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NUTRITIONAL DETERMINANTS OF DIET IN THREE TURACOS IN A TROPICAL MONTANE FOREST

CHIN SUN,[1,3] TIMOTHY C. MOERMOND,[1] AND THOMAS J. GIVNISH[2]

[1]Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA; and
[2]Department of Botany, University of Wisconsin, Madison, Wisconsin 53706, USA

ABSTRACT.—We studied nutritional characteristics of plants in the diets of three closely related, highly frugivorous turacos that inhabit a tropical montane forest in Rwanda: the Great Blue Turaco (*Corythaeola cristata*), the Ruwenzori Turaco (*Musophaga johnstoni*), and the Black-billed Turaco (*Tauraco schuettii*). The first two species also consume leaves. We compared the physical properties and nutrient contents of fruits and leaves eaten by turacos with those of common but uneaten plant species. Concentrations of hexose sugars were higher in fruits eaten by turacos than in those not eaten. In contrast, concentrations of nitrogen and fatty acids were lower in fruits eaten by turacos than in those not eaten. Leaves of plant species eaten by turacos did not differ significantly in either nitrogen or fiber content from those uneaten. Factors other than nitrogen and fiber, perhaps including secondary defensive compounds, are likely to affect leaf choice by turacos. The Great Blue Turaco ate aquatic plants containing high levels of sodium. We hypothesize that the Great Blue Turaco (which is the most folivorous of the three species) eats aquatic plants with high levels of sodium to help detoxify plant secondary compounds. *Received 14 May 1996, accepted 16 October 1996.*

NUMEROUS FACTORS affect diet choice of frugivores, including fruit morphology, fruit chemistry, spatial arrangements of fruits, and the relative abundance of other fruit species in the environment (Howe and Vande Kerckhove 1980, Janson 1983, Moermond and Denslow 1983, Gautier-Hion et al. 1985, Denslow 1986, McPherson 1987, Moermond et al. 1987, Sargent 1990, Whelan and Willson 1994). For example, some frugivores in temperate habitats prefer lipid-rich fruits (Stiles 1980, 1993; Herrera 1982; Fuentes 1994; Willson 1994), whereas others prefer fruits rich in simple sugars (Martinez del Rio et al. 1988, Martinez del Rio and Stevens 1989, Karasov and Levey 1990, Witmer 1996). Some Neotropical frugivores preferentially feed on fruits with small seeds and high pulp-to-seed ratios (Howe and Vande Kerckhove 1980), whereas Cedar Waxwings (*Bombycilla cedrorum*) in temperate forests presented with experimental diets prefer fruits with larger seeds that can be regurgitated rapidly (Levey and Grajal 1991). In this paper, we examine the size, pulp-to-seed ratio, and nutrient content of fruits eaten by three species of frugivorous turacos.

Turacos (Musophagidae) are frugivorous birds endemic to sub-Saharan Africa (Brosset and Fry 1988). Three species, the Great Blue Turaco (*Corythaeola cristata*), the Ruwenzori Turaco (*Musophaga johnstoni*), and the Black-billed Turaco (*Tauraco schuettii*), are common in a tropical montane forest in southwestern Rwanda and feed mainly on fruits, which constitute 73.3%, 92%, and 100% of their overall diets, respectively (Sun 1995).

Although they are highly frugivorous, the Great Blue and Ruwenzori turacos also eat leaves, which constitute 25% and 6.3% of their diets, respectively (Sun 1995). Obligate (i.e. absolute) frugivory is thought to be rare in birds because the availability of protein in fruits is low (Morton 1973, Foster 1978, Izhaki and Safriel 1989). Compared with fruits, leaves are rich in protein (Milton 1981, Cork and Foley 1991). However, leaves also have structural and chemical defense compounds that can deter potential herbivores. Water content and the toughness of leaves affect the extent of leaf damage by insect herbivores (Coley 1983), whereas the levels of protein, fiber, and condensed tannins, and the protein-to-fiber ratio in leaves, influence food choice by folivorous primates (Milton 1979, Oates et al. 1980, McKey et al. 1981, Rogers et al. 1990, Kar-Gupta and Kumar 1994).

To examine the attributes of fruits and leaves that may influence diet choice of turacos, we compared the morphology and nutrient content

[3] Present address: Department of Plant Pathology, University of Wisconsin, Madison, Wisconsin 53706, USA. E-mail: csun@macc.wisc.edu

of fruits and leaves eaten by turacos with those of species that were avoided by turacos. We addressed three questions: (1) Do nutrients in fruits and leaves explain the patterns of fruit and leaf choice by turacos? (2) Does fruit size or the pulp-to-seed ratio of fruits explain the patterns of fruit use by turacos? (3) Why does the Great Blue Turaco regularly eat aquatic plants?

METHODS

Study site and birds.—The Nyungwe Natural Forest Reserve is a 950-km^2 tropical montane forest located in southwestern Rwanda, Africa (2°35'S, 29°15'E). Our study site encompassed an area of approximately 3.5 km^2, ranging from 1,950 to 2,500 m in elevation. We cut over 50 km of trails to access different habitats and the home ranges of all focal birds that we studied.

Between November 1991 and December 1992, C.S. followed focal groups of turacos and recorded their activities, diets, and movements monthly. Detailed field methods are described in Sun (1995). Great Blue Turacos usually live in social groups of 6 to 20 individuals, whereas Ruwenzori Turacos and Black-billed Turacos usually live in pairs that defend year-round territories (Brosset and Fry 1988, C. Sun unpubl. data). In total, one group (15 birds) of Great Blue Turacos, four pairs of Ruwenzori Turacos, and two pairs of Black -billed Turacos were observed systematically for 433, 476, and 400 h, respectively (25 to 40 h per month per species). In addition, we recorded incidental observations on turaco feeding behavior whenever we were in the field between August 1989 and January 1993.

Fruit and leaf samples.—Between June 1991 and January 1993, we collected fleshy fruits from tree and shrub species whose fruits were accessible. Samples from species of leaves eaten by turacos were collected if possible. Because turacos fed almost exclusively on young leaves, we collected only young leaves of all species, with one exception. Because the Great Blue Turaco regularly ate mature leaves of *Maytenus acuminata*, we collected mature leaves from this species. Young leaves of five additional species not eaten by turacos also were collected. In total, we collected 14 of the 28 species of fruits and 7 of the 21 species of leaves eaten by at least one species of turaco, as well as nine species of fruits and five species of leaves that were not eaten by turacos. Selection for "not-eaten" fruits and leaves was based on their abundance relative to the species eaten; most "not-eaten" fruits and leaves included in the analyses were more abundant than "eaten" fruits and leaves.

We used densities of adult trees (dbh $>$ 20 cm) to estimate the relative abundance of different fruits. The seven species of not-eaten fruits included in our analyses comprised five trees and two shrubs. Four tree species whose fruits were not eaten had higher densities than that of *Ekebergia capensis*, a species whose fruits were eaten by all three turacos (Sun 1995). The fruit of *Bersama abyssinica*, a rare tree, was included in our analyses because its leaves were regularly eaten by Great Blue Turacos (hence, its fruit was available). Of the two shrubs whose fruits were not eaten by turacos, *Alchornea hirtella* was one of five most abundant species at our study site, and *Rubus* sp. was locally common in territories of the Ruwenzori Turacos that we followed regularly.

Of the species whose leaves were not eaten by turacos but were included in our analyses, the trees *Syzygium parvifolium* and *Carapa grandiflora* ranked second and fifth, respectively, in abundance among all 54 tree species present in vegetation plots at our study site, and the shrubs *Alchornea hirtella* and *Lasianthus kilimandscharicus* were two of the top five most common species at the study site (C. Sun unpubl. data). Compared with the three lianas whose leaves were eaten by turacos, *Monanthotaxis orophila*, the liana whose leaves were not eaten by turacos, was rarer than *Schefflera goetzenii*, but more abundant than *Embelia schimperi* and *Dalbergia lactea*, all of which were eaten (C. Sun unpubl. data; scientific names based on Troupin 1982).

Fruits and leaves that we never saw turacos eat may indeed have been actively avoided by the birds, or we may simply have missed seeing turacos feeding on them. This problem can be serious for rare fruits, not only because the birds would seldom encounter these fruits but also because it would be easy for us to miss these events. To reduce this potential bias, we included not-eaten fruits in our analyses only for species that were more abundant than the species known to be eaten by turacos. Twelve additional species of trees had densities higher than *Ekebergia capensis* (whose fruits were eaten by all turacos) but were not included in our analyses; two species produced little or no fruit during the study period, whereas 10 species produced capsule fruits, fruits with hard husks, or fruits too large for turacos to swallow (C. Sun unpubl. data).

The Great Blue Turaco regularly ate algae or filament-like tissues of rootless floating plants from clear and slow-flowing streams. This habit was well known by local people, who often trapped turacos at stream banks (F. Ngayabahiga pers. comm., C. Sun pers. obs.). In our formal study, this kind of food (hereafter, aquatic plant) represented only a very small percentage of the overall diet of the birds ($<$0.1%; Sun 1995). This low percentage can be attributed to the difficulty of following focal birds into river valleys where aquatic plants were available; we did not witness the birds foraging in the water until near the end of our study. Samples of aquatic plants were collected for mineral analyses.

Fruit morphology.—In this paper, the size of fruits or seeds refers to their width measured with calipers. Intact fruits were weighed, and seeds from each fruit were separated from the pulp, cleaned, and weighed. Pulp mass equaled the mass of the whole fruit minus the total mass of seeds. Pulp-to-seed ratio equaled the pulp mass divided by the total mass of seed(s). At least nine fruits per species were weighed. For species with small fruits, 10 to 20 fruits were weighed to obtain an average mass; the same procedure was repeated three to five times, and a total of 30 to 100 fruits were weighed.

Nutrient analysis.—Leaf and fruit samples collected in the forest were weighed and dried by the sun and in a plant drier heated by a kerosene lantern. Samples were enclosed in ziploc bags and transported to the University of Wisconsin-Madison for nutrient analyses. Fruit-pulp and leaf samples were analyzed for total nitrogen and neutral detergent fiber (hereafter, fiber) with the semi-micro Kjeldahl and Goering and Van Soest (1970) methods, respectively. Fruit-pulp samples were further analyzed for soluble carbohydrates and fatty acids (with 14- to 18-carbon chain length) by high performance liquid chromatography (McBee and Maness 1983, Hagidimitriou and Roper 1994) and gas chromatography (Sukhija and Palmquist 1988), respectively. Leaf tissues of aquatic plants and the two most important leaves in the diet of the Great Blue Turaco, the liana *Embelia schimperi* and the tree *Maytenus acuminata* (composing 11.77% of the overall diet), were analyzed for 12 minerals (P, K, Ca, Mg, S, Zn, B, Mn, Fe, Cu, Al, Na) using inductively coupled plasma emission spectrophotometry.

Data analysis.—We chose not to measure the relative preference of turacos for each species of fruits or leaves, but classified each species as "eaten"or "not eaten." Measuring preferences can be problematic because it requires information on the diet composition of the animal and the relative availability of each food in the environment. Moreover, the outcome depends critically on how many and which foods are considered relevant and included in the analyses (Johnson 1980). Because both the species composition of available fruits and leaves and the abundance of each kind of food changed among months, the preference index for each kind of food would change through time. Furthermore, because the monthly diet diversity of turacos was low, and not all fruits or leaves eaten by turacos were analyzed for nutrient content, it was not feasible to analyze data by month. Data from all 14 months of observations, therefore, were analyzed together, and only "eaten" and "not-eaten" categories were used. A species of fruit was defined as "eaten" if turacos had been seen feeding on it during either systematic or incidental observations.

Fruits of the shrubs *Chassalia subochreata, Galiniera coffeoides*, and *Rubus* sp. were available to the Ruwenzori Turaco but not to the Great Blue Turaco or the Black-billed Turaco (i.e. the latter turacos were never seen foraging in the understory). Thus, these shrubs were included in the diet analyses only for the Ruwenzori Turaco. Fruits of two species were excluded from diet analyses for all turacos (turacos were never seen eating these fruits): *Symphonia globulifera* fruits had a firm exocarp and were too big for turacos to swallow, and *Ficus ottoniifolia* was rare at our study site. However, we present nutritional data for these two fruits for comparative purposes.

We tested for differences among turaco species in nutrient contents of fruits eaten by each turaco species with MANOVA. For each species of turaco, we used ANOVA to examine morphological and nutritional differences in leaves and fruits eaten by the bird versus those not eaten. In addition, we used linear discriminant function analyses to compare all nutritional traits of fruits eaten by the bird versus those not eaten. We did not include morphological traits of fruits in discriminant analyses because the overall sample size of fruit species (23) was low relative to the number of nutritional and morphological variables we examined. Unless the ratio of sample size to the number of variables is large (e.g. 20 to 1), the standardized coefficients and the correlations in the results of linear discriminant function analyses are very unstable (Stevens 1992).

RESULTS

Fruits.—The soluble carbohydrates of fruits were composed mainly of fructose, glucose, and sucrose. Overall, fructose had the highest percent dry mass in the fruit pulp (10.16 ± SD of 1.51%, $n = 23$), glucose ranked second (7.66 ± 1.42%), and sucrose ranked lowest (1.18 ± 0.24%). Within species, the percent dry mass of either fructose or glucose was significantly higher than that of sucrose (Wilcoxon tests, $P < 0.0001$ in both cases, $n = 23$). Because fructose and glucose were similar in their percentages in fruit pulp and in their biochemical properties from the viewpoint of digestion (i.e. they are monosaccharides), these two sugars were combined and treated as "hexose" in subsequent analyses.

Total sugars were significantly higher in fruits eaten by the Great Blue Turaco than in fruits not eaten (ANOVA, $F = 10.37$, df = 1 and 16, $P = 0.005$). A similar trend existed for all three turacos (Fig. 1), although the results were not statistically significant in either the Ruwenzori Turaco ($F = 4.08$, df = 1 and 19, $P = 0.058$) or the Black-billed Turaco ($F = 0.65$, df = 1 and 16, $P = 0.434$). When the two sugars were analyzed separately, the same trend persisted in hexose but not sucrose, suggesting that the higher sugar content in the fruits turacos ate was due largely to higher hexose content (Fig. 1).

Nitrogen and fatty acid (hereafter, fat) contents generally were lower in fruits eaten by turacos than in fruits they did not eat (Fig. 1). The only significant difference, however, was between nitrogen content of fruits eaten and not eaten by the Ruwenzori Turaco ($F = 22.53$, df = 1 and 19, $P < 0.001$). The higher fat content in fruits not eaten by turacos was largely due to the fruit of *Bersama abyssinica*, which had exceedingly high fat content (Appendix 1). If *B. abyssinica* fruit was excluded from the analysis, the average fat content of fruits eaten by turacos was not different from that of fruits not eaten (Fig. 1). Nutrient contents in the fruits eaten did not differ significantly among the turaco species (MANOVA, $F = 0.06$, df = 8 and 50, $P = 0.99$).

Results from the discriminant analysis were consistent with those of univariate ANOVA; fruits eaten by the Great Blue Turaco were distinguished from those not eaten mainly by their hexose content, whereas fruits eaten by the Ruwenzori Turaco were distinguished from those not eaten by nitrogen content (Table 1). Considering only species whose fruits were available to turacos (excluding *Symphonia globulifera* and *Ficus ottoniifolia*), hexose and nitrogen content within fruits were negatively correlated ($r_s = -0.360$, $n = 21$, $P < 0.05$).

Neither pulp-to-seed ratio nor seed size differed between eaten and not-eaten fruits, both within and among turaco species (Table 2). Although only the Great Blue Turaco was large enough to swallow large fruits (e.g. *Strombosia scheffleri*), all turacos ate small fruits (Appendix 2), and fruit size did not differ significantly between eaten and not-eaten species (Table 2). Thus, morphological characters of fruits and seeds that we measured did not explain the patterns of fruit use by turacos.

Leaves.—We found no significant differences in nitrogen content, fiber content, or the ratio of nitrogen to fiber between leaves eaten and those not eaten by either species of turaco that regularly ate leaves (Table 3). Of the 12 minerals measured in leaves, the concentrations of zinc, iron, and sodium in aquatic plants were substantially higher than those in the two most important terrestrial leaves in the Great Blue Turaco's diet (Table 4).

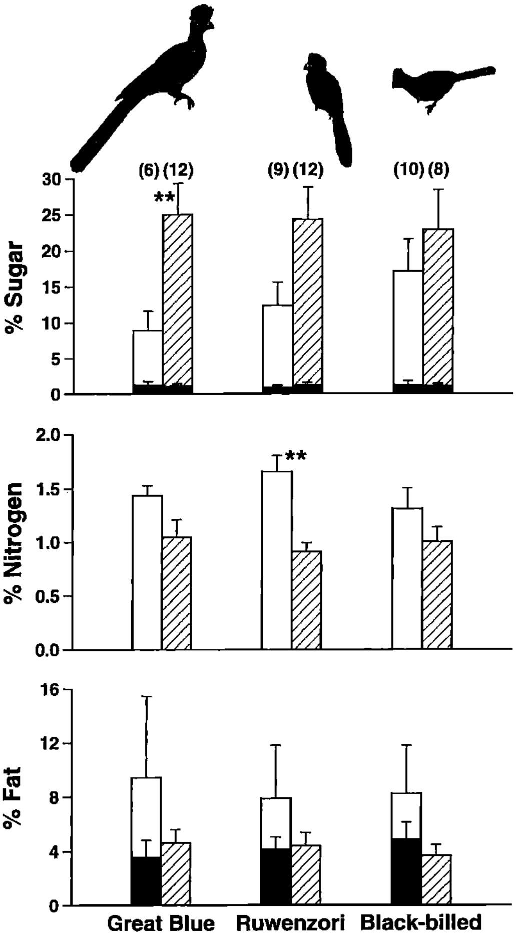

FIG. 1. Nutrient contents of fruits eaten versus not eaten by three species of turacos in Rwanda. Bars depict means and whiskers 1 SE. Empty bars represent nutrient levels of fruits not eaten, hatched bars represents those of the fruits eaten. Numbers in parentheses denote number of species of fruits analyzed. In upper panel the empty and hatched bars represent hexose content, solid bars represent sucrose content. In lower panel the empty bars represent fat content of fruits not eaten including *Bersama abyssinica*, solid bars represent fat content of fruits not eaten but excluding *B. abyssinica*. ** indicates nutrient contents between eaten and not-eaten fruits were significantly different at $P < 0.01$ (ANOVA).

DISCUSSION

Fruit nutrients.—Turacos, particularly the Great Blue Turaco, appeared to choose fruits that were high in hexose content (Table 1, Fig. 1). Although hexose content did not differ significantly between fruits eaten and not eaten by the Ruwenzori Turaco, and the pattern of fruit use by this species was explained by nitrogen content (Table 1), we hypothesize that the Ruwenzori Turaco also chose fruits that were high in hexose content; the negative correlation be-

TABLE 1. Discriminant function analysis comparing nutritional characteristics of eaten and not eaten fruits by three turacos. Correlations are between conditional dependent variables and discriminant function, and coefficients are discriminant function coefficients. Fruit traits listed in the decreasing magnitude of correlations in the Great Blue Turaco. Model indicates the overall significance of the discriminant function analysis for each species.

	Great Blue Turaco		Ruwenzori Turaco		Black-billed Turaco	
Traits	Correlation	Coefficient	Correlation	Coefficient	Correlation	Coefficient
Hexose	−0.622[a]	−1.080	−0.351	−0.251	−0.333	−0.370
Nitrogen	0.401	0.270	0.814[a]	1.017	0.536	0.677
Fats	0.274	0.669	0.167	0.600	0.421	0.846
Sucrose	0.040	0.926	−0.116	0.140	0.202	0.781
Model	$F = 3.36$, df = 4 and 13, $P = 0.043$		$F = 7.16$, df = 4 and 16, $P = 0.002$		$F = 1.43$, df = 4 and 13, $P = 0.28$	

[a] Primary nutritional trait explaining the discriminant function of the statistically significant models; no other traits differed between eaten and not-eaten fruits.

tween nitrogen and hexose content in fruits available to this turaco (all 21 species of fruits analyzed) means that the fruits high in hexose would be low in nitrogen. The high-hexose and low-nitrogen fruits eaten by turacos suggest that, within the ranges of nitrogen and hexose percentages measured here, turacos chose high-hexose over high-nitrogen fruits.

We never saw turacos eating fat-rich fruits, even though they were available (e.g. Great Blue Turacos ate the leaves but not the fat-rich fruits of *Bersama abyssinica*). Fats are absorbed passively only after emulsification and require long processing times in the gut, whereas hexoses can be absorbed immediately by active transport and require shorter processing times (Griminger 1986, Karasov 1988). Thus, the digestive traits of birds that eat predominantly hexose-rich fruits probably differ from those that eat fat-rich foods (Martinez del Rio and Restrepo 1993). Turacos appear to specialize on hexose-rich fruits, and their gut-retention times may be too short to accommodate a fat-rich diet.

Fruit morphology.—Fruit choice by turacos was not explained by pulp-to-seed ratio, seed size, or fruit size. Similar conclusions have been reached for other species of birds and likely stem from non-nutritive factors that affect fruit choice (Johnson et al. 1985, Foster 1990, Willson 1994). However, fruit size does limit accessibility of some fruits to birds, because the upper size limit that a bird can swallow is dictated by gape size (Wheelwright 1985; Appendix 2). The two dominant morphological traits of fruits that could limit their use by avian frugivores may be exocarp hardness (which may hamper birds from eating fruits in piecemeal fashion) and fruit size (which may prevent birds from swallowing them whole; Wheelwright 1985, Levey 1987).

Leaf nutrients.—Our results suggest that neither nitrogen content nor fiber content affect leaf choice by Great Blue Turacos and Ruwenzori Turacos. However, this may be due to our small sample sizes. Frugivorous bats have been found to ingest the liquid extract of leaves to supplement their protein requirements (Kunz and Ingalls 1994, Kunz and Diaz 1995). Because turacos are highly frugivorous and rarely eat insects (Sun 1995), it remains possible that they eat leaves to supplement their protein needs.

Other factors probably affect leaf choice by turacos. The leaves of a common shrub (*Alchornea hirtella*) and a tree (*Psychotria mahonii*) had high nitrogen and low fiber contents but were not important in the diets of either the Great Blue Turaco (2.2%) or the Ruwenzori Turaco (0%; Sun

TABLE 2. Morphology traits ($\bar{x} \pm$ SE) of fruits eaten versus not eaten by turacos.

	Great Blue Turaco			Ruwenzori Turaco			Black-billed Turaco		
Trait	Eaten	Not eaten	P[a]	Eaten	Not eaten	P	Eaten	Not eaten	P
Pulp-to-seed ratio	2.5 ± 0.5	5.5 ± 2.4	0.15	4.0 ± 1.5	2.7 ± 0.9	0.52	5.0 ± 2.4	2.7 ± 0.6	0.27
Seed width (mm)	7.8 ± 1.7	7.0 ± 1.6	0.75	6.6 ± 1.3	10.1 ± 2.1	0.15	6.6 ± 2.2	8.2 ± 1.3	0.53
Fruit width (mm)	13.8 ± 2.0	16.1 ± 2.5	0.48	12.7 ± 1.9	17.5 ± 2.5	0.14	14.8 ± 2.5	14.4 ± 2.0	0.90
n[b]	12	6		12	9		8	10	

[a] ANOVA comparing fruits eaten vs. not eaten by turacos.
[b] Number of fruit species analyzed.

TABLE 3. Nutrient contents (% dry mass; $\bar{x} \pm$ SE) of leaves eaten versus not eaten by turacos.

	Great Blue Turaco			Rowenzori Turaco		
Variable	Eaten	Not eaten	P^a	Eaten	Not eaten	P
Nitrogen	2.91 ± 0.24	2.19 ± 0.11	0.17	2.53 ± 0.09	2.84 ± 0.23	0.49
Fiber	29.74 ± 2.83	24.45 ± 2.45	0.38	31.40 ± 3.56	28.60 ± 3.26	0.66
Nitrogen-to-fiber ratio	0.10 ± 0.02	0.09 ± 0.01	0.69	0.08 ± 0.01	0.16 ± 0.02	0.43
n^b	7	2		3	9	

[a] ANOVA comparing fruits eaten vs. not eaten by turacos.
[b] Number of leaf species analyzed.

1995). In contrast, the leaves of *Maytenus acuminata* were relatively low in nitrogen but constituted the highest percentage (7.8% of overall diet) in the leaf diet of the Great Blue Turaco (Sun 1995). This differential use of leaves was not due to availability, because *Psychotria mahonii* was more abundant than *Maytenus acuminata* (8.7 times by density and 6.4 times by basal area; Sun unpubl. data). This evidence suggests that factors other than nitrogen and fiber content, such as plant secondary defense compounds, influence leaf choice by turacos.

Nutrients in aquatic and terrestrial plants.—To our knowledge, the ingestion of aquatic plants by fruit-eating birds has not been described previously. The aquatic plant eaten by Great Blue Turacos had higher levels of sodium, zinc, and iron than the leaves of the two terrestrial species that we analyzed (Table 4), a result confirmed by other studies comparing minerals in aquatic versus terrestrial plants (Oates 1978, Fraser et al. 1984). Zinc, iron, and sodium are essential for birds, but sodium is needed in the highest quantity (National Research Council 1994). However, most fruits have very low sodium content (<0.05% dry mass; Consumer Nutrition Center 1982, Burguera et al. 1992).

Sodium often is a limited mineral for mammalian herbivores (Weir 1972; McNaughton 1988, 1990), some of which lose sodium when detoxifying and metabolizing plant secondary compounds (Freeland et al. 1984, Reichardt et al. 1984, Foley and McArthur 1994). Although folivory occurs in 14 avian families (Morton 1978), little is known about how plant secondary compounds affect sodium balance in birds (Jakubas et al. 1995). If turacos require additional sodium to metabolize plant secondary compounds (as do some mammals), then meeting sodium requirements could be a serious concern for the Great Blue Turaco, because 25% of its diet consists of leaves (Sun 1995). We propose that the Great Blue Turaco eats aquatic plants to meet its needs for sodium.

In summary, turacos were selective in using the food resources in their environment. They appeared to prefer hexose-rich fruits over fruits rich in nitrogen or fats. Although turacos might eat leaves to supplement their protein intake, factors influencing leaf choice by turacos are likely to be complex. We hypothesize that the Great Blue Turaco, the most folivorous of the three turacos we studied, requires additional sodium to metabolize secondary compounds in the leaves it ingests. Detoxifying leaf secondary compounds may explain the ingestion of aquatic plants by Great Blue Turacos.

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TABLE 4. Mineral content of aquatic plants and of the two most important terrestrial leaves (*E. schimperi* and *M. acuminata*) in the diet of Great Blue Turaco.

	% dry mass						P.P.M. dry mass					
Species[a]	P	K	Ca	Mg	S	Na	Zn	Mn	Fe	Cu	Al	B
Aquatic species	0.09	0.35	0.16	0.17	0.19	1.69	737	698	4250	3.41	—[b]	<3
Embelia schimperi	0.29	1.83	0.31	0.17	0.17	0.01	19.9	85.5	73.7	12.1	55.5	28.6
Maytenus acuminata	0.17	0.82	0.33	0.17	0.25	0.03	20.3	757	119	13.7	106	20.2

[a] Young leaves of *E. schimperi* and mature leaves of *M. acuminata*.
[b] Omitted because the sample was stored in aluminum foil.

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APPENDIX 1. Nutrient content of fruit pulp ($\bar{x} \pm$ SD).

		% dry mass						Bird species		
Species	% Water	Glucose	Fructose	Sucrose	Nitrogen	Fat	Fiber	CC[a]	MJ	TS
			Aquifoliaceae							
Ilex mitis	75.9	19.76	19.81	1.44	0.64	5.0	21.0	X[b]	X	X
			Clusiaceae							
Symphonia globulifera	66.2	8.58	11.10	2.03	0.57	3.26	24.3	N/A	N/A	N/A
			Euphorbiaceae							
Macaranga neomildbraediana	67.2	0.56	1.90	0.41	1.45	7.76	35.2	—	—	—
			Flacourtiaceae							
Casearia runssorica	80.1	0.92	4.65	1.55	1.60	2.60	—	—	X	X
			Lauraceae							
Beilschmiedia troupinii	82.4	0.54	1.53	0.42	2.46	0.66	40.2	X	—	—
			Melastomataceae							
Memecylon walikalense	75.7	19.04	20.80	4.35	0.86	4.01	9.0	X	X	—
			Meliaceae							
Ekebergia capensis	79.3	16.62	17.63	0.91	0.91	5.77	13.2	X	X	X
			Melianthaceae							
Bersama abyssinica	38.8	0.12	0.17	0.17	1.07	38.86	—	—	—	—
			Moraceae							
Ficus oreodryadum	87.3	0.48	0.19	0.15	0.76	0.56	52.0	X	X	X
Ficus ottoniifolia	86.2	1.73	7.63	0.0	1.13	2.63	31.7	N/A	N/A	N/A
			Myrsinaceae							
Maesa lanceolata	—	20.45	17.3	2.61	1.06	5.43	19.0	X	X	X
Rapanea melanophloeios	—	15.76	23.71	0.80	0.56	9.69	10.0	X	X	—
Embelia schimperi	—	6.29	10.53	0.0	1.02	11.37	24.8	X	X	—
			Myrtaceae							
Syzygium parvifolium	72.6	14.04	12.09	1.95	0.69	3.69	28.8	X	X	X
			Olacaceae							
Strombosia scheffleri	84.5	4.18	18.88	0.78	1.64	4.77	35.9	X	—	X
			Rosaceae							
Robus sp.	—	3.50	4.56	0.45	2.04	5.37	17.9	N/A	—	N/A
			Rubiaceae							
Chassalia subochreata	—	11.30	18.15	0.43	1.86	6.20	20.2	N/A	—	N/A
Galiniera coffeoides	—	6.81	5.23	0.11	0.82	0.59	34.5	N/A	X	N/A
Rytigynia sp.	78.0	6.44	8.11	2.56	1.18	0.98	17.8	—	—	—
Sericanthe leonardii	82.7	6.63	11.51	2.33	1.31	2.44	29.1	X	X	—
			Sapotaceae							
Chrysophyllum gorungosanum	78.7	1.85	4.73	2.55	1.49	0.96	—	—	—	—
Chrysophyllum rwandense	86.6	6.93	9.36	1.21	1.81	4.91	17.2	—	—	—
			Theaceae							
Balthasarea schliebenii	—	3.72	4.01	0.0	0.68	0.71	56.7	X	X	X

[a] CC, Great Blue Turaco; MJ, Ruwenzori Turaco; TS, Black-billed Turaco.

[b] X, fruit was eaten; —, fruit was not eaten; N/A fruit was not available to the particular species of turaco or was not assigned to either category.

APPENDIX 2. Fruit size, seed size, and pulp-to-seed ratio ($\bar{x} \pm$ SD) of fleshy fruits and their use by turacos. Sample size in parenthesis; numbers in brackets under pulp-to-seed ratio indicate batches of fruits used in the calculation. Species are presented in the ascending order based on fruit width.

Species	Fruit width (mm)	Fruit length (mm)	Seed width (mm)[a]	Pulp-to-seed ratio[b]	Bird species[c]		
					CC	MJ	TS
		Myrsinaceae					
Maesa lanceolata	4.2 ± 0.5 (10)	4.5 ± 0.5	0.5	—	X[d]	X	X
Rapanea melanophloeos	5.6 ± 0.5 (37)	8.3 ± 1.2	4.4 ± 0.5 (35)	3.85	X	X	—
Embelia schimperi	6.1 ± 0.4 (25)	7.8 ± 0.6	4.1 ± 1.9 (25)	1.98 ± 0.27 [3]	X	X	—
		Rubiaceae					
Psychotria mahonii	6.2 ± 1.0 (36)	7.2 ± 1.4	3.50	5.20	X	X	—
		Aquifoliaceae					
Ilex mitis	6.6 ± 0.4 (22)	7.4 ± 0.4	5.0	3.27	X	X	X
		Euphorbiaceae					
Macaranga neomildbraediana	6.6 ± 0.4 (26)	7.4 ± 0.4	4.0	3.67 ± 0.38 [3]	—	—	—
		Rubiaceae					
Galiniera coffeoides	7.4 ± 0.6 (35)	8.0 ± 0.8	3.4 ± 0.4 (2)	0.57 ± 0.25 (10)	N/A	X	NA
		Rosaceae					
Prunus africana	8.9 ± 0.7 (9)	11.8 ± 1.3	6.2 ± 0.8 (7)	1.81 ± 0.48 (7)	X	X	X
		Oleaceae					
Olea hochstetteri	10.0 ± 1.2 (12)	14.6 ± 2.0	7.3 ± 0.4 (12)	1.51 ± 0.18 (12)	X	X	X
		Rubiaceae					
Rytigynia sp.	11.8 ± 1.8 (27)	13.7 ± 1.0	5.1 ± 1.1 (22)	2.15 ± 0.51 (15)	—	—	—
		Myrtaceae					
Syzygium parvifolium	13.6 ± 2.2 (27)	14.6 ± 2.1	13.0 ± 1.2 (3)	0.60 ± 0.08 (3)	X	X	X
		Podocarpaceae					
Podocarpus milanjianus	14.0[e]	—	9.4 ± 1.2 (9)	0.54 ± 0.77 (8)	X	X	X
		Moraceae					
Ficus oreodryadum	14.9 ± 1.7 (54)	15.9 ± 1.9	2.0	5.25 ± 0.20 [3]	X	X	X
		Rubiaceae					
Sericanthe leonardii	15.9 ± 2.4 (28)	17.0 ± 2.8	8.7 ± 1.8 (14)	1.58 ± 0.85 (10)	X	X	—
		Theaceae					
Balthasarea schliebenii	16.1 ± 2.0 (15)	36.1 ± 3.9	1.5	—	X	X	X
		Sapotaceae					
Chrysophyllum rwandense	18.0 ± 1.1 (21)	30.1 ± 2.4	13.2 ± 1.0 (16)	1.51 ± 0.50 (19)	—	—	—
		Melianthaceae					
Bersama abyssinica	18.0	—	5.0	0.29 ± 0.05 (19)	—	—	—

APPENDIX 2. Continued.

Species	Fruit width (mm)	Fruit length (mm)	Seed width (mm)[a]	Pulp-to-seed ratio[b]	Bird species[c] CC	MJ	TS
			Flacourtiaceae				
Casearia runssorica	18.4 ± 1.5 (12)	27.0 ± 4.2	4.0	14.96 ± 3.02 (10)	—	X	X
			Lauraceae				
Beilschmiedia troupinii	18.7 ± 3.8 (51)	39.6 ± 7.1	14.7 ± 2.2 (4)	3.69 ± 2.12 (9)	X	—	—
			Melastomataceae				
Memecylon walikalense	19.7 ± 1.3 (16)	20.8 ± 1.6	12.8 ± 1.4 (13)	3.00 ± 0.98 (16)	X	X	—
			Meliaceae				
Ekebergia capensis	20.2 ± 2.1 (11)	22.6 ± 2.8	8.8 ± 1.0 (66)	4.50 ± 0.64 (11)	X	X	X
			Sapotaceae				
Chrysophyllum gorungosanum	23.8 ± 2.4 (43)	43.7 ± 4.1	10.4 ± 1.2 (23)	12.62 ± 7.46 (31)	—	—	—
			Moraceae				
Ficus ottoniifolia	24.7 ± 2.3 (15)	31.8 ± 6.5	2.5	3.56 ± 0.28 (10)	N/A	N/A	N/A
			Olacaceae				
Strombosia scheffleri	25.5 ± 3.8 (25)	28.4 ± 3.5	18.9 ± 2.0 (30)	1.09 ± 0.26 (15)	X	—	X[f]
			Clusiaceae				
Symphonia globulifera	36.6 ± 5.0 (9)	44.2 ± 4.5	26.9 ± 1.3 (9)	0.94 ± 0.25 (9)	N/A	N/A	N/A

[a] Values for species without SD and sample size are averages or midpoints of values presented in Troupin (1982).
[b] Pulp-to-seed ratio determined by wet mass; values without SD and sample size are averages of 20–60 fruits.
[c] CC, Great Blue Turaco; MJ, Ruwenzori Turaco; TS, Black-billed Turaco.
[d] X, fruit was eaten; —, fruit was not eaten; N/A, fruit was not available to the particular species of turaco or was not assigned to either category.
[e] The edible part of *Podocarpus milanjianus* fruit is an aril attached to two seeds. Fruit size refers to entire unit of aril and seeds.
[f] The Black-billed Turaco seen attempting to swallow smaller fruits of *Strombosia scheffleri*.