

NUTRITION ADVISORY GROUP HANDBOOK



FRUIT BATS: NUTRITION AND DIETARY HUSBANDRY^a

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Bats (order: Chiroptera) account for one-fourth of the world's living mammals. Their closest taxonomic relatives are still debated, but Chiroptera are commonly included in a supraordinal grouping along with the Dermoptera (flying lemurs), Primates, and Scandentia (tree shrews).⁵⁸ There are over 900 species of bats, divided into two suborders: Megachiroptera, consisting of the single family Pteropodidae, and Microchiroptera, consisting of 16 highly diverse families. Megachiroptera are primarily limited to the Old World tropics and subtropics, whereas Microchiroptera are found throughout the world.

Bats exhibit a great ecological, behavioral, and physiological diversity that makes them popular exhibit animals in zoological parks and fascinating subjects of research. Species in the Megachiropteran family Pteropodidae are primarily plant-visiting bats and feed on fruit and on flower resources (nectar and pollen), although some have been observed practicing folivory by leaf fractionation. They chew the leaves, swallow the juices, and spit out the residue. The 16 families of Microchiroptera include species that eat primarily fruit (frugivorous), nectar and pollen (nectarivorous), insects (insectivorous), blood (sanguivorous), small mammals, birds, lizards, and frogs (carnivorous), or fish (piscivorous).^{22, 23,77}

^aAdapted (and updated) from Dempsey, J.L. 1998. Recent advances in fruit bat nutrition. Pp. 354-360 in Fowler, M.E. and R.E. Miller (eds.). *Zoo and Wild Animal Medicine: Current Therapy 4*. W.B. Saunders Co., Philadelphia, PA.

This diversity in feeding strategies, along with limited knowledge of environmental and physiologic requirements, limits the species that can be successfully maintained in captivity. The frugivorous and nectarivorous bat species found in the families Pteropodidae (Megachiroptera) and Phyllostomidae (Microchiroptera) have been maintained in captivity with the greatest success, due in large measure to their preferences for soft, sweet fruits and the ability of zoos to satisfy those preferences with adequate diets. It has been demonstrated that the golden-mantled flying fox (*Pteropus pumilus*) and the greater musky fruit bat (*Ptenochirus jagori*) can use olfaction to locate fruit and assess its ripeness.³⁹ Diets for captive fruit bats have traditionally been based on feeding habits in the wild. Studies on wild bats include attempts to collect and analyze food items that they have been observed eating and to identify foods consumed through examination of fecal or stomach contents.^{23,30,42,48,57,65,70,74} These data, while important, are not sufficient to set nutrient requirements, and the specific nutrient needs of frugivorous and nectarivorous bats remain virtually unknown. The studies of nutrient requirements that have been conducted and diets that have been successfully used in captivity are discussed in the following pages.

Digestive Tract Morphology and Physiology

Fruit bats are highly efficient in extracting the liquid portion of chosen foods. They have fewer teeth than insectivores,¹⁰ and their teeth are broad and relatively flat for crushing fruits, allowing the bats to squeeze out and swallow the juices.²³ The fibrous portion remaining is much reduced in moisture and is spit out in tightly compressed pellets (ejecta). Seeds also may be swallowed, but many of those from figs appear to pass whole into the feces.^{23,48} To meet nutrient needs, daily food intakes (on a wet basis) range as high as 2.5 times body mass.^{14,15,16,26,31,48,63,70} These large volumes of food are processed through the digestive tract rapidly, with transit times ranging from 15-100 min.^{30,48,69}

The gastrointestinal tract of the fruit bat species that have been studied is highly modified compared to bat species with other feeding strategies. The stomach is large and more complex, the small intestine is long and convoluted, the cecum is absent, and the large intestine is short and nearly indistinguishable from the small intestine.^{30,68,69} There appear to be no areas of fermentation analogous to the rumen of ruminants, and significant concentrations of gastrointestinal fermenting anaerobes have not been found.³⁰ Rather, it is thought that the enlarged, complex stomach and long, convoluted intestine provide the space and surface area required for digestion and absorption of nutrients from the large volumes of liquid consumed.

Nutrient Content of Foods

Upon comparison with established nutrient requirements of other mammals and the foods needed to provide them, fruit, when consumed alone, would seem to constitute an inadequate diet. Analyses of most cultivated fruits indicate that the concentrations of many nutrients are quite low. However, there are few documented analyses of the nutrients in wild fruit species, and *A. jamaicensis* has been reported to feed on fruits from over 70 genera.²³ Thus, it may be important to distinguish between cultivated and wild fruits. Limited compositional data on proximate fractions and minerals in both are presented in Tables 1 and 2. The cultivated fruits listed tend to be lower in fiber, ash, and calcium (dry basis), with some higher in moisture, than the listed wild fruits.^{8,19,25,31,59,60,66} Comparisons between cultivated and wild fruits in concentrations of vitamins could not be made because published vitamin values for wild

fruits were not found.

Fruit bats in the wild appear to meet their nutrient needs by consuming large quantities of a mixture of native fruits, with some consumption of flower parts, leaves, and insects.^{2,11,12,21,23,28,33,34,36,37,38,46-49,61,78} In captivity, fruit sources are limited to those that are cultivated and readily available. As a consequence, it may be important to ensure that all essential nutrients are supplied by using other nutritionally complete foods. To formulate such foods, it is important to know which nutrients are essential to fruit bats and in what amounts they should be supplied.

Nutrient Requirements

Despite differences in diet and feeding strategy among mammals, most species that have been studied appear to have similar qualitative nutrient needs for normal tissue metabolism. Presumably, these similarities also apply to fruit bats. Approximately fifty nutrients have been identified as dietary essentials for mammals. That is, they must be obtained from the diet or through the activity of gastrointestinal microbes because they cannot be endogenously synthesized in quantities appropriate to meet animal needs.⁷²

Water

Water is the easiest and least expensive nutrient to provide in captivity. A supply of water is crucial due to its involvement in a variety of essential functions within the body. The need for liquid water is influenced by variables such as ambient air temperature and humidity, solar and thermal radiation, metabolic rates, and food composition and intake.⁶⁴ Fruit bats have been maintained in laboratory settings on mixed fruit diets without free access to liquid water and appear to obtain the water they need from their high-moisture fruit diet and presumably from water released during metabolism of absorbed energy sources (metabolic water). However, many species have been observed to actively consume water both in captivity and in the wild. Wild species of *Pteropus* on oceanic islands have been observed consuming sea water, and their kidneys appear well-adapted to excreting salt.²⁹ Therefore, considering the limited food choices and, in some cases, fluctuating environmental conditions, it is prudent to provide *ad libitum* access to fresh water in captivity.

Protein and amino acids

Proteins contain nitrogen, are major constituents of the animal body, and are vital to all tissues. Amino acids are the functional building blocks of proteins, and animals with relatively simple stomachs and little or no capacity for fermentation require a dietary source of 10-12 amino acids that cannot be synthesized metabolically at an adequate rate (dietary essentials).^{64,72} Essential amino acid requirements for bat species are not known nor has the amino acid composition of many foods consumed by bats been determined, although Herbst²⁶ has reported relative concentrations of arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, and valine in fruit pulp protein of four plant species (*Cecropia peltata*, *Chlorophora tinctoria*, *Ficus ovalis*, and *Piper amalago*). It is not known whether the amino acid composition of protein in juice squeezed out of the pulp and swallowed by fruit bats is the same as that in the pulp.

Fruit, as the only food item, is considered by many researchers to constitute an inadequate diet because of its low protein content when compared to other plant and animal food sources, although the quality of that protein is relevant to such a conclusion. It has been argued that both pteropodid and phyllostomid fruit bats must supplement their fruit diets with relatively higher protein items, including a more complementary array of amino acids, such as might be found in insects,⁴⁸ pollen,³⁵ or leaves^{32,33,38,78} in order to meet protein needs. However, other researchers maintain that fruit bats can meet their protein requirements exclusively with fruits,^{9,15,26,67,70} and fruit bats (*Carollia brevicauda* and *Sturnira ludovici*) in Costa Rica showed a strong preference for fruit (*Acristus arborescens*) that was not infested with insect larvae.²⁰ Further, it has been proposed that most fig wasps will have departed figs by the time they become ripe and are consumed by bats, and residual corpses are unlikely to contribute significantly to protein intake.⁸

Recent research supports the latter hypothesis, at least for maintenance of adults. These studies have been conducted using diets that approximate the protein concentration of fruits (both cultivated and wild) or by using wild fruits alone, thus suggesting that fruit bats have the ability to meet their protein requirements for maintenance on very low protein diets. This may be accomplished in part through minimal nitrogen excretion,³¹ and by adjusting dry matter intake to meet protein needs, regardless of dietary energy concentration.⁶³ A diet containing about 9% crude protein (DM basis) was consumed by captive fruit bats (*Pteropus hypomelanus*, *P. pumilus*, *P. vampyrus*) at 28% of body weight on an as-fed basis or 7% as dry matter.¹⁶ Studies of the protein needs of *A. jamaicensis* (phyllostomids) weighing 39-50 g found that 0.28-0.30 g/day were required for adult maintenance, or about 5% of dietary dry matter.^{48,63} In another study, adult *A. jamaicensis* bats weighing 36.8 g achieved nitrogen balance at protein intakes of 0.17 g/day on a “high-energy” diet and 0.46 g/day on a “low-energy” diet.¹⁵ Maintenance protein requirements for adult *Carollia perspicillata* (phyllostomids) were estimated to be 0.14 g/day.¹⁴ Adult *Rousettus aegyptiacus* (pteropodids) weighing 144-157 g achieved nitrogen balance at protein intakes of 0.36-0.83 g/day.^{15,31} It should be noted that when stable-N isotope analyses were used to quantify the relative importance of plants (fruits) and animals (insects) as sources of assimilable N for five species of free-ranging frugivorous New World bats (*Artibeus jamaicensis*, *Uroderma bilobatum*, *Dermanura phaetis*, *Sturnira lilium*, and *Carollia brevicauda*), fruits were by far the most important throughout the year. However, at the end of the rainy season and beginning of the dry season, there was a trend in all species for a decline in the relative proportion of plant protein in the diet, and in some individuals of *S. lilium* and *C. brevicauda*, insects became a significant source of protein. It was suggested that fruit bat species may vary in their foraging strategy, with some relying almost entirely on fruits throughout the year, whereas others may switch to insects when fruits are less abundant.²⁷

It is difficult to estimate exact requirements because quite different diets have been used in published studies, and the factors to convert nitrogen to protein may have, in some cases, been incorrect.^{9,26,43} Assuming appropriate amino acid concentrations in the protein, 4-6% protein in the dry matter consumed and digested appears sufficient for maintenance. Requirements for reproduction or growth may be higher but have not been experimentally determined. Presumably, the essential amino acid composition of dietary proteins as compared to amino acid needs would influence the amounts of protein required for any of the above functions.

Energy

Digestible energy and metabolizable energy are terms used to describe an animal's energy needs and to characterize the usable energy concentrations in food fed to that animal. Because animal species vary in the way they digest and metabolize nutrient sources, the digestible energy or metabolizable energy concentration in a food varies with the gross energy of that food, the amount of food consumed, and the digestive and/or metabolic abilities of the animal to which the food is fed. A more complete description of energy terms can be found in a National Research Council publication.⁵²

Due to their high concentrations in fruit, carbohydrates are quantitatively important sources of energy in the diets of fruit bats. Dietary fat is a potentially important source of energy, as well, but generally is a minor constituent of high-sugar fruits. Protein in the diet also can be broken down for energy, but that is probably minimal on low-protein diets in which the balance of essential amino acids is just adequate to meet amino acid requirements.

Fruit bats presumably have no difficulty meeting energy needs during periods of food abundance because they consume large amounts of high carbohydrate fruits, both in captivity and in the wild. There is controversy among researchers whether or not fruit bats must “over-ingest” energy in order to meet protein requirements. This is due to the relatively high energy:protein ratio of most fruits. High food (and energy) intakes were necessary to meet protein needs in pteropodids (*Epomops buettikoferi*, *Micropteropus pusillus*, and *Pteropus poliocephalus*) when fed some low-protein fruits but not when fed others.^{67,70} *Carollia perspicillata* (phyllostomids) did not need to consume excessive energy to meet maintenance protein needs if appropriate wild foods were available and selected.²⁶

Estimates of metabolizable energy requirements for adult maintenance of *A. jamaicensis* have been made by a number of researchers, and range from 12 to 34.3 kcal/day.^{15,48,63} The intermediate value of 17.2 kcal/day found by Reiter⁶³ is equivalent to 43.9 kcal of metabolizable energy/100 g body mass/day (mean body mass 39.2 g) or a metabolizable energy density in ingested dry matter of 3.16 kcal/kg, a metabolizable energy concentration found in many domestic fruits.

Estimates of metabolizable energy requirements for adult maintenance of *C. perspicillata* weighing 18.5 g were 16.1 kcal/day/bat¹⁴ and were 40.1 kcal/day for *R. aegyptiacus* with a mean body mass of 144 g,³¹ or 76.3 to 91.9 kcal/day for *R. aegyptiacus* with a mean body mass of 156.7 g.¹⁵

Care must be taken when interpreting published data on energy requirements of fruit bats because species, experimental diets, and levels of permitted activity varied appreciably among studies. Basal energy expenditures of bats appear to vary with species (particularly body mass and foraging and roosting behavior), sexual dimorphism in body mass, precision of body temperature regulation, tendency to enter torpor, and the environmental circumstances within which they evolved.^{40,41} In addition, both dietary digestibility and metabolizability have usually been estimated rather than directly determined. Some fruit bats eating very low protein diets may consume large amounts of food to meet protein requirements, thus elevating energy intakes. Researchers generally have noted little change in body mass, but studies of changes in body composition appear not to have been made. With respect to energy needs for flight, requirements are surely higher than for resting, and the amount of flight activity required in the wild will vary with food abundance and distribution. In captivity, it is likely that energy requirements for resting and for flight can be met by offering *ad libitum* quantities of nutritionally appropriate food.

Essential fatty acids

Apart from serving as sources of dietary energy and promoting fat-soluble vitamin absorption, fats also provide essential fatty acids (n-6 and n-3 series). The most important dietary fatty acids for the mammal species that have been studied are n-6 fatty acids, such as linoleic and arachidonic, and n-3 fatty acids, such as α -linolenic and longer chain fatty acids in this series. Qualitative requirements for essential fatty acids have been demonstrated in a number of mammalian species although quantitative requirements are mostly undefined. Fruit bats are likely to have dietary fatty acid requirements similar to other mammals. The recommendation for most mammals is to include essential fatty acids in the diet at 1-2% of the total metabolizable energy intake, with linoleic acid comprising the largest proportion of the total. However, the amounts of total essential fatty acids and the proportions of each may vary with species, age, and physiologic state.^{64,72} Cultivated fruits generally have very low levels of fat and essential fatty acids.^{60,73} Essential fatty acid concentrations in the wild fruits eaten by bats are largely unknown.

Vitamins and minerals

Specific vitamin and mineral requirements have not been determined for fruit bats, and there is no information on the nutrient requirements of their closest taxonomic relatives. Limited data are available on a few primate species.⁵⁰ The National Research Council (NRC) has established vitamin and mineral requirements for a variety of domestic and laboratory animals.^{50,53-56} NRC nutrient requirements for rats and mice are shown in Table 3.⁵⁵ The range in body mass of laboratory rats and mice is similar to that of several species of fruit bats, although relative intakes of dietary dry matter and energy are typically higher for bats. Thus, when nutrient requirements are expressed per unit of dietary dry matter, bats would be expected to consume larger amounts of these nutrients per day than would rats or mice of comparable mass and physiologic state. As a consequence, until specific requirements are determined, diets for captive bats may be presumed sufficient if formulated to provide bioavailable¹ vitamin and mineral levels within the ranges of nutrients for the listed laboratory species. It is known that some bat species lack the ability to synthesize vitamin C and therefore require a dietary source.³ Despite serum levels of 25-hydroxyvitamin D <4 ng/ml in both captive and wild populations of the Egyptian fruit bat (*Rousettus aegyptiacus*), small amounts of 1,25-dihydroxyvitamin D were found, serum mineral concentrations were well regulated, and pathologic signs usually associated with vitamin D deficiency were not evident.⁷ Others reported plasma concentrations of 1.5 ng 25-hydroxyvitamin D/ml and 93-108 pg 1,25-dihydroxyvitamin D/ml in captive *Pteropus hypomelanus* and *P. vampyrus* fed a diet containing 400 IU vitamin D₃/kg DM and exposed to natural sunlight immediately prior to the study.¹⁷

Qualitative information on some vitamin and mineral requirements of fruit bats is available from observations of deficiencies or toxicities in captivity. Methodology must be carefully considered when interpreting the quantitative implications of such results. One report has described dilated cardiomyopathy in pteropodid fruit bats as a result of hypovitaminosis E.²⁴ Hemochromatosis (iron storage disease) has been reported in three species of pteropodid fruit bats (*Rousettus aegyptiacus*, *Pteropus giganteus*, and *P. poliocephalus*), and was ascribed to dietary iron overload.¹³ The diet contained 400 mg of iron/kg of dry matter, by analysis. The principal unintended iron source was monocalcium phosphate, which was used as a phosphorus supplement and contained 11,860 mg iron/kg.

Unusually high vitamin C supplementation (estimated intake of 7,500 mg/kg dry diet) may have compounded the problem by enhancing iron uptake.^{44,45} Studies of hematologic values and iron status of wild and captive fruit bats (*Rousettus aegyptiacus*) found lower plasma iron concentrations in wild (175 ng/dl) than in captive (286-316 ng/dl) subjects.⁷⁵

Investigators studying the cause of nodular bone lesions in the same three species of pteropodid fruit bats proposed fluoride toxicity as the probable cause.¹⁸ The diet contained shrimp meal, which is naturally high in fluoride, dicalcium phosphate, which may contain significant fluoride if a fertilizer-grade rather than a feed-grade product is used, fruit, and other supplements. Although the concentration of fluoride in the total diet was not reported, the estimated amounts of fluoride consumed by the bats were well above maximum tolerable levels reported for other species.⁵¹ Recently, several more cases of suspected fluoride toxicosis have been reported in pteropodid species (six *Pteropus rodricensis*, one *Rousettus aegyptiacus*) at one institution.⁷¹ The affected bats exhibited periosteal hyperostosis of long bones, similar to the previous study, as well as curled phalanges. The fluoride concentrations (by analysis) of all dietary items and water sources, as well as other potential sources of fluoride contamination (e.g., exhibit rock-work, flooring, and heating system condensate) were well below maximum tolerable levels for domestic species. Signs of periosteal hyperostosis were not seen after municipal tap water was replaced by distilled water for drinking.⁷¹ Quantitative fluoride requirements have not been established for most species. However, excessive levels have been shown to cause bone and tooth lesions, anorexia, lameness, necrosis of gastrointestinal mucosa, and cardiac failure.⁵¹ The results of these studies are not conclusive since requirements and tolerances of bats for fluoride have not been established.

Diets for Captive Frugivorous and Nectarivorous Bats

When formulating diets for captive fruit bats, foods available and appropriate for meeting probable nutrient needs must be identified. Bats that are primarily frugivorous or primarily nectarivorous are commonly fed similar diets. Nutritionally complete nectar formulas are sometimes included in diets for species that consume large amounts of nectar in the wild. Cultivated fruits are readily accepted by both groups. However, the concentrations of several nutrients in cultivated fruits are typically low or imbalanced, and an additional food source must generally be provided to ensure that nutrient concentrations in the total diet will be within the range required by other nonruminant mammalian species.^{50,53-56} The preferred method for ensuring dietary adequacy is to provide nutritionally complete feeds such as low-fiber, dry primate diets or dry diets formulated for frugivorous birds. These feeds should be formulated to meet the currently known requirements of the species for which they have been designed. The use of individual vitamin and mineral compounds as nutrient supplements is not recommended unless they are provided in a preparation specifically formulated for fruit bats. Over- or under-dosing, when using individual vitamin or mineral supplements, is common, as are the consequent toxicity and/or deficiency signs.

The nutritionally complete feed used should be as finely ground as possible to promote adequate consumption. Mixing fruit nectars, such as peach or apricot, with the ground feed will soften and/or suspend the diet and encourage intake, since fruit bats tend to be attracted to fruit nectars. Fruit also may be added to this mixture. However, it is advisable to chop the fruit into very small pieces or to mix ingredients in a blender so bats cannot preferentially consume fruit only. Because this mixture may gel if

not mixed correctly and will ferment in a hot environment, its condition should be assessed periodically and the mixture replaced when necessary. Behavioral enrichment in the form of hanging whole fruits may be used to encourage natural feeding behavior, providing fruit intakes relative to intakes of the complete diet are carefully monitored and are not excessive.

Microchiropteran and megachiropteran fruit bats are sometimes offered insects in addition to fruit, nutritionally complete feeds, and nectar formulas. A number of “home made” nectar formulas used successfully in captivity have been previously described.⁶² However, these formulations contain a variety of supplements that can be dangerous if misused. Nutritionally complete nectar powders formulated for hummingbirds are currently available with varying protein concentrations and may be appropriate for nectarivorous bats. Megachiroptera also are sometimes offered leafy vegetables and browse, both of which are readily accepted.^{34,36,37} Preliminary research suggests that certain browses are consumed preferentially,^{32,33,38} but the reasons for these choices are not entirely clear.²

The total diet should be formulated so that the items consumed will provide the probable nutrient requirements. Formulas and nutrient specifications for three diets that have been used successfully for 5 years, with generally minor modifications, are shown in Table 4.

Summary

Although specific nutrient requirements for frugivorous and nectarivorous bats remain virtually unknown, information exists which provides practical guidelines for formulating diets for captive bats. This information must be reviewed critically, applied sensibly, and compared with what is known for other mammalian species until more specific research is conducted. Opportunities for research in bat nutrition abound and, in view of the diversity of species, the information derived would improve not only our understanding of the nutrient requirements and dietary husbandry of bats but also of other species with similar dietary habits and feeding strategies.

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Table 1. Comparison of the macronutrient composition of cultivated and native fruits.

Fruit type	Expressed on a dry matter basis							
	Moisture %	Gross energy Kcal/g	Protein %	Nitrogen %	Fat %	Fiber %	Carbo- hydrates %	Ash %
Cultivated ^{a,b}								
Apple	84.50	3.66 ^f	1.03	0.16	2.00	3.55	95.46	1.55 ^g
Banana	74.30	3.74 ^f	4.08	0.63	2.06	2.06	91.03	3.11 ^g
Cantaloupe	91.00	3.57 ^f	8.88	1.38	2.69	3.33	85.55	5.68 ^g
Orange	86.80	3.70 ^f	7.58	1.21	0.54	3.26	88.25	3.47 ^g
Native								
Fig (<i>F. ovalis</i>) ^c	78.50	4.08	2.10	0.60	0.80	35.40	43.40	5.20
Fig (<i>F. sycomorous</i>) ^d	83.70	3.60	3.50	0.56	2.10	5.20	84.70	4.50
Fig (Belize native) ^e	72.08	---	7.85	1.26	---	---	---	7.96
<i>Piper</i> fruit (<i>P. amalago</i>) ^c	73.00	3.95	6.00	1.90	1.40	10.90	86.70	23.00
<i>Carob</i> (<i>C. siliqua</i>) ^d	20.50	3.90	6.50	1.04	0.95	7.60	82.40	2.60

^aData from Pennington and Church.⁶⁰

^bFruit without skin or peel, includes seeds.

^cData from Herbst.²⁵ Sum of values for protein, fat, fiber, carbohydrates, and ash deviate significantly from 100%. Errors in reported values are suspected but are presented as published. N=130 for *F. ovalis*, N=200 for *P. amalago*.

^dData from Korine et al.³¹ Samples analyzed were pooled from 20 specimens of each fruit species.

^eData from Silver et al.⁶⁶ Samples were pooled from multiple *Ficus sp.*, N=6.

^fData provided by Debra A. Schmidt and Monty S. Kerley, Department of Animal Sciences, Nutrition Laboratory, University of Missouri-Columbia. Values are for fruit pulp only, no skin, peel or seeds.

^gData from USDA, Agricultural Handbook No. 8 Composition of Foods.⁷³

Table 2. Comparison of the mineral content of cultivated and native fruits.

Fruit type	Moisture %	Expressed on a dry matter basis			
		Ca %	P %	Fe ppm	Se ppm
Cultivated ^{a,b}					
Apple	84.50	0.03	0.05	4.5	0.02
Banana	74.30	0.02	0.08	11.9	0.04
Cantaloupe	89.78	0.11	0.17	21.5	0.04
Orange	86.80	0.30	0.11	7.6	0.04
Native					
Fig (<i>F. pertusa</i>) ^c - ripe fruit	77.20	0.74	0.12	56.6	0.03
Fig (<i>F. trigonata</i>) ^c - unripe fruit	83.70	0.74	0.23	49.9	0.10
Fig (Belize native) ^d	72.08	2.04	0.18	58.1	---
Fig (Indonesia native) ^e	---	1.21	0.33	65.7	---
Fig (Uganda native) ^e	---	1.52	0.18	94.7	---

^aData from Pennington and Church.⁶⁰

^bFruit without skin or peel, includes seeds.

^cData from Edwards.¹⁹ N=3 for *F. pertusa*, N=1 for *F. trigonata*.

^dData from Silver et al.⁶⁶ Samples were pooled from multiple *Ficus sp.*, N=5.

^eData from O'Brien et al.⁵⁹ Indonesia N=20, Uganda N=10.

Table 3. Vitamin and mineral requirements of laboratory mice and rats in dietary dry matter.^a

<u>Nutrient</u>	<u>Mice</u>	<u>Rats</u>
<u>Vitamins</u>		
A, IU/kg	2,600	2,600
D ₃ , IU/kg	1,100	1,100
E (<i>RRR</i> - α -tocopherol), mg/kg	24	20
K (phylloquinone), mg/kg	1.1	1.1
Thiamin, mg/kg	5.6	4.4
Riboflavin, mg/kg	7.8	4.4
Niacin, mg/kg	17	17
Pantothenic acid, mg/kg	18	11
Vitamin B ₆ , mg/kg	9	7
Folic acid, μ g/kg	555	1,100
Biotin, μ g/kg	220	220
Vitamin B ₁₂ , μ g/kg	11	55
Choline, mg/kg	2,222	833
<u>Minerals</u>		
Calcium, %	0.6	0.7
Phosphorus, %	0.33	0.4
Magnesium, %	0.06	0.07
Sodium, %	0.06	0.06
Potassium, %	0.22	0.4
Iron, mg/kg	39	83
Copper, mg/kg	7	9
Manganese, mg/kg	11	11
Zinc, mg/kg	11	28
Iodine, mg/kg	0.17	0.17
Selenium, mg/kg	0.17	0.4

^aRequirements for most demanding life periods.⁵⁵

Table 4. Formulas of and calculated nutrient concentrations in three sample fruit bat diets.

Ingredient	Percent by weight, as fed		
	Diet A ^a	Diet B ^b	Diet C ^c
Fruits, whole ^d	5.2	42.0	---
Fruits, chopped ^d	30.5	13.2	17.0
Vegetables, chopped ^e	7.3	1.65	1.0
Starchy vegetables, chopped ^f	2.0	1.65	2.0
Leafy green vegetables, chopped ^g	10.4	---	7.0
PMI Prolab High Protein monkey diet 5045 ^h	13.7	2.99	---
Marion Jungle Biscuit ⁱ	---	---	22.0
Calcium phosphate, dibasic	0.30	0.41	---
Peach nectar, canned	6.0	38.1	22.0
Orange juice, frozen, reconstituted	6.0	---	---
Water	18.6	---	29.0
	100.0	100.0	100.0
Nutrient	Calculated concentration, DM basis		
Dry matter, %	25.2	20.6	29.0
Crude protein, %	16.2	6.5	18.3
Crude fat, %	3.8	1.8	6.4
Vitamin A, IU/kg	23,419	6,240	10,484
Vitamin D ₃ , IU/kg	3,595	958	2,877
Vitamin E, mg/kg	49	20	252
Vitamin C, mg/kg	588	752	444
Thiamin, mg/kg	10.6	4.0	6.5
Riboflavin, mg/kg	6.2	3.2	7.8
Niacin, mg/kg	72	32	59
Pantothenic acid, mg/kg	37	15	21
Vitamin B ₆ , mg/kg	12	8	9
Folic acid, µg/kg	6,144	1,907	4,458
Biotin, µg/kg	>103	>28	>301
Vitamin B ₁₂ , µg/kg	26	7	23
Choline, mg/kg	>980	>261	>1,079
Calcium, %	0.85	0.63	0.85
Phosphorus, %	0.61	0.52	0.58
Magnesium, %	0.17	0.09	0.15
Sodium, %	0.19	0.06	0.21
Potassium, %	1.16	0.90	0.84
Iron, mg/kg	411	352	140
Copper, mg/kg	14	7	15
Manganese, mg/kg	84	30	38
Zinc, mg/kg	90	29	78
Iodine, mg/kg	0.98	0.26	>0.8
Selenium, mg/kg	0.13	0.05	0.28

^aFed to Rodriguez fruit bats (*Pteropus rodricensis*) at Brookfield Zoo for 5 years (Ca phos., dibasic, added at 3 yr).

^bFed to Neotropical fruit bats (*Artibeus jamaicensis*) at Brookfield Zoo for 5 years.

^cFed to Rodriguez fruit bats (*Pteropus rodricensis*) at Philadelphia Zoo for 5 years.

^dWhole fruits include apple, banana and orange; chopped fruits include apple, banana, blueberries, currants, grapes, mango, and raisins.

^eVegetables (nonstarchy type) consisted of carrots, either steamed or raw.

^fStarchy vegetables consisted of sweet potatoes, either steamed or raw.

^gLeafy green vegetables included celery, romaine lettuce, and spinach.

^hPurina Mills, LLC, 1401 S. Hanley Rd., St. Louis, MO 63144 (800-227-8941).

ⁱMarion Zoological Inc., 2003 E. Center Circle, Plymouth, MN 55441 (800-327-7974).