

CHEMICAL COMPOSITION OF FRUITS AND LEAVES EATEN BY SHORT-NOSED FRUIT BAT, *Cynopterus sphinx*

J. RUBY,¹ P. T. NATHAN,¹ J. BALASINGH,¹ and T. H. KUNZ^{2,*}

¹Department of Zoology, St. John's College
Palayamkottai, 627 002, South India

²Department of Biology, Boston University
Boston, Massachusetts 02215

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Abstract—We evaluated organic and macromineral composition of selected fruits and leaves consumed by the short-nosed fruit bat, *Cynopterus sphinx* in South India. Results of principal components analysis (PCA) comparing soluble carbohydrates, crude protein, and crude fats indicate a higher percentage of protein in leaves and a higher percentage of carbohydrates and lipids in fruits. However, results of a paired *t* test comparing these organic components indicated no differences between fruits and leaves. Among the fruits analyzed, *Musa x paradisiaca* had the highest percentage of carbohydrates, and *Psidium guajava* had the highest percentage of lipids. Leaves of *Cassia fistula*, *Moringa oleifera*, *coccinia cordifolia*, and *F. religiosa* had the highest percentage of protein. PCA of selected macrominerals (Ca, Na, K, and P) indicate higher levels of Ca in leaves than in fruits. Results of *t* tests comparing these macrominerals revealed a difference between fruits and leaves for Ca, but not for the other macrominerals. Among the leaves analyzed, Ca was highest in mature leaves of *C. fistula* and lowest in leaves of *F. religiosa*. Leaves of *M. oleifera* and fruits of *Achras sapota* were highest in sodium. Among fruits analyzed for macrominerals, Ca was highest in *F. bengalensis* and lowest in *Prosopis juliflora*, *A. sapota*, and *M. x paradisiaca*. Potassium levels were highest in leaves of *C. cordifolia* and fruit pods of *Prosopis juliflora*. Phosphorus content was highest in leaves of *M. oleifera* and fruits of *M. x paradisiaca*. The relatively high concentrations of protein and calcium in leaves eaten by *C. sphinx* supports the hypothesis that leaves are important dietary sources for this plant-visiting bat.

Key Words—Bats, calcium, folivory, frugivory, nutrition, protein, Pteropodidae.

*To whom correspondence should be addressed; e-mail: kunz@bu.edu

INTRODUCTION

Plant-visiting bats in the Neotropics and Paleotropics are known to feed on a variety of plant parts, including flowers, pollen, fruit, nectar, and leaves (e.g., Gardner, 1977; Marshall, 1983, 1985; Dobat and Peikert-Holle, 1985; Fleming, 1988, 1993; Law, 1992; Richards, 1995; Uzzurum, 1995; Tan et al., 1998; Kalko et al., 1996; Banack, 1998). They appear to gain access to the nutrient content of leaves and fruit by so-called "wodging," a behavior that involves mastication and formation of an oral bolus of fiber and/or seeds as a wodge or spat (see Reynolds et al., 1998), swallowing the liquid fraction, and expelling the fibrous pulp and seeds (Richards and Provic, 1984; Lowry, 1989; Zortea and Mendes, 1993; Kunz and Ingalls, 1994; Kunz and Kiaz, 1995; Tan et al., 1998; Banack 1998). Some plant-visiting bats also may feed on insects (Gardner, 1977; Courts, 1998).

Fruits are generally rich in nonstructural carbohydrates, although they are typically low in fats and proteins (e.g., Mattson, 1980; Herrera, 1987; Martinez del Rio and Restrepo, 1993; Corlett, 1996). Because leaves of several plant species are rich in protein (Telek and Martin, 1983; Kunz and Diaz, 1995), they should provide an important source of nitrogen for plant-visiting bats (Kunz and Diaz, 1995).

Calcium is necessary for maintenance and reproduction in animals (Sadler, 1969; Robbins, 1993), and fruits and leaves of some species are rich in this important macromineral (Raweiler, 1977; O'Brien et al., 1998). Calcium is essential for maintaining normal cellular (acid-base balance), neuromuscular, and skeletal functions (Currey, 1984, 1990; Nordin and Frankel, 1989). Reduced calcium intake can lead to retarded growth, decreased food consumption, osteoporosis and rickets, bone fractures, and ultimately reduced survivorship (Robbins, 1993; Favus, 1996). Additionally, bats may experience large shear stresses and torsional loads during powered flight (Swartz et al., 1992, Swartz, 1998), especially when females withdraw calcium from their bone reserves during lactation (Kwiecewski et al., 1987; Bernard and Davison, 1996). Thus, calcium may be a limiting nutrient for both survival and reproductive success (Barclay, 1994, 1995). Other macrominerals, such as sodium, potassium, and phosphorus are essential for nearly every aspect of an animal's metabolism, including muscle contraction, neural transmission, and nucleic acid formation, as well as carbohydrate, fat, and amino acid metabolism (Robbins, 1993).

The present study was designed to assess the composition of organic and selected macrominerals in leaves and fruits commonly eaten by the short-nosed fruit bat, *Cynopterus sphinx* Vahl. We tested the hypothesis that leaves, relative to fruits, provide rich sources of both protein and calcium. We also evaluated the organic components and macrominerals present in young and mature leaves of *Cassia fistula*, a plant whose leaves are consumed year-round by *C. sphinx*.

METHODS AND MATERIALS

Cynopterus sphinx is a common plant-visiting bat that ranges throughout the Indomalayan region (Storz and Kunz, 1999). Individuals and small social groups typically roost in altered foliage of palm trees—*Borassus flabellifer* (Brosset, 1962) and *Caryota urens* (Bhat and Kunz, 1995); mast trees—*Polyalthia longifolia*; beneath the altered stems of climbing vines—*Vernonia scandens* (Balasingh et al., 1995); and sometimes beneath eaves, awnings, and other manmade structures (Bhat, 1994; Storz and Kunz, 1999; Storz et al., 2000). Food items of *C. sphinx* include fruits of at least 23 plant species, leaves of eight species, and flowers of two other plant species (Bhat, 1994; Rajan et al., 1999).

The study was conducted on the campus of St. Johns College, in the town of Palayamkottai, South India (8°44'N, 77°42'E), where several tree species, including *Azadirachta indica*, *Pithecalobium dulce*, *Psidium guajava*, *Terminalia catappa*, and *Cassia fistula* were regularly visited by *C. sphinx*. Samples of ripe fruits and leaves were collected, weighed, and chopped into small pieces after seeds were removed. Fruit pulp and leaves were dried to constant mass at 60°C and ground with a mortar and pestle. Samples were stored in separate containers until chemical analyses were completed.

Crude protein was determined by using the Kjeldahl method (Pierce and Hanisch, 1948; Williams, 1984), lipid content was analyzed after Bligh and Dyer (1959), and soluble carbohydrate was determined with the Anthrone method (Sadasivam and Manickam, 1992). We estimated the percentage of crude protein by multiplying total nitrogen by 4.4 (Milton and Dintzis, 1981). The latter value is similar to those reported by Herbst (1986) for converting total nitrogen to crude protein in fruits of *Piper amalago* (3.12) and *Cecropia peltata* (4.13). Recent chemical analyses of fruits and leaves revealed that a conversion factor of 6.25 is too large for most wild species of plants (Conklin-Brittain et al., 1999). Thus, when cited values of percent protein were based on $N \times 6.25$, we corrected these by using $N \times 4.4$ for comparison with our results. Phosphorus was analyzed by a colorimetric method, and calcium, sodium, and potassium were analyzed with flame photometry (Trivedi and Goel, 1984; Misra, 1968; Jayaraman, 1985). All samples were run in triplicate and expressed as percent dry matter (organic matter) or milligrams per gram dry mass (minerals).

Because plant-visiting bats often chew leaves and fruits, ingest the liquid fraction, and expel spats (e.g., Lowry, 1989; Studier and Wilson, 1991; Kunz and Ingalls, 1994; Kunz and Diaz, 1995; Banack, 1998), we tested the hypothesis that the nutritious composition of the expelled fraction of leaves (spats) was lower than that of whole leaves. We assumed that the observed differences between the expelled spats and whole leaves represented nutrients ingested by and available to the bats. We selected *Cassia fistula* because leaves of this species

are consumed year-round by *C. sphinx* in India (Balasubramanian, 1988; Bhat, 1994; Rajan et al., 1999).

We used principal components analysis (PCA) to evaluate the patterns of variation between fruits and leaves in amounts of organic matter and macrominerals. This ordination method accounts for the maximum amount of variation in data based on the fewest number of factors (Pimentel, 1979). PCA was used to examine and describe multivariate patterns of organic matter and macrominerals. PCA of both organic and mineral nutrients revealed that the first two factors were defined in relation to the original variables by examining the magnitude and sign of the associated factor loadings. For PCA, we assumed that all input variables were linearly related (Kachigan, 1991). To test this assumption, bivariate scatter plots of each combination of variables were examined for nonlinearity. Natural log transformations were used to remove nonlinearity from the data.

Differences in composition of each organic and macromineral component also were evaluated by using two-tailed *t* tests. The Kolmogorov-Smirnov test was used to evaluate assumptions of normality for each variable, and Levene's test was used to evaluate the assumption of homogeneity of variances between groups (Sokal and Rohlf, 1995). All assumptions were met after data were transformed by natural logs. All statistical analyses were run with Minitab statistical software (version 11) (Ryan et al., 1994).

RESULTS

Chemical composition of organic components in fruits and leaves is summarized in Table 1. PCA of these organic components identified two principal factors that together explain 74.5% of the variation (Table 2). Factor 1 loaded strongly and negatively for protein, and moderate to positive for carbohydrates and lipids. A plot of the factor scores for each sample indicated a relatively clear separation of fruits and leaves along factor 1 (Figure 1A), indicating that leaves have greater amounts of crude protein than fruits.

We found no significant differences, based on *t* tests, when we compared the organic components in fruits with leaves (Table 1). Carbohydrates were highest in fruits of *Musa x paradisiaca* (72%) and lowest in *Psidium guajava* (15%). Protein was highest in fruits of *Achras sapota* (14.9%) and lowest in *P. guajava* (2.2%). Lipids were highest in fruits of *P. guajava* (10%) and lowest in *Ficus bengalensis* and *Prosopis juliflora* (4%).

Young leaves of *Cassia fistula* had the highest concentration of carbohydrates (25.7%), and mature leaves of *P. guajava* had the lowest (7.8%). Mature leaves of *C. fistula* had the highest percentage of protein (14.3%) and *Tamarindus indica* had the lowest (5.4%). Young leaves of *C. fistula* and mature leaves of *Coccinia cordifolia* contained the highest percentage of protein (17.7%

TABLE 1. PROXIMATE COMPOSITION OF LEAVES AND FRUITS FROM PLANTS VISITED BY *Cynopterus sphinx* IN SOUTH INDIA^a

Species	Composition (%)		
	Carbohydrate	Protein	Lipid
Leaves			
<i>Psidium guajava</i> *	7.77	5.67	3.5
<i>Moringa oleifera</i>	12.07	14.04	3.0
<i>Coccinia cordifolia</i>	13.33	16.26	5.0
<i>Tamarindus indica</i>	14.80	5.41	3.0
<i>Ficus religiosa</i>	19.20	13.55	2.5
<i>Cassia fistula</i> , young	25.67	17.73	6.0
<i>Cassia fistula</i> , mature	13.60	14.30	5.0
Mean	15.21	12.42	4.0
± SD	5.32	4.92	1.23
Fruits			
<i>Psidium guajava</i>	15.00	2.22	10.0
<i>Ficus bengalensis</i>	21.25	2.46	4.0
<i>Prosopis juliflora</i>	31.83	9.12	4.0
<i>Achras sapota</i> *	24.67	14.78	5.0
<i>Musa × paradisiaca</i> *	72.00	6.65	6.0
Mean	32.95	7.05	5.8
± SD	20.27	5.21	2.23
<i>t</i> test (leaves vs. fruits)			
<i>t</i>	1.64	1.80	1.47
<i>p</i>	0.18	0.11	0.20

^aAll samples were run in triplicate and expressed as percent dry matter. Percent protein was calculated as N × 4.4 (after Milton and Dintzis, 1981). Orchard trees are denoted with an asterisk.

and 16.3%), respectively. Young and mature leaves of *Cassia fistula* and mature leaves of *Coccinia cordifolia* had the highest concentration of lipids (5–6%).

Macromineral composition of selected leaves and fruits are summarized in Table 3. PCA identified two factors that together explain 82.8% of the variation (Table 2). Factor 1 loaded strongly and negatively for Na, K, and P, and factor 2 loaded strongly and negatively for Ca. A plot of the factor scores for these samples (Figure 1B) indicates a moderate separation of leaves and fruit along factor 2, supporting the hypothesis that calcium concentration is higher in leaves than in fruit. Results of *t* tests show that levels of Ca, but not Na, K, or P, were significantly different between leaves and fruits.

Among the fruits evaluated for macrominerals (Table 3), calcium was highest in *Ficus bengalensis* (1.76 mg/g) and lowest in *Prosopis juliflora*, *A. sapota*, and *Musa × paradisiaca* (0.40 mg/g). Sodium was highest in *P. juliflora* (0.6 mg/g) and lowest in *Achras sapoto* (0.08 mg/g). Potassium was highest in *P.*

TABLE 2. PCA FACTOR LOADING BASED ON LEVELS OF ORGANIC AND MINERAL NUTRIENTS IN RIPE FRUITS AND LEAVES OF SELECTED PLANT SPECIES INGESTED BY *Cynopterus sphinx* IN SOUTH INDIA

	Factor 1	Factor 2
Organic nutrients		
Eigenvalue	1.364	0.873
Percent variation	45.4	29.1
Carbohydrates	0.538	0.759
Protein	-0.564	0.647
Lipids	0.627	-0.069
Mineral nutrients		
Eigenvalue	2.422	0.891
Percent variation	60.5	22.3
Calcium	-0.388	-0.747
Sodium	-0.582	-0.257
Potassium	-0.582	0.257
Phosphorus	-0.503	-0.274

juliflora (2.3 mg/g) and lowest in *A. sapota* (0.2 mg/g). Phosphorus was highest in *M. x paradisiaca* (0.9 mg/g) and lowest in *A. sapota* (0.3 mg/g).

Among the mature leaves evaluated for macrominerals (Table 3), those of *Cassia fistula* had the highest concentration of calcium (2.73 mg/g) and *Psidium guajava* had the lowest (1.52 mg/g). Leaves of *Moringa oleifera* were highest in sodium (1.4 mg/g) and lowest in *C. fistula* (0.10 mg/g). Potassium was highest in *Coccinia cordifolia* (2.25 mg/g) and lowest in *Tamarindus indica* (0.41 mg/g). Phosphorus was highest in *Ficus religiosa* and young leaves of *C. fistula* (1.12 mg/g) and lowest in *P. guajava* (0.4 mg/g).

Analysis of both organic and mineral components of leaves of *C. fistula* (Tables 1 and 3) suggests that carbohydrates, proteins, fats, potassium, and phosphorus were highest in young leaves, and calcium was highest in mature leaves. Sodium appears to be present in equal concentrations in both young and mature leaves. The calcium concentration in mature leaves of *C. fistula* was greater than in young leaves, but the phosphorus concentration in mature leaves was less than in young leaves. The Ca/P ratio in leaves (2.3 ± 1.0 SD) and fruits (1.2 ± 0.82 SD), was not significant (Table 3). Among leaves, the highest Ca/P ratio was in *Psidium guajava* (3.8) and the lowest in *Moringa oleifera* (1.3). Among fruits, the highest Ca/P ratio was in *F. bengalensis* (2.5) and the lowest was in *Musa x paradisiaca* (0.44). The Ca/P ratio in mature leaves of *C. fistula* was higher in immature leaves (Table 3).

Estimates of nutrient extraction efficiencies of organic and macromineral components from leaves chewed by *C. sphinx* ranged from 17.6% to 56.4% for carbohydrates, from 55.1% to 63.8% for protein, and from 40.0% to 50.0% for

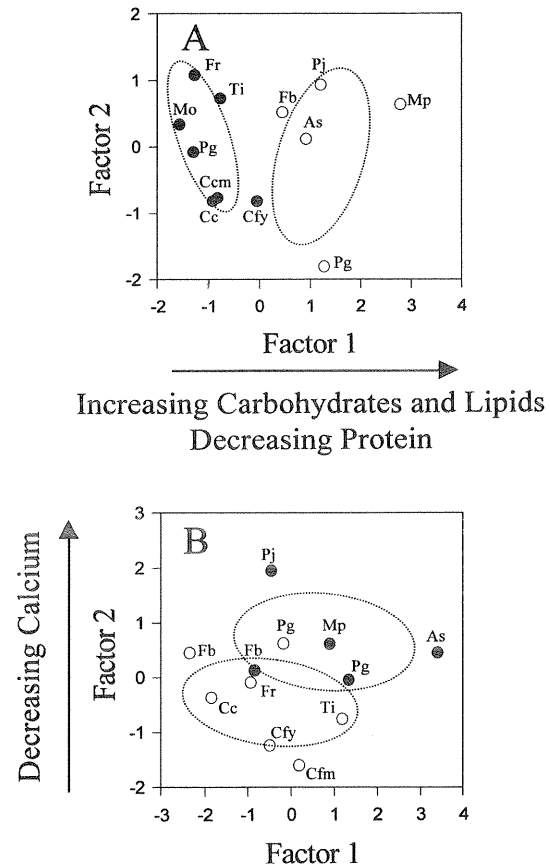


FIG. 1. Results of principal components analysis (PCA) for organic nutrients (A) and minerals (B) comparing fruits and leaves for factor 1 (increasing carbohydrates and lipids and decreasing protein) and factor 2 (decreasing calcium). Solid circles are leaves and open circles are fruits. Ellipses for each analysis depict 95% confidence limits. Principal component scores are coded for the species they represent (PG = *Psidium guajava*, Mo = *Moringa oleifera*, Cc = *Coccinia cordifolia*, Ti = *Tamarindus indica*, Fr = *Ficus religiosa*, Cfy = *Cassia fistula* (young), Cfm = *Cassia fistula* (mature), Fb = *Ficus bengalensis*, Pj = *Prosopis juliflora*, Mp = *Musa x paradisiaca*), As = *Achras sapota*).

lipids (Table 4). A comparison of organic components in leaves from *Cassia fistula* versus those from the extracted fraction (spats) suggests that *C. sphinx* is moderately efficient at extracting carbohydrates, fats, and proteins from foods that it masticates. Estimates of nutrient extraction efficiencies by *C. sphinx* for minerals from leaves of *Cassia fistula* indicate that this varied from 15.4% to

TABLE 3. MINERAL COMPOSITION OF LEAVES AND FRUITS FROM PLANTS VISITED BY *Cynopterus sphinx* IN SOUTH INDIA^a

Species	Amount (mg/g dry matter)				Ca/P
	Ca	Na	K	P	
Leaves					
<i>Psidium guajava</i> *	1.52	0.40	1.91	0.40	3.8
<i>Moringa oleifera</i>	1.84	1.40	1.95	0.14	1.3
<i>Coccinia cordifolia</i>	2.65	0.50	2.25	1.11	1.6
<i>Tamarindus indica</i>	1.60	0.15	0.41	0.56	2.9
<i>Ficus religiosa</i>	1.28	0.30	1.55	1.12	1.9
<i>Cassia fistula</i> , young	2.08	0.10	1.50	1.12	1.9
<i>Cassia fistula</i> , mature	2.73	0.10	0.75	0.87	3.1
Mean	1.96	0.42	1.47	0.95	2.3
± SD	0.56	0.23	0.87	0.35	1.0
Fruits					
<i>Psidium guajava</i>	0.72	0.10	0.70	0.6	1.20
<i>Ficus bengalensis</i>	1.76	0.40	1.86	0.7	2.51
<i>Prosopis juliflora</i>	0.40	0.60	2.28	0.7	0.57
<i>Achras sapota</i>	0.40	0.08	0.23	0.3	1.33
<i>Musa × paradisiaca</i> *	0.40	0.16	0.74	0.9	0.44
Mean	0.74	0.27	1.16	0.6	1.21
(± SD)	0.59	0.22	0.87	0.2	0.82
<i>t</i> -test (leaves vs fruits)					
<i>t</i>	3.68	0.63	0.83	1.48	1.99
<i>P</i>	0.01	0.55	0.44	0.17	0.09
Difference	2.64	1.55	1.26	1.58	1.90

^aAll mineral samples were run in triplicate matter. Orchard trees are denoted with an asterisk.

35.5% for calcium and from 33.3% to 50.0% for potassium. By contrast, extraction efficiency for phosphorus ranged from 17.2% to 35.7% (Table 4). Extraction efficiency of sodium was nil for both young and mature leaves. Because we could not distinguish between the spats produced from young versus mature leaves in our study, we were unable to determine whether extraction of macrominerals was related to leaf maturity.

DISCUSSION

PCA analysis indicates a marked separation of leaves and fruits, suggesting that leaves contain higher concentrations of proteins and calcium than do fruits. However, we found no difference between fruits and leaves, however, when organic components were compared by using *t* tests. The latter result may reflect small sample size and the high variance in organic nutrients present in

TABLE 4. ORGANIC AND MINERAL COMPOSITION OF YOUNG AND MATURE LEAVES OF *Cassia fistula* AND EXTRACTION EFFICIENCY OF NUTRIENTS BY *Cynopterus sphinx* IN SOUTH INDIA^a

Sample	Organic composition (% dry matter)			Minerals (mg/g)			
	Carbohydrate	Protein	Lipid	Ca	Na	K	P
Young leaves	25.7	25.2	6.0	2.08	0.10	1.5	1.12
Mature leaves	13.6	20.3	5.0	2.73	0.10	0.75	0.87
Expelled leaf spats (wedges)	11.2	9.1	3.0	1.76	0.10	0.5	0.72
Estimated extraction efficiency (%)							
Young leaves	56.4	63.8	50.0	15.4	0	50.0	17.2
Mature leaves	17.6	55.1	40.0	35.5	0	33.3	35.7

^aAll samples were analyzed in triplicate and are expressed as mean values.

the leaf and fruit samples that we analyzed. Corlett's (1996) analysis of 153 species of fruits consumed by frugivorous vertebrates, including two species of Paleotropical plant-visiting bats (*Cynopterus sphinx* and *Rousettus leschenaulti*), indicated that the percentage of protein in fruits ranged from 0.9% to 15%, with most species (approximately 89%) having a protein content of less than 7%.

Because many fruits consumed by bats are rich in soluble carbohydrates and poor in crude protein, Thomas (1984) suggested that plant-visiting bats would need to overingest fruits and dump carbohydrates to meet their protein requirements. This hypothesis was supported by Steller (1986), based on experimental feeding trials with *Pteropus poliocephalus*. However, if plant-visiting bats supplement their fruit diet with protein-rich leaves (Kunz and Diaz, 1995; Zortea and Mendes, 1993) and insects (Gardner, 1977; Courts, 1998), they would not need to overingest carbohydrate-rich fruits. Among leaves regularly eaten by *C. sphinx*, the highest concentrations of protein were found in young leaves of *C. fistula* (17.3%), *Cocinia cordifolia* (16.3%), and mature leaves of *Cassia fistula* (14.3%). These values are similar to concentrations of proteins in leaves of *Erythrina poeppigiana* eaten by *Artibeus jamaicensis* (Kunz and Diaz, 1995), but lower than protein concentrations in leaves from *Albizia lebbek* consumed by *Pteropus electo* (Lowry, 1989).

Many plant-visiting bats appear to have overcome the problem associated with the high fiber content present in leaves. They often do so by extracting the liquid fraction rather than by ingesting whole fruits and leaves (Thomas, 1984; Studier and Wilson, 1991; Kunz and Ingalls, 1994; Dudley and Vermeij, 1994; Banack, 1998). Folivory and frugivory by wodging (extraction of liquid fractions by chewing fruits and leaves and forming and expelling an oral bolus or spat),

combined with rapid gut transit time allows bats to process a greater amount of food per unit time than would be possible if large volumes of pulp were consumed and gut retention time were prolonged. Thus, some bats apparently have evolved a strategy for both maximizing nutrient intake and minimizing gut retention time. Fractionation or wadding of fruits and leaves minimizes the ingestion of pulp and fiber and thus can be expected to reduce wing-loading and energy expenditure while in flight (Kunz and Ingalls, 1994).

The highest concentration of protein in young leaves of *Cassia fistula* is consistent with reports that protein content decreases with leaf maturity (Feeny, 1970; Telek and Martin, 1983), although young leaves have higher concentrations of proteinase-inhibiting compounds such as tannins (Feeny, 1970; Ryan and Green, 1974; Rhoades and Cates, 1976; Sanderson et al., 1976; Telek and Martin, 1983; Harborne, 1991).

Relative to fruits, which have patchy distributions in space and time (Fleming, 1992; Terborgh, 1986), leaves of some tropical plant species are ubiquitous and are available year-round, although they may vary considerably in phenology as well as fiber and chemical composition (Ganzhorn, 1992). Plant-visiting bats that selectively feed on leaves should gain a higher yield of protein per unit foraging effort compared to those that feed only on protein-poor fruits (Kunz and Diaz, 1995). The net result of feeding on leaves is that this behavior potentially provides *C. sphinx* with a food source that is rich in both protein and calcium. That plant-visiting bats expel fruit and leaf pulp high in fiber content should increase the rate of gut passage and improve the digestibility of extracted juices (see Van Soest, 1967).

Whether nitrogen is a limiting organic nutrient in free-ranging, plant-visiting bats remains unclear. Korine et al. (1996) determined the digestible nitrogen requirements for free-ranging *Rousettus aegyptiacus* (134 mg N/kg^{0.75}/day), and concluded that energy rather than nitrogen was the limiting factor in this species. DeLorme and Thomas (1996) determined the digestible nitrogen requirements of captive *Carollia perspicillata* (292.8 mg N/kg^{0.75}/day), and concluded that nonreproductive individuals were able to meet their nitrogen requirements without overingesting energy-rich fruits. More recently, Delorme and Thomas (1999) evaluated the nitrogen and energy requirements of captive *Artibeus jamaicensis* and *Rousettus aegyptiacus* and concluded that these two species may be specialized for the retention of nitrogen, especially if they are faced with low nitrogen availability. Whether these results reflect dietary differences in captive versus free-ranging conditions remains to be determined. Notwithstanding, all of the protein ingested by plant-visiting bats may not be available because condensed and hydrolyzable tannins may deter or inhibit protein digestion in animals (Harborne, 1991).

Some fruits consumed by *C. sphinx* have crude lipid contents ranging from 6% to 10%, with the highest values found in *Psidium guajava* (Table 1). How

much of this dietary fat is available for metabolism remains unknown. Cox (1984) reported that *Pteropus samoensis* preferred flower parts rich in carbohydrates and fats, although most tropical fruits typically are low in lipids (Herrera, 1987). The high glycogenolytic activity associated with carbohydrate and fat metabolism in *Artibeus jamaicensis* and *Phyllostomus discolor* (Yacoe et al., 1982) indicates that these plant-visiting bats readily convert dietary sugars and fats into glycogen as a temporary energy reserve. *Eidolon helvum*, an Old World fruit bat, converts dietary carbohydrates and fats into glycogen (Okon et al., 1978), and glycogen rather than fat is the primary source of energy for roosting activities and flight (Okon et al., 1978; Van der Westhuyzen, 1978).

The high calcium levels in *Cassia fistula*, relative to other leaves and most fruits, including *Ficus* spp., may explain why leaves of *C. fistula* are consumed by *C. sphinx* year-round (Bhat, 1994; Rajan et al., 1999). The mean level of calcium in leaves was more than two times greater than the mean value in fruits (Table 3). *Ficus bengalensis* was the only species with calcium levels in fruits comparable to those in leaves. Given the high concentration of calcium in *Ficus* fruits (O'Brien et al., 1998) (Table 3), it is not surprising that they are preferred as food by many plant-visiting bats (Gardner, 1977; Marshall 1983, 1985; Morrison 1978, 1980; Handley et al., 1991), including *Cynopterus sphinx* and *C. brachyotis* (Bhat, 1984; Boon and Corlett, 1989; Tan et al., 1998).

Calcium is critical for successful reproduction in both wild and domesticated mammals (Sadler, 1969; Robbins 1993). Batzli (1986) demonstrated that low calcium levels in the diet of female California voles (*Microtus californicus*) led to a reduction in reproductive performance. Calcium was judged to be a limiting nutrient for milk production (Kunz et al., 1995) and postnatal growth (Studier and Kunz, 1995; Papadimitriou et al., 1996) in the insectivorous bat, *Tadarida brasiliensis*. Similarly, Stern et al. (1997) considered calcium a limiting nutrient during lactation in the omnivorous bat *Phyllostomus hastatus*.

Of the calcium present in leaves and fruits, not all may be available to plant-visiting bats, since dietary fiber is known to bind calcium and reduce its bioavailability (Weaver et al., 1991). Moreover, while some leaves and fruits may be high in calcium, it may not be readily available if the Ca/P ratio is less than the optimum range of 1 to 2 (Robbins, 1993). The high Ca/P ratio observed in leaves relative to fruits in the present study (Table 3) suggests why leaves may be exploited by bats. Notwithstanding, *Ficus* fruits have higher Ca/P ratios than leaves and most other wild fruits (O'Brien et al., 1998) (Table 3), which may further explain why these native fruits are preferred by tropical frugivores.

Sodium is one of the most sought after minerals by animals, especially in tropical regions (Moe, 1993; Emmons and Stark, 1979). The relatively low sodium levels in fruits (Herrera, 1987; O'Brien et al., 1998) and leaves (Table 3), and the apparent lack of oral extraction of sodium from leaves by *C. sphinx* (Table 4), suggests that sodium may be a limiting nutrient for this species. That

some members of the Pteropodidae drink seawater further supports the hypothesis that sodium is a limiting nutrient for this and other plant-visiting bats (F. Bonaccorso, personal communication). As in other mammals (Weeks and Kirkpatrick, 1976), the relatively low potassium levels observed in fruits and leaves (Table 4) may reduce the sodium requirements for *C. sphinx* as well as other plant-visiting bat species.

Early reports of low survival rates for Old World fruit bats maintained in captivity were attributed to diets that consisted largely of cultivated fruits (Rasweiler, 1977). Because of recent advances in the captive care and management of plant-visiting bats, dietary supplements of green leaves and multivitamins are now recommended (Fascione, 1995), with expected increases in survival and reproductive success. These observations are supported by studies that indicate that domestic fruits have lower concentrations of calcium and sodium than native fruits (O'Brien et al., 1998; Nelson et al., 2000). In the present study, calcium levels in leaves were higher than in fruits, and the Ca/P ratio in leaves was nearly twice that of fruits, suggesting that leaves may be selected by bats for their relatively high mineral content.

Our estimates of extraction efficiency of organic and macromineral nutrients by *C. sphinx* from leaves of *Cassia fistula* are based on comparisons of whole leaves to spats. However, the maturity of leaves (young vs. mature leaves) formed into spats by bats was not determined. Thus, whether the apparent differences in extraction efficiency of young versus mature leaves reflect the nutrient quality of the leaves or differences in the extraction of minerals from leaves at different stages of maturity remains to be determined. What is clear, however, is that extraction efficiencies vary depending on the nutrient being considered, ranging from 50.0% to 63.8% for organic nutrients and from 0 to 35.7% for macrominerals. By comparison, Morrison (1980) reported that 43% of the metabolizable energy in fruits of *Ficus insipida* was retained by *Artibeus jamaicensis*. Similarly, Stellar (1986) found that 29.1% of the dry matter content was retained by *Pteropus poliocephalus*, with the remainder ejected as spats. These findings point to the variation that can be expected in extraction and retention efficiencies and emphasize the need for additional data from plant-visiting bats throughout the year, especially as they feed on leaves and fruits at different stages of maturity and ripeness.

The fact that many plant-visiting bats are sequential dietary specialists (Marshall, 1983; Banack, 1998) highlights the need to evaluate the nutritional quality of foods on a year-round basis. Whether *C. sphinx* and other bats feed selectively on leaves when fruit abundance is low, or when nutrient demands are high, remains to be established. Bhat (1994) and Rajan et al. (1999) reported that *C. sphinx* fed on leaves year-round in western India, as did Tan et al. (1998) for *C. brachyotis* in Malaysia.

In summary, our findings suggest that leaves are valuable sources of organic

and mineral nutrients for plant-visiting bats. If *C. sphinx* and other plant-visiting species were able to meet their protein and calcium requirements with minimal energy expenditure, we would expect folivory (by wodging) to be a consistent year-round feeding strategy. Moreover, assuming that requirements for protein and calcium increase during pregnancy and lactation, we predict that folivory should reach a peak during these nutrient-demanding periods.

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