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Articles

MACRONUTRIENT PATTERNS OF 19 SPECIES OF PANAMANIAN FRUITS FROM BARRO COLORADO ISLAND

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Abstract

To attract seed dispersal agents, most Neotropical tree species produce edible fruits. Animals eat the fruits, often swallowing the seeds, which may be deposited away from the parent tree. Data show that not all frugivores in a given habitat are equally attracted to the same fruit species. Though numerous factors can influence fruit choice, the nutrient value of the pulp to the disperser is clearly of key importance. Here data are presented on the macronutrient content (total crude protein, fat and nonstructural carbohydrate) of 19 fruit species collected from a single forest site, Barro Colorado Island in central Panama. The only criterion for analyses was that each species produce fruits consumed by at least two primate species at this site. Though all fruit species contained a measurable amount of each macronutrient class, there were often striking differences in the amount contributed per class. Overall, two species (10.5% of the total sample) were highest in protein, five (26%) were highest in fats and twelve (63%) were highest in nonstructural carbohydrates. Fruit species in the same family or genus did not necessarily show the same macronutrient pattern. Similar data from a range of Neotropical sites could prove useful in formulating hypotheses related to community fruit-disperser relationships.

Key Words: Tropical forest, Panama, fruits, nutrients, protein, fats, nonstructural carbohydrates, frugivores, seed dispersal.

Resumen

Para atraer a los agentes dispersores de semillas, muchas de las especies de árboles Neotropicales producen frutos comestibles. Los animales comen los frutos, a menudo tragando las semillas, las cuales pueden ser depositadas lejos del árbol parental. Los datos muestran que no todos los frugívoros en un hábitat dado son igualmente atraídos por las mismas especies de frutos. A pesar de que numerosos factores pueden influir la selección de frutos, el valor nutricional de la pulpa para el dispersor es claramente de fundamental importancia. Aquí se presentan datos del contenido de macronutrientes (proteína cruda total, grasa y carbohidratos no estructurales) de 19 especies de frutos colectados en un solo bosque en la Isla de Barro Colorado, región central de Panamá. El único criterio para el análisis fue que cada especie produjera frutos consumidos por al menos dos especies de primates en dicho sitio. Aunque todas las especies de frutos contuvieron una cantidad apreciable de cada clase de macronutriente, hubo a menudo marcadas diferencias en la cantidad aportada por cada clase. En general, dos especies (10.5% de la muestra total) tuvieron más alta proteína, cinco (26%) más alto contenido de grasas y doce (63%) más alto contenido de carbohidratos no estructurales. Las especies de frutos de una misma familia o género no mostraron necesariamente el mismo patrón de macronutrientes. Datos similares de diferentes sitios en el neotrópico serían muy útiles para formular hipótesis acerca de las relaciones de las comunidades de dispersores de semillas.

Palabras Clave: Bosque tropical, Panamá, frutos, nutrientes, proteína, grasas, carbohidratos no estructurales, frugívoros, dispersión de semillas.

Introduction

The overwhelming majority of tropical tree species rely on animal vectors to disperse seeds to potential germination sites away from the parent (van der Pijl, 1969; Snow, 1971; Howe and Vande Kerckhove, 1979; Howe, 1993; Stiles, 1993; Herrera, 2002). To facilitate dispersal, seeds are enveloped in an edible matrix—fleshy mesocarps, pericarps, arils and the like—that serves as an attractant for potential dispersal agents. Animals enter the tree to eat the fruit, often swallowing the seeds, which may later be regurgitated or defecated some distance away. Some frugivores (*e. g.*, various bat species) carry fruits away from the parent tree to consume elsewhere, often dropping quantities of seeds below the feeding perch. Studies show that not all frugivores in a given habitat are equally attracted to the same fruit species (Snow, 1962; McDiarmid *et al.* 1977; Howe and de Stevens, 1979; Milton, 1981; Chen *et al.*, 2001; Herrera, 2002; Dew, 2005). Fruit choices at times appear deliberate in that individuals of a particular species will ignore available ripe fruits of one tree species while feed-

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ing heavily on ripe fruits from another. Such behavioral disparities may influence patterns of seed distribution and thereby affect forest structure and composition (Clark *et al.* 2001).

Considerable effort has been devoted to examination of the attractant relationship between fruit species and their dispersal agents, with particular attention paid to avian dispersers. Fruit traits examined include fruit size, color, hardness, nutrient composition, seed size and number, secondary metabolites, distribution patterns in space and time, and accessibility, among others (Denslow and Moermond, 1982; Howe, 1993; Fleming *et al.,* 1993; Corlett, 1996; Alves-Costa and Lopez, 2001; Herrera, 2002). These traits must then be integrated with features of the external and internal morphology and physiology of potential dispersal agents (Milton, 1981; Witmer and Van Soest, 1989; Stiles, 1993; Alves-Costa and Lopez, 2001; Levey and Martinez del Rio, 2001; Martinez del Rio and Karasov, 1991). Due to this complex array of factors, many questions related to seed-disperser interactions remain unanswered or incompletely understood as information to address them is scarce, inconclusive or simply non-existent (Herrera, 2002).

As the edible pulp or aril is the "reward" typically offered to dispersers, its nutrient value would seem to be a critical element in plant-disperser interactions (*e. g.*, Stiles, 1993, p. 228: "Birds eat fruits to gain the nutritional rewards in fruit pulp. The preferences exhibited by birds must, in part, be influenced by the nutritional components assimilated.") (see also Herrera, 2002). Yet to date, in spite of numerous elegant papers on aspects of fruit selection and seed dispersal by a wide range of dispersal agents, there is little comparative data on the nutrient composition of a representative array of mammal-consumed wild fruits from tropical forest sites (Howe, 1993). This absence is particularly striking for Barro Colorado Island (BCI) in the Republic of Panama, as this 1600 ha nature reserve has been the site of numerous studies of mammalian dietary ecology and there is also an unusual wealth of information on BCI forest composition and phenology and the maintenance of forest diversity (Knight, 1975; Leigh *et al*., 1982; Hubbell and Foster, 1990; Milton, 1991).

Here I present data on the macronutrient content of 19 species of wild fruits collected on Barro Colorado Island. All species have seeds dispersed by various mammals as well as other vertebrates and/or invertebrates. Unlike many studies, fruit species analyzed were not selected because of the dietary focus of any particular species—rather they are regarded as a composite sample of macronutrient patterns of mammal-consumed fruits from the BCI forest. Results of analyses provide a quantitative basis for characterizing fruit nutrient profiles for fruits at this site. Similar information from a number of Neotropical lowland forest sites might prove useful in refining hypotheses related to fruit-disperser relationships, niche-partitioning and the predicted composition of particular disperser communities as well as the role played by primate and other mammalian dispersers in influencing and maintaining forest composition.

Methods

Study site

Fruits were collected from adult trees, hemiepiphytes or lianas growing in the forest on Barro Colorado Island, Panama. Detailed descriptions of this moist lowland tropical forest and of climatic features characteristic of this region can be found in the literature (Allee, 1926; Croat, 1978; Leigh *et al*., 1982; Hubbell and Foster, 1990).

Study species

The 19 fruit species analyzed were not collected according to any predetermined plan and can be regarded as an arbitrary sample of edible fruit flesh from this forest. The only criterion for acceptance was that each species produce fruit flesh of a type generally accepted as functioning to attract mammalian feeders (van der Pijl, 1969) and known to be consumed by at least two of the four non-human primate species on BCI. I typically noted a particular fruiting tree because some mammal, often a howler monkey (*Alouatta palliata*) or spider monkey (*Ateles geoffroyi*), was feeding on its fruits. If sufficient fruit could be obtained for analysis, I collected a sample. Each sample was composed of fresh, ripe, undamaged fruit dropped under the parent tree by feeding monkeys or removed by a climber with a tree pruner.

Ultimately fruits were collected from four hemiepiphytes (*Ficus bullenei, F. costaricana, F. obtusifolia, F. trigonata*), one liana *(Doliocarpus major)* and 14 tree species (see Table 1 for list of all species). Four of the 14 tree species are among the 50 most abundant species in the 50-hectare survey plot of Hubbell and Foster (Hubbell and Foster, 1990; S. Lao, personal communication). Six of the fruit species analyzed are members of the genus *Ficus*; there are 17 *Ficus* species identified thus far on Barro Colorado Island and one to three species of the other genera represented in my sample (Wendeln *et al.*, 2000; S. Lao, personal communication). Wendeln *et al.* (2000) examined the nutrient content of 14 species of *Ficus* fruit from BCI, including the six species I analyzed. Their work looked at *Ficus* species only. The array of families and genera represented in my study extend their findings on *Ficus* into a broader comparative framework. Fruits analyzed ranged from ~1 cm in diameter when ripe (*F. costaricana*) to ~9 cm in diameter (*Gustavia superba*). Most species produced fruits ~2-3 cm in diameter and ~3-5 cm. in length. The *Ficus* species contained many dozens of tiny seeds; *Gustavia superba* fruit contained an average of 12 seeds per fruit, each seed ~2.5 cm in length. The rest of the species contained one to a few moderate sized (~0.5-1.5 cm long) seeds per fruit.

Treatment of samples

Each sample was composed of the flesh or arils of various fruits collected at the same time from a single parent tree.

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Ripe fruits of a given species can show notable differences in nutrient composition between trees or even when collected from the same tree on the same or different days (Howe, 1980; Wheelwright, 1993; Chapman *et al.*, 2003). Though the exact percentage of protein, fat or carbohydrate in a given ripe fruit may vary within or between trees of a particular species, the profile of the three macronutrient groups in relation to one another should generally remain consistent. In other words, one would not expect to find that ripe fruits from tree 1 of species X at a given site would predominate in protein while ripe fruits of tree 2 of species X at that same site would predominate in fats. For this reason, analytical results presented here are regarded as a composite overview of the distribution profile of the three macronutrient groups both for ripe fruits from that tree and for ripe fruits of that species on BCI. Fruits of all species except *Ficus* spp. were opened shortly after collection and the flesh or aril separated from the seeds. The *Ficus* fruits were broken apart to facilitate drying but seeds were not removed (more on this point below). Samples were dried in an oven at 55° C until a constant weight was reached. The dried flesh was then ground in a Wiley mill using a 20-mesh screen. Samples were stored in sealed plastic containers placed in a desiccator and later analyzed for crude protein, crude fat and total nonstructural carbohydrates (TNC) at the Palmer Research Laboratory, University of Alaska, using techniques described below.

Crude protein

Total nitrogen (N) in each sample was determined by the macro-Kjeldahl technique. Results were then multiplied by the standard 6.25 conversion factor to get an estimate of crude protein present in each sample.

Crude fat

The crude fat (= all fats, oils and waxes) content of each sample was determined by the Randall extractor method (Randall 1974). In this technique each sample is immersed in hot ethyl ether for ten minutes, rinsed out of the solvent and further extracted and rinsed with solvent condensate for 20 minutes. The ethyl ether is then removed by evaporation and the residue is weighed. The difference in weight of the sample prior to and following ether extraction is used as an estimate of the crude fat content of the sample.

Total nonstructural carbohydrates

The modified Weinmann technique as described in Milton (1979) was used to determine the total nonstructural carbohydrate (TNC = sugars, starches and fructosans) content of each sample.

Results and discussion

Results of analyses are presented in Table 1. All values are expressed as percent dry weight of fruit pulp. Results are discussed first in terms of each macronutrient class and then in terms of the proportion contributed per class per species.

Protein

Protein content of the flesh or arils of the 19 species ranged from a low of 3.2% (*Tetragastris panamensis*) to a high of 15.2% (*Gustavia superba*). Mean protein content for the

Table 1. The percent dry weight of each macronutrient group (crude protein, crude fat, total nonstructural carbohydrates, TNC) in flesh or arils of 19 Panamanian fruit species.

Family	Species	Crude Protein	Crude Fat	TNC
Anacardiaceae	*Spondias mombin*	4.3	1.3	40.0
Anacardiaceae	*Spondias radlkofera*	11.7	3.9	24.6
Bombacaceae	*Quararibea asterolepis*	5.4	0.2	31.0
Burseraceae	*Tetragastris panamensis*	3.2	0.2	56.3
Dilleniaceae	*Doliocarpus major*	4.5	3.8	21.1
Lauraceae	*Beilschmiedia pendula*	6.2	25.4	11.9
Lecythidaceae	*Gustavia superba*	15.2	42.3	5.1
Meliaceae	*Trichilea tuberculata*	7.8	38.3	15.6
Moraceae	*Brosimum alicastrum*	9.3	1.2	20.7
Moraceae	*Ficus bullenei*	7.1	3.4	3.7
Moraceae	*Ficus costaricana*	6.9	3.9	6.4
Moraceae	*Ficus insipida*	7.0	5.8	14.5
Moraceae	*Ficus obtusifolia*	4.1	3.6	8.7
Moraceae	*Ficus trigonata*	5.6	6.4	10.5
Moraceae	*Ficus yoponensis*	7.5	6.0	11.3
Myristicaceae	*Virola nobilis*	4.5	42.5	18.6
Palmae	*Astrocaryum standleyanum*	4.8	1.4	45.5
Palmae	*Scheelea zonensis*	3.6	22.3	15.1
Rubiaceae	*Faramea occidentalis*	4.1	0.1	38.8

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combined samples was 6.5% ± 3.0%. This is a low protein content when compared with that of tree leaves from this same forest. On Barro Colorado Island, young tree leaves averaged 19.5% ± 7.2% protein (Kjeldahl technique; n = 6 species; K. M., unpubl. data; see also Milton 1979 for estimates of leaf protein using summed amino acid technique). Data compiled by Leung (1969) show that insects (*i. e.*, flying ants, beetles, crickets, caterpillars, grasshoppers, locusts and termites) average 16.2% ± 8.5% protein. Some insect larvae contain ≥ 42% protein (Jenkins and Milton, 1993). When compared both to young leaves and insects, most ripe fruits are low in protein. The actual protein content of fruits analyzed may be even lower than estimates suggest as using nitrogen as a proxy for protein may over-estimate the protein content of fruit pulp (Levey and Martinez del Rio, 2001).

Fat

The crude fat content of the 19 species ranged from a low of 0.1% (*Faramea occidentalis*) to a high of 54.2% (*Virola surinamensis*). Mean fat content for the combined samples was 11.8% ± 16.5%. Though most species were decidedly low in fat, five species contained a substantial (> 22% dry wt.) amount (Table 1). Leaves are generally quite low in fat. Young leaves from the Barro Colorado forest average 2.4% ± 2.3% crude fat (Randall technique, n = 10 species; K. M., unpubl. data). Insects examined by Leung (1969, see list above) averaged 9.5% ± 9.9% fat. Some insect larvae may have fat contents > 42% (Jenkins and Milton, 1993). Though most fruit species in the BCI sample were not high in fat, a few species were notably high.

Total nonstructural carbohydrates

The total nonstructural carbohydrate content (TNC) of the 19 species ranged from a low of 5.1% (*Gustavia superba*) to a high of 56.3% (*Tetragastris panamensis*). Mean TNC content for the combined samples was 21.0% ± 14.8%. Leaves are generally low in TNC. Mature leaves from the Barro Colorado forest average 3.7% ± 3.5% TNC and young leaves 4.0% ± 2.2% (Weinmann technique; n = 6 species for each category; Milton, 1979). Data from Leung (1969) show that insects average 2.7% ± 1.6% TNC. Therefore, in contrast to both leaves and insects, many ripe fruit species contain a notable amount of nonstructural carbohydrate.

Nutrient content by species

Though all species contained some measurable proportion of each macronutrient class, there were often striking differences in the amount contributed per class per species. In terms of the three nutrient classes, two species (10.5% of the total sample) were highest in protein, five (26%) were highest in fats and twelve (63%) were highest in nonstructural carbohydrates. Species predominating in TNC showed a wide range of values. In contrast, results suggest that when a given plant taxon uses fat as the principal caloric attractant, it will use a high percentage, as all five species in this category had > 22% fat. *Gustavia superba,* with a fat content of 42.3%, is clearly in the high fat group but unlike the other four species predominating in fat, *Gustavia* had the highest protein content (15.2%) and one of the two lowest TNC contents in the entire sample. Therefore, it was an anomalous species in comparison with the other eighteen and has its own distinct pattern of nutrient allocation. The two species predominating in protein were both *Ficus* species. It is likely that the protein content of the flesh of all *Ficus* species was confounded by the protein content of the many indigestible fig seeds in each fruit and for this reason overestimated. Fig seeds are degraded by chemicals used in analyses but, if swallowed intact, (that is, not crushed by the teeth of the feeder) apparently are not degraded by the action of digestive enzymes in the guts of most fig-eating animals and are excreted intact (Hladik and Hladik, 1969; Morrison, 1980). On BCI, *Ficus* fruits are made up of approximately 50% pulp and 50% seeds dry weight and the two components show somewhat different nutrient profiles, with flesh higher in water-soluble carbohydrates than seeds and seeds higher in protein and fiber than flesh (Wendeln *et al.*, 2001).

Howler monkeys and some other fig-eating mammals crush some, but by no means all, fig seeds when eating the fruits (Hladik and Hladik, 1969; Wendeln *et al.*, 2001; K.M., pers. obs.). For this reason, it is difficult to provide an estimate of the proportion of pulp versus seed nutrient intake for many fig-eating animals. All values presented in Table 1 for *Ficus* species include both flesh and seeds; the precise nutrient contribution of one or the other component in a given animal's diet would depend on an array of factors particular to that feeder. With one exception, the TNC content of *F. insipida*, in comparison to all other species in the analyses, *Ficus* species were not outstandingly high in any nutrient group in spite of the fact that all estimates likely include augmentation from seed macronutrients.

The nutrient patterns present in fruit species from particular locales presumably reflect a long evolutionary interplay between tree species and seed dispersal agents (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977; Howe, 1993; Herrera, 2002). The manufacture of fruit flesh is costly and theoretically each parent tree is seeking to maximize returns from such investments. If we view these 19 fruit species as a type of "grab sample" of macronutrient patterns present in vertebrate-consumed fruit species in this forest, it is clear that the majority of species predominate in nonstructural carbohydrates. In terms of caloric value, TNC may not always dominate per unit mass ingested, but it predominates as a chemical constituent in terms of the three macronutrient groups. If we assume that, over evolutionary time, each plant species has been free to elaborate fruit nutrients in whatever proportions seem most expedient for seed dispersal success, it is clear that most species in this sample have "chosen" to emphasize TNC over protein or fat. A priori, there is apparently no physiological reason why all fruit flesh could not be high in protein or fat rather than TNC if either of these were more favored mode of

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nutrient allocation, since there are fruit species, both on BCI and elsewhere, showing such patterns (Snow, 1962; McDiarmid *et al.*, 1977; Styles, 1993; Herrera, 2002). On a community-wide basis, soluble carbohydrates appear to be the most commonly utilized disperser attractant.

The dominance of nonstructural carbohydrates in wild fruit flesh is seen in data from other Neotropical locales. For example, in a list of 40 wild fruit species eaten by frugivores in Guatemala, 38 were highest in TNC and two in fat (Coelho *et al.*, 1976). Similarly, in most Neotropical plant communities for which data are available, lipids appear restricted to a small subset of species producing fleshy fruits. For example, only 20% of the fleshy-fruited species in a Costa Rican plant community had a lipid content > 10% dry weight (Stiles 1993). Protein content appears low for most wild fruit species, regardless of locale. A mean protein content of 8.9% ± 0.6% was reported for 122 fruit species in the Neotropics while an overall mean protein content of 5.5% ± 0.4% was reported for fruit species in Europe and 5.2% ± 0.4% for species in North America (Stiles 1993). Several reasons can be suggested for the use of nonstructural carbohydrates rather than protein or fat as the predominant fruit attractant. Generally, nonstructural carbohydrates are the most rapidly and inexpensively digested of the three nutrient groups (Maynard and Loosli, 1969). This factor may be of special importance to a wide array of smaller-bodied frugivores, since they need to turn over considerable food energy each day to meet metabolic demands. In herbivorous mammals, as body size decreases, metabolic costs per unit mass increase exponentially while gut capacity increases proportionate to body mass (Parra, 1978). Thus, in general, smaller homeotherms should be greatly attracted to foods offering high and rapid energetic returns.

Flesh from six of the 19 fruit species used in these analyses, and likewise collected by KM on BCI, were analyzed for sugar composition by I. and H. Baker, using methodologies presented by Baker and colleagues (1998). In all cases (100%) fruit flesh predominated in glucose and fructose and sucrose was uniformly low (Milton, 1999). In striking contrast, data on the sugar composition of a wide range of cultivated fruits show that sucrose is generally the predominant fruit sugar (Milton, 1999). Sugar composition of flesh could have important implications for the fruit preferences of particular seed dispersal agents (Freeman and Worthington, 1989; Ko *et al.*, 1998; Martinez del Rio *et al.*, 1989; Martinez and Karasov, 1991). The digestion of the hexoses glucose and fructose does not require manufacture of a sucrase, necessary if sucrose were the principal sugar attractant. This metabolic "savings" may benefit many frugivores, particularly smaller bodied frugivores. Fats typically take considerably longer to digest than nonstructural carbohydrates and are more costly to digest in terms of their specific dynamic effect. In addition, most animals find it necessary to maintain a balance between energy and protein in the diet. The source of the energetic calories can affect the amount of protein required to maintain this balance. Experimental data show that for each 4% of extra fat input into the diet, the protein content must go up 1% by weight to maintain a constant protein to non-protein caloric ratio (Crampton and Lloyd, 1959). A certain threshold in body size and/or digestive specializations may be required to utilize quantities of fatty foods efficiently (Stiles, 1993; Martinez del Rio and Karasov, 1990; Levey and Martinez del Rio, 2001; Dew, 2005).

As noted, there are already various sources of high quality protein available in tropical forests, including young leaves, insects and other animal matter. For this reason, tree species producing protein-rich flesh would not be offering a particularly novel attractant. As most vertebrates do not require large quantities of protein in the diet each day, smaller-bodied species in particular might rapidly become satiated on protein-rich flesh which would lower the number of fruits eaten per visit and thereby depress the number of seeds dispersed. Protein ingested in excess of what the body actually requires also tends to be wasted in so far as its specific functions are concerned, since only the most marginal amounts can be stored. And dietary protein must be catabolized, a process that is energetically expensive because of the high specific dynamic effect of protein digestion (Maynard and Loosli, 1969). The striking exception to the low protein pattern in the BCI sample was *Gustavia superba*. It was by far the largest fruit in the sample—softball-sized— and its unique nutrient profile (and large seeds) suggests that it may seek to attract large terrestrial frugivores as seed dispersal agents. Offering notable protein and energy as a reward may help ensure the specialized dispersal services required for unusually large seeds. Fruits rarely comprise the entire diet of mammals and birds, as fruit pulp provides primarily energy (Rode and Robbins, 2000). Not only do fruits generally lack a sufficiency of protein and various other nutrients animals require, a high carbohydrate-low protein intake is not desirable over the long term as it greatly elevates energy metabolism (Rode and Robbins, 2000). To obtain an optimal balance of energy and nutrients, most vertebrates must therefore move away from fruiting trees each day to seek out other types of foods. A fruit species that provided feeders with complete nutrition would likely disperse few seeds as animals would cluster around such trees until the fruit crop was exhausted. In the case of *Gustavia superba,* a high protein content might not be disadvantageous in terms of seed dispersal, as trees of this species produce only a few ripe fruits at any given time and all trees are small in size. Large frugivores would thus be forced to move about the forest each day to obtain sufficient food and in doing so would move *Gustavia* seeds away from the parent. Rodent predation on *Gustavia* seeds is high at some sites (Sork 1987) and for this reason, movement of seeds well away from parent trees may be of particular value.

In choosing to emphasize TNC in fruit flesh, species may also be seeking to maximize their possibilities for future reproductive success. As no plant can predict where a given seed will land, it seems most expedient to use the

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disperser attractant with the widest appeal. If seed dispersal agents present in the parent habitat are absent in new habitats where seeds arrive and germinate, other frugivorous species should still be attracted to sugar-rich fruits. This might not happen so easily with a high protein or fat reward as most dispersal agents depend largely on other sources (leaves, insects, larvae, other vertebrates) for these nutrients. It therefore appears that on BCI, nonstructural carbohydrate is the most "popular" reward offered seed dispersal agents. By providing a source of readily assimilated energy, largely in the form of fructose and glucose, sugary flesh gives dispersal agents the fuel required for an active life style that should facilitate the movement of seeds away from the parent plant. Sugary fruits also give dispersers the energy needed to move about the forest in search of foods containing other nutrients they require. Many primates preferentially eat fruits early in the day and leaves later in the day (Chivers, 1977; Milton, 1980). This feeding pattern suggests that many frugivores actively seek out energy-rich food sources at their first opportunity and feed heavily from them in order to ensure the energy required for their other daily activities. Such a feeding pattern, in turn, should enhance seed dispersal efficiency.

As noted, the six *Ficus* species in this sample were not notably high in any nutrient group. In keeping with this finding, data suggest that most Neotropical frugivores are not attracted to fig fruits because of their high nutrient value. On BCI, spider monkeys (*Ateles geoffroyi*), for example, will ignore fruiting fig trees if other more preferred fruit species are available (Milton, pers. obs.). Neotropical *Ficus* species often produce large ripe fruit crops at times of year when many other fruit species are in short supply (Foster, 1978; Milton, 1980; Terborgh, 1983; Milton, 1993). It would appear that many Neotropical frugivores are attracted to *Ficus* fruit largely because it is the "only game in town" at some times of year (Terborgh, 1983). Various Neotropical mammals that show strong dependence on fig fruits throughout the year appear to have either an energetically inexpensive life style (e.g., howler monkeys, *Alouatta palliata*; Milton, 1980) or a technique for eating fig fruits such that nutrient returns are maximized and the intake of bulky indigestible material is kept low (e.g., fruit bats; *Artibeus jamaicensis*, Morrison, 1980; Wendeln *et al.*, 2001).

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