1)	1.3	4.8	0.8	35.2	26.5	10.4	59.0
	Xylopia rubescens (1)	2.2	4.9	3.9	52.4	32.6	7.6	
	Xylopia sp. (1)	1.2	9.2	1.5	56.3	39.2	9.8	20.7
	Xylopia staudtii (1)	1.6	8.6	6.5	43.7	32.2	4.4	21.4
Apocynaceae	*Rauwolfia macrophylla* (2)	7.5	7.6	10.5	24.1	19.3	8.4	10.4
Arecaceae	*Elaeis guineensis* (2)	2.2	3.1	3.7	18.5	11.7	6.6	69.4
	Eremospatha macrocarpa (1)	3.0	7.4	24.5	45.5	29.9	17.3	
	Lacosperma secundiflorum (1)	3.0	6.9	30.8	39.6	23.1	12.9	
	Raphia monbuttorum (2)	3.0	3.7	14.3	32.0	23.3	9.4	29.7
Burseraceae	*Canarium schweinfurthii* (2)	3.8	3.7	3.7	39.6	38.9	30.3	33.1
	Canarium schweinfurthii (1)	5.9	8.9	3.9	44.4	30.2	18.1	
Combretaceae	*Pteleopsis hylodendron* (2)	7.4	12.8	1.1	60.3	48.3	19.2	8.7
Connaraceae	Unknown (2)	9.1	5.5	5.3	16.9	9.4	7.6	67.5
Dracaenaceae	*Dracaena arborea* (1)	1.9	7.7	44.7	9.5	5.4	1.1	10.6
Euphorbiaceae	*Bridelia* sp. (1)	2.8	7.2	20.7	37.3	32.8	24.1	
	Macaranga sp. (1)	3.0	5.6	12.8	13.0	5.9	3.6	47.5
	Uapaca paludosa (2)	4.7	3.1	20.5	50.0	53.5	41.6	5.4
	Uapaca sp. (2)	4.5	3.7	7.1	68.6	71.1	56.1	2.5
Meliaceae	*Guarea cedrata* (3)	2.5	8.2	41.9	8.9	3.9	1.4	14.0
	Trichilia sp. (1)	2.0	6.7	12.5	14.6	11.6	6.1	13.9
	Trichilia sp. (1)	2.9	7.0	12.6	14.3	10.9	5.4	20.9
	Trichilia sp. *(welwitschii?)* (1)	3.1	10.3	16.7	13.8	10.3	5.2	14.4
Moraceae	*Ficus* spp. (5)	4.4	5.4	5.3	66.9	54.8	30.6	2.6
	Trilepisium madagascariense (1)	6.5	8.9	18.4	23.3	18.2	12.7	
Myristicaceae	*Pycnanthus angolensis* (1)	1.0	3.4	3.4	17.5	6.2	4.0	
	Staudtia kamerunensis (2)	1.6	7.6	13.7	50.6	36.2	30.5	
Olacaceae	*Heisteria zimmereri* (1)	3.7	12.5	17.3	9.2	5.0	4.5	
	Strombosiopsis tetrandra (1)	4.4	7.6	35.0	40.4	35.2	20.8	
Rhamnaceae	*Maesopsis eminii* (1)	3.4	8.9	22.5	46.7	43.1	28.2	
Sapindaceae	*Blighia welwitschii* (1)	3.6	19.5	4.3	33.3	22.8	17.8	
	Eriocoelum macrocarpum (1)	0.6	6.3	30.6	83.9	34.8	34.8	
Sterculiaceae	*Eribroma oblongum* (2)	5.0	5.2	0.9	40.6	33.3	7.6	29.9
Ulmaceae	*Celtis tessmannii* (1)	4.5	6.7	17.4	32.3	19.4	13.2	

A major assumption made here was the substitution of the proportional representation of each fruit in hornbill diets for the total dry mass of each food item eaten during a time period. Even though feeding observations are relatively simple data to collect in the field, it is not obvious how well they substitute for the actual dry mass of fruit consumed. The fraction of feeding observations is a sample more of how long birds are spending at feeding sites (foraging time, t_{ti}) than of how much of their diet that item represents. If we assume that foraging time is a good proxy for dry mass consumed, the system is simplified and estimation of the water content and foraging efficiency is avoided. Differences in foraging efficiency between fruit may be partly compensated for by differences in water content. It is plausible that larger wetter fruits will be more efficiently harvested (i.e. more mass consumed per unit time) than smaller, drier fruits. Thus the product of efficiency and dry mass may be closer to a constant than either alone. To the degree that this is true, the simplification of removing dry mass and foraging efficiency from the calculation will not affect the variance of the result.

In the Dja, hornbills appear to actively select a diet based on nutritional content, including mineral concentration. They are eating a diet significantly higher in calcium before and during egg-laying and they are then selecting a fruit diet that is significantly higher in fat (energy) and iron through the end of the breeding season while

supplementing with invertebrates for protein to feed their young (Table 5).

The two indices presented in this study show seasonal variation in nutrient flows in the Dja, producing results that match expectations based on known breeding biology and timing. The assumptions of a calorically adequate diet, of consistent nutritional and water content of fruit over time, of the proportionality of foraging time to dry mass consumed, and the proportionality of dbh to fruit production (to name a few) may lessen the precision of the results, but the indices accurately reflect expectations of how these birds will modify their diets to meet seasonal shifts in nutrient and energy demands. We conclude that these indices are useful in making comparisons between the chosen versus neutral diets and for predicting breeding success from seasonal diet data for these tropical avian frugivores.

ACKNOWLEDGEMENTS

We are grateful to the government of the Republic of Cameroon, in particular the Ministry of Environment and Forests (MINEF) and the Ministry of Higher Education and Scientific Research (MINREST), for permission to conduct this research. In particular we wish to thank J. M. Mengang, J.-P. Boyogueno and V. S. Balinga. Financial and logistical support were generously provided by NYZS/The Wildlife Conservation Society, the National Science Foundation Graduate Fellowship Program, the GAANN and MIRT fellowship programmes of San Francisco State University, and ECOFAC Cameroun. For assistance in the field we thank S. Benge, M. Biederman, A. L. Bowersox, B. L. Demarest, F. E. Eanet, C. Gjerdrum, E. R. Hekkala, N. A. Helme, C. Hess, D. A. Kilimnik, M. Kimura, D. LeFer, D. Marnel, T. W. Richardson, M. R. Russell, R. E. Rynning, J. G. Schuetz, A. P. Smyth, D. Sonwa, E. Springborn, J. Witkin, T. A. Worth and G. M. Yanega. Residents of Bifolone and Somalomo, particularly A. Siec, D. Amazieh, J. Mann, M. Mbenge and B. Bokama, generously shared their knowledge of the forest with us. We wish to acknowledge the unique contributions of J.-M. Froment, J.-P. Vautherin, R. C. Fotso, P. Muchaal, S. Weise, B. Brennand, S. Scheffler and T. & H. Hockey.

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Appendix 1. Tree-plot data used to generate the model of nutrient availability (Fogiel 2007). Average dbh and species density were estimated from surveys of trees greater than 10 cm dbh in two belt transects, 32 40-m^2 plots and three 100-m^2 plots in 1994.

Species	Average dbh (cm)	Density (stems ha^{-1})
Anopyxis klaineana Pierre	86.7	–
Blighia welwitschii (Hiern.) Radlk.	37.1	–
Canarium schweinfurtii Engl.	91.2	0.39
Celtis tessmannii Rendle	40.6	–
Cleistopholis glauca Pierre ex Engl. & Diels	26	1.76
Cleistopholis patens Engl. & Diels	28.1	0.78
Coelocaryon preussii Warb.	29.7	1.56
Dacryodes edulis (G.Don) H.J.Lam	61.3	–
Dracaena arborea Hort.Angl. ex Link	106	–
Enantia chlorantha Oliv.	21.8	6.25
Eriocoelum macrocarpum Gilg ex Engl. & Radlk.	21.1	6.84
Eribroma oblongum (Mast.) Pierre ex A.Chev.	29.2	1.17
Ficus sp.	47.4	0.2
Heisteria zimmereri Engl.	55	–
Lannea welwitschii (Hiern) Engl.	71.4	–
Macaranga sp. Thouars	35.3	–
Maesopsis eminii Engl.	13.4	0.2
Pachypodanthium staudtii Engl. & Diels	47.5	–
Polyalthia suaveolens Engl. & Diels	18.8	12.11
Pycnanthus angolensis (Welw.) Exell	90.0	–
Rauwolfia macrophylla Stapf	44.6	0.39
Staudtia kamerunensis Warb.	26.1	0.59
Strombosiopsis tetrandra Engl.	21.3	18.75
Uapaca sp.	88.3	–
Uapaca paludosa Aubrév. & Leandri	48.3	–
Xylopia aethiopica A.Rich.	48.3	–
Xylopia rubescens Oliv.	22.1	2.93
Xylopia staudtii Engl. & Diels	38.5	0.98

Appendix 2. Diet of *Bycanistes albotibialis* and *Ceratogymna atrata* observed in the Dja reserve, Cameroon during the study period. Observations were taken during daily walks of the trail system at the BRS between December 1994 and December 1999.

Family	Species	*C. atrata* (%) N = 1877	*B. albotibialis* (%) N = 1288
	Bark	1 (0.03%)	
	Invertebrates	98 (3.10%)	82 (6.37%)
	Lichen	3 (0.09%)	
	Unknown fruit	56 (1.77%)	53 (4.11%)
Anacardiaceae	*Lannea nigritiana*	17 (0.54%)	69 (5.36%)
	Lannea sp.		2 (0.16%)
	Lannea welwitschii	27 (0.85%)	57 (4.43%)
Anisophylleaceae	*Anopyxis klaineana*	2 (0.06%)	2 (0.16%)
Annonaceae	*Cleistopholis glauca*	135 (4.27%)	76 (5.90%)
	Cleistopholis patens	7 (0.22%)	5 (0.39%)
	Cleistopholis sp.	1 (0.03%)	
	Enantia chlorantha	97 (3.06%)	56 (4.35%)
	Pachypodanthium staudtii	1 (0.03%)	2 (0.16%)
	Polyalthia suaveolens	15 (0.47%)	10 (0.78%)
	Xylopia aethiopica	5 (0.16%)	1 (0.08%)
	Xylopia hypolampra	69 (2.18%)	50 (3.88%)
	Xylopia rubescens	24 (0.76%)	10 (0.78%)
	Xylopia staudtii	8 (0.25%)	2 (0.16%)
Apocynaceae	*Alstonia boonei*	5 (0.16%)	5 (0.39%)
	Futumia elastica	1 (0.03%)	1 (0.08%)
	Rauwolfia macrophylla	21 (0.66%)	26 (2.02%)
Arecaceae	*Elaeis guineensis*	22 (0.70%)	
	Lacosperma secundiflorum	10 (0.32%)	2 (0.16%)
	Raphia monbuttorum	15 (0.47%)	1 (0.08%)
Bombacaceae	*Bombax buonopozense*		1 (0.08%)
Burseraceae	*Canarium schweinfurthii*	112 (3.54%)	43 (3.34%)
	Dacryodes edulis	11 (0.35%)	4 (0.31%)
	Santiria trimera	14 (0.44%)	1 (0.08%)
Chrysobalanaceae	*Maranthes glabra*	2 (0.06%)	1 (0.08%)
Clusiaceae	*Allanblackia floribunda*	1 (0.03%)	1 (0.08%)
	Garcinia punctata	1 (0.03%)	
	Garcinia sp.	1 (0.03%)	
Combretaceae	*Pteleopsis hylodendron*	2 (0.06%)	4 (0.31%)
	Terminalia superba	2 (0.06%)	1 (0.08%)
Dracaenaceae	*Dracaena arborea*	28 (0.88%)	9 (0.70%)
Ebenaceae	*Diospyros bipindensis?*	1 (0.03%)	
Euphorbiaceae	*Discoglypremna caloneura*	5 (0.16%)	3 (0.23%)
	Macaranga sp.	2 (0.06%)	
	Margaritia discoidea	1 (0.03%)	1 (0.08%)
	Uapaca guineensis	1 (0.03%)	
	Uapaca acuminata		1 (0.08%)
	Uapaca paludosa	4 (0.13%)	3 (0.23%)
	Uapaca sp.	5 (0.16%)	6 (0.47%)
Fabaceae	*Albizia ferruginea*	1 (0.03%)	
	Cylicodiscus gabunensis	2 (0.06%)	1 (0.08%)
	Distemonanthus benthamianus	8 (0.25%)	4 (0.31%)
	Erythrophloem suaveolens	2 (0.06%)	2 (0.16%)
	Pentaclethra macrophylla	2 (0.06%)	
	Hylodendron gabonense		2 (0.16%)
	Piptadeniastrum africanum	6 (0.19%)	5 (0.39%)
	Pterocarpus mildbraedii	1 (0.03%)	1 (0.08%)
	Pterocarpus soyaxii	3 (0.09%)	2 (0.16%)
	Tessmannia africana	1 (0.03%)	
Icacinaceae?	*Lasiathera? africana?*		1 (0.08%)
Irvingiaceae	*Desbordesia glaucescens*	9 (0.28%)	10 (0.78%)
	Irvingia grandifolia	2 (0.06%)	
	Klainedoxa gabonensis		2 (0.16%)
	Klainedoxa macrocarpa	2 (0.06%)	2 (0.16%)
Lecythidaceae	*Petersianthus macrocarpus*	4 (0.13%)	4 (0.31%)
Lepidobotryaceae	*Lepidobotrys staudtii*	1 (0.03%)	1 (0.08%)

Appendix 2. Continued

Family	Species	*C. atrata* (%) N = 1877	*B. albotibialis* (%) N = 1288
Meliaceae	*Entandophragma cylindricum*	1 (0.03%)	2 (0.16%)
	Entandrophragma angolense	1 (0.03%)	
	Guarea cedrata	49 (1.55%)	43 (3.34%)
	Guarea thompsonii	18 (0.57%)	30 (2.33%)
	Trichilia sp.	6 (0.19%)	8 (0.62%)
	Trichilia welwitschii	11 (0.35%)	6 (0.47%)
	Turraeanthus africanus		1 (0.08%)
Moraceae	*Ficus dekdekena?*	1 (0.03%)	2 (0.16%)
	Ficus sp.	25 (0.79%)	67 (5.20%)
	Milicia excelsa	1 (0.03%)	1 (0.08%)
	Musanga cercropioides	1 (0.03%)	2 (0.16%)
	Trilepisium madagascariense		1 (0.08%)
Myristicaceae	*Coelocaryon preussii*	37 (1.17%)	1 (0.08%)
	Pycnanthus angolensis	300 (9.48%)	34 (2.64%)
	Staudtia kamerunensis	257 (8.12%)	102 (7.92%)
Myrtaceae	*Syzygium* sp.	1 (0.03%)	1 (0.08%)
Olacaceae	*Heisteria zimmereri*	12 (0.38%)	10 (0.78%)
	Ongokea gore	2 (0.06%)	
	Strombosia grandifolia	1 (0.03%)	
	Strombosia pustulata	2 (0.06%)	2 (0.16%)
	Strombosia scheffleri	1 (0.03%)	
	Strombosiopsis tetrandra	1 (0.03%)	1 (0.08%)
Rhamnaceae	*Maesopsis eminii*	214 (6.76%)	310 (24.07%)
Rubiaceae	Rubiaceae sp.	1 (0.03%)	1 (0.08%)
Sapindaceae	*Blighia welwitschii*	15 (0.47%)	2 (0.16%)
	Eriocoelum macrocarpum	11 (0.35%)	5 (0.39%)
Sapotaceae	*Breviea sericea*		1 (0.08%)
	Gambeya lacourtiana	2 (0.06%)	
	Gambeya perpulchra?	3 (0.09%)	
Sterculiaceae	*Eribroma oblongum*	14 (0.44%)	17 (1.32%)
Ulmaceae	*Celtis mildraedii*	9 (0.28%)	10 (0.78%)
	Celtis tessmannii	1 (0.03%)	
Verbenaceae	*Vitex* sp.	2 (0.11%)	