

Folivory in Fruit-Eating Bats, with New Evidence from *Artibeus jamaicensis* (Chiroptera: Phyllostomidae)

Author(s): Thomas H. Kunz and Carlos A. Diaz

Source: *Biotropica*, Vol. 27, No. 1 (Mar., 1995), pp. 106-120

Published by: The Association for Tropical Biology and Conservation

Stable URL: <http://www.jstor.org/stable/2388908>

Accessed: 18/05/2009 22:08

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=tropbio>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



The Association for Tropical Biology and Conservation is collaborating with JSTOR to digitize, preserve and extend access to *Biotropica*.

Folivory in Fruit-eating Bats, with New Evidence from *Artibeus jamaicensis* (Chiroptera: Phyllostomidae)¹

Thomas H. Kunz

Department of Biology, Boston University, Boston, Massachusetts 02215, U.S.A.

and

Carlos A. Diaz

U.S. Fish and Wildlife Service, Caribbean Field Office, Boqueron, Puerto Rico 00622, U.S.A.

ABSTRACT

We review reports of leaf-eating by bats and present new evidence for folivory by leaf fractionation for the neotropical bat *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Leaf-eating has been reported for at least 17 species of Old-World Megachiroptera and four species of New World Microchiroptera. Leaves eaten by bats include at least 44 species of plants represented by 23 different families. Plant families which account for the greatest species richness (numbers of species given in parentheses) include the Leguminosae (12), Moraceae (4), and Solanaceae (4). Evidence for folivory by *A. jamaicensis* is based on captures of bats carrying leaves, and collections of whole and partially chewed leaves and discarded pellets recovered from beneath feeding roosts. Whole leaves carried into caves by *A. jamaicensis* and partially chewed, but discarded leaves included *Erythrina poeppigiana*, *Ficus* sp., and *Calophyllum calaba*, in decreasing order of frequency. Bats captured while carrying *Erythrina* leaves were most often mature males. *Erythrina poeppigiana* leaves are relatively high in protein (>19% dry-matter content) and low in fat (~1%). Our observations that *A. jamaicensis* selects and chews leaves high in protein and rejects protein-poor, fibrous pellets, support the hypothesis that these bats extract liquid fractions which contain a reliable source of dietary protein. Although we have no direct evidence that male or female *A. jamaicensis* transport leaves to feeding roosts located outside of caves, we suggest that liquid fractions derived from leaves may provide females with an important source of protein, especially during periods of pregnancy and lactation. Folivory, once thought to be rare among plant-visiting bats, may in fact be quite common and widespread, especially among species that feed largely on fruits which are low in protein.

Key words: *Artibeus jamaicensis*; *Erythrina poeppigiana*; folivory; leaf-fractionation; Megachiroptera; Microchiroptera; Phyllostomidae; protein.

THE RICH SOURCE OF SOLUBLE NUTRIENTS AND ENERGY PRESENT in leaves presumably was a major factor in the evolution of obligate folivory for many terrestrial mammals. Most modern-day folivorous mammals have evolved highly specialized structures and enzymes which facilitate the extraction of lignin- and cellulose-bound nutrients and energy (Eisenberg 1978, Hume 1989). Many of these taxa also have evolved unique specializations that reduce the adverse effects of secondary compounds present in leaves (Freeland & Janzen 1974, Rhodes & Oates 1976). Among the most important adaptations leading to the evolution of folivory in mammals are selection for specialized dentition and gut morphology that enhances mechanical digestion and prolongs gut retention, and microbial digestion needed to extract nutrients and energy from undigestible plant fibers.

Although the dentition and digestive tract of phytophagous bats are highly specialized for processing fruits and nectar (Forman *et al.* 1979, Tedman & Hall 1985, Richardson *et al.* 1987, Forman 1990), these flying mammals lack the elongated, enlarged, and specialized compartments of the gut found in strictly folivorous taxa. In fact, the intestine of tropical frugivorous bats is only about one-third the length of a comparable size folivorous rodent, and food transit-time is relatively rapid in most bats, usually less than 30 min (Klite 1965, Tedman & Hall 1985, Fleming 1988). The relatively short gut and rapid food transit time in bats are thought to be adaptations associated with the evolution of aerial locomotion (Norberg & Rayner 1987, Norberg 1990, Kunz & Ingalls 1994). Leaf- or fruit-fractionation, by the mastication of leaves and fruit into a bolus, swallowing the liquid fraction, and discarding the bolus as a fibrous pellet (Lowry 1989, Handley & Morrison 1991), appears to be one way that plant-visiting bats are able to exploit the nu-

¹ Received 13 August 1993; revision accepted 29 March 1994.

trients in leaves without increasing the size of their digestive tract and food load (Kunz & Ingalls 1994).

Plant-visiting bats from the Neo- and Paleotropics are known to feed on a variety of plant products, including flowers, pollen, fruit, nectar, and leaves (Gardner 1977, Marshall 1985, Wiles & Fujita 1992). Notwithstanding, direct evidence for the consumption of leaves, or their liquid fractions, has rarely been observed or been reported for bats (but see Cunningham van Someren 1972, Richards & Provic 1984, Lowry 1989, Zortea & Mendes 1993, Bhat 1994, Zortea 1994). This paucity is not surprising when one considers that liquid fractions of leaves, as well as nectar and fruit juices, are not likely to be detected using standard fecal or stomach-content analyses, especially when these fractions coexist with relatively easily identified seeds, pollen, and insect parts. Based on fecal analysis or stomach-content analysis, even nectar and fruit will be judged as uncommon, unrecognizable, or absent. For example, Fleming (1988) noted that the stomach contents of *A. jamaicensis* collected in Costa Rica contained (by volume) 66 percent "plant material," 25 percent insects, and nine percent "unclassified material." We suspect that some of the plant and unclassified material in Fleming's and similar studies, in which food habits of frugivorous species have been reported, may reflect the highly masticated fruits and liquid fractions of fruits and leaves. Nectar consumption is often inferred from direct observation, by the presence of pollen in stomach contents and feces, or from its occurrence on the pelage of bats (Law 1992). Consumption of insects can be inferred by the presence of finely chewed insect parts in the feces or from culled parts dropped by bats beneath feeding roosts. Rejected seeds and culled insect parts are most likely to be observed beneath feeding roosts in a forest than would the culled parts of leaves and rejected, fibrous leaf-pellets.

Whole or partially chewed leaves dropped by bats beneath feeding roosts are quite likely to be overlooked in forested regions if the partially chewed leaves are attributed to the activities of leaf-eating insects, if they decompose rapidly, or if they are inconspicuous among other plant materials that may be deposited or dropped onto the forest floor. Partially chewed leaves and leaf pellets are more likely to be observed and attributed to bats if they are found beneath traditional feeding roosts in caves or on roads and other man-made surfaces in urban areas. It is interesting to note that Handley and Morrison (1991) observed discarded pellets beneath feeding roosts in trees based on the consumption of

fruit by *Artibeus jamaicensis*, but they did not report discarded leaf pellets. Bhat (1994) reported leaf pellets beneath feeding roosts of *Cynopterus sphinx* in urban areas.

Most reports of folivory by Old-World fruit bats (Megachiroptera: Pteropodidae) and New World fruit bats (Microchiroptera: Phyllostomidae) are anecdotal (Table 1). These findings reveal that leaf-eating has been observed in at least 17 species of the Megachiroptera and four species of the Microchiroptera. Notwithstanding, there are few reports of year-around leaf consumption based either on the analysis of fecal remains, leaf parts discarded beneath roosts (Lowry 1989, Parry-Jones & Augee 1991a, Bhat 1994), or direct observation (Zortea & Mendes 1993). Periodic episodes of relatively high leaf intake (16.9–22.4% by volume) have been reported for *Pteropus poliocephalus* (Parry-Jones & Augee 1991a) and *Cynopterus sphinx* (Bhat 1994). Bhat (1994) noted that leaf-eating was common in each month of the year for *C. sphinx*, and reported that in addition to feeding on fruit of 23 species of plants, it also consumed leaves from eight species (see Table 1). Leaves are also eaten year-around by the New World phyllostomid, *Artibeus lituratus*, with the greatest number of species consumed in August and September (Zortea and Mendes 1993). The latter authors found that the consumption of leaves and fruit by *A. lituratus* (based on dry mass of pellets) accounted for 5.6 percent and 94.4 percent respectively. Zortea (1994) also found that *Platyrrhinus (Vampyrops) lineatus* consumed leaves in a manner similar to that reported for *A. lituratus*.

Published reports of leaf consumption and evidence that the liquid fractions of some leaves are high in protein (Telek & Martin 1983, Lowry 1989) suggests that leaves provide an important source of dietary protein for fruit-eating bats. In fact, it is well-known that other fruit-eating mammals (e.g., some primates) regularly supplement their protein-poor diets with insects, buds, and leaves (Table 2). Although there have been several anecdotal reports of whole or partially chewed leaves found beneath roosts of New World bats (*A. jamaicensis*, *A. lituratus*, *Platyrrhinus lineatus*, and *Micronycteris hirsuta*), evidence for folivory generally has been indirect and circumstantial. This includes reports of *Ficus religiosa* leaves being found beneath roosts of *Artibeus lituratus* in Trinidad (Goodwin & Greenhall 1961), "twigs and leaf pellets" found beneath cave roosts of *A. jamaicensis* in Mexico (Tuttle 1968), leaves of *Ficus maxima* found beneath roosts of *A. jamaicensis* in Cuba (Silva-Taboada 1979), and leaves of *Solanum torvum* beneath cave roosts

TABLE 1. Plant species of which the leaves, leaf buds, and petioles are eaten wholly or partially by phytophagous bats.

Plant family and species	Bat species	Plant part	Location	Reference
Araucariaceae				
<i>Araucaria heterophylla</i>	<i>Eidolon helvum</i>	Leaves	Ivory Coast	Malagnoux and Gautun 1976
<i>Araucaria cunninghamii</i>	<i>Eidolon helvum</i>	Leaves	Ivory Coast	Malagnoux and Gautun 1976
Caricaceae				
<i>Carica papaya</i>	<i>Pteropus voeltzkowii</i>	Leaves	Pemba Islands	Mickleburgh <i>et al.</i> 1992
Cucurbitaceae				
<i>Sechium edule</i>	<i>Cynopterus</i> sp.	?	?	van der Pijl 1957
Elaeagnaceae				
<i>Elaeagnus</i> sp.	<i>Pteropus dasymallus</i>	Leaves	Tokara Islands	Funakoshi 1989
Fagaceae				
<i>Castanopsis sieboldii</i>	<i>Pteropus dasymallus</i>	Leaf buds	Okinawajima Island	Maruyama 1980
Gingkoaceae				
<i>Gingko</i> sp.	<i>Pteropus dasymallus</i>	Leaves	Tokara Islands	Funakoshi 1989
Guttiferae				
<i>Calophyllum calaba</i>	<i>Artibeus jamaicensis</i>	Leaves	Puerto Rico	Present study
Hamamelidaceae				
<i>Liquidambar</i> sp.	<i>Pteropus</i> sp.	Leaves	Australia	Parry-Jones and Augée 1991b
Lauraceae				
<i>Cinnamomum camphora</i>	<i>Pteropus</i> sp.	Leaves	Australia	Parry-Jones and Augée 1991b
Leguminosae				
<i>Albizia lebbek</i>	<i>Pteropus alecto</i>	Leaves	Australia	Lowry 1989
<i>Albizia procera</i>	<i>Pteropus poliocephalus</i>	Leaves	Australia	Richards and Prociw 1984
<i>Albizia (samanea) saman</i>	<i>Pteropus rodricensis</i>	Leaves	Rodrigues Island	Carroll 1983-1984
<i>Albizia</i> sp.	<i>Eidolon helvum</i>	Leaves	Africa	Marshall 1985
<i>Cassia fistula</i>	<i>Cynopterus sphinx</i>	Leaves	India	Balasubramanian 1988
<i>Cassia fistula</i>	<i>Cynopterus sphinx</i>	Leaves	India	J. Balasingh, pers. comm.
<i>Cassia fistula</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
<i>Cassia siamca</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
<i>Cynometra ramiflora</i>	<i>Pteropus mariannus</i>	Leaves	Mariana Islands	Wiles 1987
<i>Erythrina albyssinica</i>	<i>Rousettus</i> sp.	Leaves	Africa	Cunningham van Someren 1972
<i>Erythrina indica</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
<i>Erythrina poeppigiana</i>	<i>Artibeus jamaicensis</i>	Leaves	Puerto Rico	Present study
<i>Erythrina verna</i>	<i>Artibeus lituratus</i>	Leaves	Brazil	Zortea and Mendes 1993
<i>Erythrina</i> sp.	<i>Eidolon helvum</i>	Leaves	Africa	Marshall 1985

TABLE 1. Continued.

Plant family and species	Bat species	Plant part	Location	Reference
<i>Erythrina</i> sp.	<i>Pteropus</i> sp.	Petioles	Australia	Parry-Jones and Augée 1991b
<i>Leucaena leucocephala</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
<i>Tamarindus indica</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
Moraceae				
<i>Artocarpus altilis</i>	<i>Pteropus mariannus</i>	Leaves	Caroline Islands	Wiles et al. 1991
<i>Chlorophora excelsa</i>	<i>Eidolon helvum</i>	Leaves	Uganda	Okon 1974
<i>Ficus citrifolia</i>	<i>Artibeus jamaicensis</i>	Leaves	Puerto Rico	This study
<i>Ficus maxima</i>	<i>Artibeus jamaicensis</i>	Leaves	Cuba	Silva-Taboada 1979
<i>Ficus microcarpus</i>	<i>Pteropus dasymallus</i>	Leaves	Japan	Funakoshi 1989
<i>Ficus religiosa</i>	<i>Artibeus lituratus</i>	Leaves	Trinidad and Tobago	Greenhall 1957
<i>Ficus religiosa</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
<i>Ficus religiosa</i>	<i>Rousettus aegyptiacus</i>	Leaves	Lebanon	Lewis and Harrison 1962
<i>Ficus religiosa</i>	<i>Rousettus aegyptiacus</i>	Leaves	Israel	Makin and Mendlesohn 1986
<i>Ficus superba</i>	<i>Pteropus dasymallus</i>	Leaves	Japan	Funakoshi 1989
<i>Ficus</i> sp.	<i>Cynopterus</i> sp.	Leaves	?	Marshall 1985
<i>Morus australis</i>	<i>Pteropus dasymallus</i>	Leaves	Okanawajima Island	Maruyama 1980
Moringaceae				
<i>Moringa glauca</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
Myrtaceae				
<i>Acmena smithii</i>	<i>Pteropus</i> sp.	Leaves	Australia	Parry-Jones and Augée 1991b
<i>Eucalyptus nicholii</i>	<i>Pteropus</i> sp.	Leaves	Australia	Parry-Jones and Augée 1991b
Pandanaceae				
<i>Pandanus tectorius</i>	<i>Pteropus samoensis</i>	Leaf buds	Fiji	D. E. Wilson, pers. comm.
Rubiaceae				
<i>Gnetterda speciosa</i>	<i>Pteropus mariannus</i>	Leaves	Marianus	Wiles 1987
Salicaceae				
<i>Populus</i> spp.	<i>Pteropus poliocephalus</i>	Leaves	Australia	Parry-Jones and Augée 1991a, b
<i>Salix</i> spp.	<i>Pteropus</i> sp.	Leaves	Australia	Parry-Jones and Augée 1991b
Solanaceae				
<i>Solanum hazenii</i>	<i>Artibeus jamaicensis</i>	Leaves	Columbia	T. Lemke, pers. comm.
<i>Solanum swartzianum</i>	<i>Artibeus lituratus</i>	Leaves	Brazil	Zorrea and Mendes 1993
<i>Solanum</i> sp. 1	<i>Artibeus lituratus</i>	Leaves	Brazil	Zorrea and Mendes 1993
<i>Solanum</i> sp. 2	<i>Artibeus lituratus</i>	Leaves	Brazil	Zorrea and Mendes 1993
<i>Solanum</i> sp. 1	<i>Platyrrhinus lineatus</i>	Leaves	Brazil	Zorrea 1994
<i>Solanum</i> sp. 2	<i>Platyrrhinus lineatus</i>	Leaves	Brazil	Zorrea 1994

TABLE 1. Continued.

Plant family and species	Bat species	Plant part	Location	Reference
Sonneratiaceae				
<i>Sonneratia alba</i>	<i>Pteropus mariannus</i>	Leaves	Marianus	Wiles 1987
<i>Sonneratia alba</i>	<i>Pteropus mariannus</i>	Leaves	Yap	Falanrow 1988
Sterculiaceae				
<i>Theobroma cacao</i>	<i>Eidolon helvum</i>	Leaves	Nigeria	Funmilayo 1976
<i>Theobroma cacao</i>	?	Leaves	Thailand	Pakarnseree 1986
Tamaricaceae				
<i>Tamarix aphylla</i>	<i>Pteropus</i> sp.	Leaves	Australia	Parry-Jones and Augée 1991b
<i>Tamarix articulata</i>	<i>Pteropus scapulatus</i>	Leaves	Australia	Mickleburgh et al. 1992
Ulmaceae				
<i>Holoptelea intergrifolia</i>	<i>Cynopterus sphinx</i>	Leaves	India	Bhat 1994
Verbenaceae				
<i>Avicennia marina</i>	<i>Pteropus poliocephalus</i>	Leaves	Australia	Parry-Jones and Augée 1991a
<i>Avicennia</i> sp.	<i>Pteropus seychellensis</i>	Leaves	Seychelles	Cook 1979
<i>Avicennia</i> sp.	<i>Pteropus</i> sp.	Leaves	?	Marshall 1985
Zygophyllaceae				
<i>Balanites wilsoniana</i>	<i>Epomopborus wahlbergi</i>	Leaves	Africa	Wickler and Seibr 1976
Unidentified plant taxa				
	<i>Artibeus jamaicensis</i>	Leaves	Panama	Tuttle 1968
	<i>Artibeus lituratus</i>	Leaves	Brazil	Zortea and Mendes 1993
	<i>Cynopterus brachyotis</i>	Leaf epidermis	Indonesia	Kitchener et al. 1990
	<i>Cynopterus titthaescheilus</i>	Leaf epidermis	Indonesia	Kitchener et al. 1990
	<i>Pteropus poliocephalus</i>	Leaves	Australia	Nelson 1965
	<i>Eidolon helvum</i>	Leaves	Africa	Jensen and Eisentraut 1945
	<i>Syconycteris crassa</i>	Leaves	Africa	Jensen and Eisentraut 1945
	<i>Myonycteris birsuta</i>	Leaves	Costa Rica	Wilson 1971
	<i>Myonycteris lagochillus</i>	Leaves	Africa	Jensen and Eisentraut 1945
	<i>Myonycteris pusillus</i>	Leaves	Ivory Coast	Thomas 1984

TABLE 2. Mean percent dry-matter content (% DM) of protein reported for selected food items eaten by phytophagous bats (C) and primates (P).

Plant family and species	Plant part	Percent DM	Reference	Mammal taxon
Anacardiaceae				
<i>Mangifera indica</i>	Fruit	4.6	Hladik <i>et al.</i> 1971	P
<i>Spondias mombin</i>	Fruit	4.3	Hladik <i>et al.</i> 1971	P
<i>Spondias mombin</i>	Fruit	3.4	Fleming 1988	C
Guttiferae				
<i>Calophyllum walkeri</i>	Mature leaves	7.3	Oates <i>et al.</i> 1980	P
Leguminosae				
<i>Erythrina poeppigiana</i>	Mature leaves	19.1	Present study	C
<i>Erythrina poeppigiana</i>	Leaves	23.6	Telek and Martin 1983	C
<i>Erythrina excelsa</i>	Mature leaves	20.2	Choo <i>et al.</i> 1981	C
<i>Acacia collinsi</i>	Fruit	2.6	Fleming 1988	C
<i>Albizia lebbek</i>	Leaves	30	Irvine 1961	C
<i>Albizia lebbek</i>	Leaves	38	Lowry 1989	C
<i>Leucaena leucocephala</i>	Leaves	21.23	Telek and Martin 1983	C
<i>Tamarindus indica</i>	Leaves	8.17	Telek and Martin 1983	C
Moraceae				
<i>Cecropia peltata</i>	Mature leaves	12.50	Hladik <i>et al.</i> 1971	P
<i>Cecropia peltata</i>	Fruit	5.0	Hladik <i>et al.</i> 1971	P
<i>Cecropia peltata</i>	Fruit	3.9	Fleming 1988	C
<i>Cecropia eximia</i>	Young leaves	10.11	Hladik <i>et al.</i> 1971	P
<i>Ceiba pentandra</i>	Young leaves	22.31	Milton 1981	P
<i>Chlorophora tinctora</i>	Fruit	3.2	Fleming 1988	C
<i>Ficus capensis</i>	Fruit	4.0	Thomas 1984	C
<i>Ficus insipida</i>	Fruit	1.54	Morrison 1980	C
<i>Ficus insipida</i>	Mature leaves	10.59	Milton 1981	P
<i>Ficus ovalis</i>	Fruit	2.1	Fleming 1988	C
<i>Ficus ovata</i>	Fruit	2.9	Thomas 1984	C
<i>Ficus yopensis</i>	Young leaves	11.56	Milton 1981	P
<i>Ficus vallis-choudae</i>	Fruit	3.32	Hladik <i>et al.</i> 1971	P
Musaceae				
<i>Musa sapientum</i>	Fruit	3.40	Hladik <i>et al.</i> 1971	P
<i>Musa paradisiaca</i>	Fruit	1.31	Calvert 1985	P
Myrtaceae				
<i>Psidium guajava</i>	Fruit	0.60	Hladik <i>et al.</i> 1971	P
Piperaceae				
<i>Piper amalago</i>	Fruit	6.0	Fleming 1988	C
<i>Piper jacquemontianum</i>	Fruit	4.0	Fleming 1988	C
Solanaceae				
<i>Solanum</i> spp.	Fruit	13.4	Calvert 1985	P

of *A. jamaicensis* in Colombia (T. Lemke, pers. comm.). Chewed leaves also have been reported beneath a cave roost of *Micronycteris hirsuta* (Wilson 1971), although since this species is a gleaning insectivore, it is quite likely that leaves were taken fortuitously by this bat, or perhaps were deposited by another leaf-eating species. Recent observations reported by Zortea and Mendez (1993) and Zortea (1994) provide solid evidence of folivory by New World phyllostomids.

In the present study, we report new observations of folivory by leaf-fractionation for the phyllostomid

bat *A. jamaicensis*, and discuss these and other reports of folivory by bats from the perspectives of nutritional ecology and life-history characteristics. *Artibeus jamaicensis* is a common neotropical member of the family Phyllostomidae. It roosts singly or in small groups in hollow trees, caves, and beneath foliage (Goodwin & Greenhall 1961; Goodwin 1970; Foster & Timm 1976; Morrison 1979, 1980; Morrison & Morrison 1981; Kunz *et al.* 1983; Timm 1987; Handley *et al.* 1991; Kunz *et al.* 1994). *Artibeus jamaicensis* has a polygynous mating system, where single, mature males defend

tree hollows (Morrison & Morrison 1981), solution cavities in caves (Kunz *et al.* 1983), and leaf-tents (Kunz & McCracken 1995) from intrusions by other males. This bat is considered to be mostly frugivorous in its diet (Gardner 1977, Bonaccorso 1979, Morrison 1980, Handley *et al.* 1991), although reports of insect, nectar, and pollen suggest that other items are sometimes taken.

MATERIALS AND METHODS

In the course of our study on the social organization of cave-roosting *A. jamaicensis* in Puerto Rico (Kunz *et al.* 1983), we observed several whole and partly-chewed leaves of *Erythrina poeppigiana* and fresh leaf-pellets discarded beneath harem roosts in Aguas Buenas Cave. To substantiate these observations, we sampled discarded leaves and other plant parts, fruit and leaf pellets, and feces, that were deposited beneath both harem and feeding roosts of *A. jamaicensis* at this and several other caves in Puerto Rico. Observations of leaf eating (and leaf transport) were made during each month of the year, although most observations and collections were made in the months of January, May, June, and July (1985–1992).

To sample diet composition, we placed litter traps beneath five active harem roosts in Aguas Buenas Cave. Each trap consisted of a 1 m² wood frame (lined with opaque plastic sheeting) and attached in the center to a 1.5 m-long wooden pole. The free end of each pole was forced into the soil of the cave floor to prevent rats, snails, and land crabs from either disturbing or devouring the samples. Plastic linings were removed each day and the records of leaves, leaf pellets, fruit pellets, and fecal "splats" were collected. Leaf samples and leaf pellets were stored in plastic vials. Fecal splats were outlined on the plastic liner with a colored marker, scraped from the plastic, and placed in plastic vials. These samples were then frozen in liquid nitrogen or placed on dry ice and transported to Boston University where they were then analyzed.

In the period from May through July 1985, we set mist nets at weekly intervals at one of the upper entrances to Aguas Buenas Cave, and continuously tended these nets from sunset to sunrise. As bats were removed from the net, we noted their sex, age class (adult or juvenile), and whether they were carrying plant parts. We also recorded their body mass (0.1 g) and forearm length (0.1 mm). Females were palpated to determine whether they were pregnant, lactating, or in non-breeding con-

dition. For males we also measured the length of the testes. All linear measurements were taken with metric dial calipers, and body mass was taken with a Pesola spring scale (after Kunz *et al.* 1983). Each bat was marked on the forearm with a plastic, numbered wing band (A.C. Hughes, Ltd.) and released at the site of capture after being processed.

Leaf samples of *Erythrina poeppigiana* were collected from trees near Aguas Buenas Cave and at several localities in western Puerto Rico, near Mayaguez, and frozen on dry ice for later analysis. Dry-mass protein content was determined by the methods of Marks *et al.* (1985). Lipid content of leaves was determined using petroleum-ether extraction (Herbst 1988). We have used the nomenclature of Little *et al.* (1977) for the plant taxa in Puerto Rico.

RESULTS

Leaf-eating has been reported for at least 17 species of Old-World Megachiroptera and four species of New World Microchiroptera (Table 1). Leaves of at least 44 species of plants representing 23 different families are eaten by these bats. Plant families which account for the greatest species richness (numbers of species given in parentheses) include the Leguminosae (12), Moraceae (4), and Solanaceae (4). In addition to leaves, some members of the Pteropodidae eat other non-conventional plant parts, including leaf petioles, flower buds, and stems. Whether these parts provide essential nutrients or provide sources of energy during food shortages has not been determined. We suspect that whole leaves are seldom consumed by most species of bats, but rather the leaves probably are chewed and the soluble contents are extracted by what Lowry (1989) referred to as "green-leaf fractionation" (see Telek & Martin 1983). Essentially, green-leaf fractionation involves bats chewing whole leaves, extracting the soluble contents while forming fibrous pellets, and later rejecting the pellets upon the completion of chewing. Leaves reportedly taken by bats include both new and mature leaves, although there has been no systematic examination of leaf quality or quantity, or whether leaves are selectively consumed by all or only some members of a particular species.

We collected discarded fruit parts, whole and partially chewed leaves, discarded leaf and fruit pellets, and seeds of nine species of plants beneath harem and feeding roosts of *Artibeus jamaicensis*. Species identified from discarded fruit parts include *Calophyllum* sp., *Clusia rosea*, *Piper aduncum*, and *Spondias mombin*. The only flower parts (calaces)

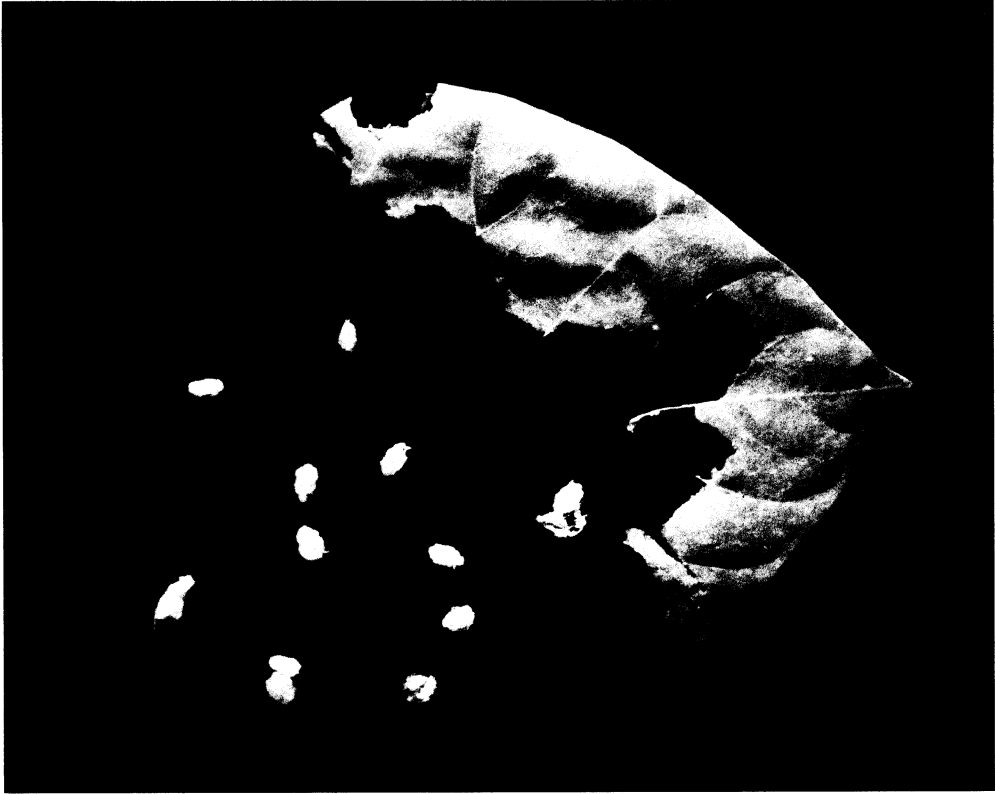


FIGURE 1. Partially chewed *Erythrina poeppigiana* leaf and rejected leaf pellets collected beneath a harem roost of *Artibeus jamaicensis* in Aguas Buenas Cave, Puerto Rico.

taken in the traps were from *Eugenia jambos*, but since fruits often retain their inflorescences, we suspect that fruits and not flowers were eaten. Small seeds were common in fecal samples, with seeds of *Ficus citrifolia* recorded in 76 out of 149 fecal samples, as was *Solanum torvum* (56%) and *Cecropia peltata* (13%). Insect remains were recorded in 25 percent of the fecal samples, although some of the insects (2 coleopterans, 5 hymenopterans, 1 dipteran) were found intact, suggesting that there was contamination of feces by cavernicolous flying insects which may have been attracted to the feces and discarded fruit parts.

Discarded whole leaves, partially chewed leaves, and leaf pellets from *Calophyllum calaba*, *Ficus* sp., and *E. poeppigiana* were found in fecal traps, but only those from *E. poeppigiana* were recorded consistently ($N = 25$ nights). We found no evidence that only certain parts of leaves were selectively eaten or rejected, although in many instances the basal lobes of leaves, including the petiole, were missing from the discarded or dropped leaves (Fig. 1). From

these observations it appears that leaves, including the petioles, are regularly eaten by *A. jamaicensis*. Most, if not all, of the whole leaves and leaf parts that we found beneath roost sites were mature. Trees of each of the above species were abundant in the vicinity of Aguas Buenas Cave. Since whole leaves or leaf parts from *Calophyllum* and *Ficus* were only recorded on two occasions, this suggests that *A. jamaicensis* may prefer leaves of *E. poeppigiana* over other species.

Pellet counts made daily at each harem roost indicated that 6 to 12 leaf pellets were discarded each night. Freshly discarded leaf pellets were typically green, highly fibrous, and could be distinguished from rejected fruit pellets, which were mostly yellow or orange (but sometimes green) and less fibrous than the pellets of leaves. We do not know how many pellets are produced from a single leaf. Discarded leaf pellets formed by *A. jamaicensis* were relatively uniform in shape and size (Fig. 1). Typically, leaf pellets were ovoid and slightly flattened, with average length, width, and depth measure-

ments ($N = 42$) of $6.7 \pm 0.46 \times 4.4 \pm 0.23 \times 3.0 \pm 0.68$ mm, respectively. Our nutrient analyses of several mature *Erythrina* leaves indicate a mean dry-matter protein content of 19.1 ± 0.7 mg/100 mg and an extractable lipid component of 1.8 ± 0.10 mg/100 mg.

Of the 348 bats captured in 1985 as they were entering Aguas Buenas Cave, six were carrying *Erythrina* leaves. Each of the six bats was a mature male, although we could not confirm whether they were harem males since they were taken in mist nets (Kunz *et al.* 1983). When the leaf-carrying bats were removed from the net, each had a whole leaf, including the petiole, in its mouth. Several other *A. jamaicensis* were captured while carrying whole leaves, but they either dropped them as they became entangled in the mist or they escaped before we could determine their sex and reproductive status. Since these individuals could not be positively identified to sex or reproductive status we have not included them as evidence of leaf carrying.

DISCUSSION

Our collections of discarded leaf parts, whole leaves, and rejected leaf pellets beneath roosts of *A. jamaicensis*, and captures of mature males carrying fresh leaves provide additional evidence for folivory, by leaf-fractionation, by plant-visiting phyllostomids. As in other parts of its range, *A. jamaicensis* in Puerto Rico feeds mostly on fruits, but the leaves of *E. poeppigiana* appear to comprise an important dietary component, at least on a seasonal basis. *Erythrina* leaves are also eaten by *A. jamaicensis* in Colombia (T. Lemke, pers. comm.). Whether the protein-rich leaves of *Erythrina* are preferred by *A. jamaicensis*, or whether this bat takes the most abundant and available leaves remains to be established. Consumption of *Erythrina* leaves has been reported in megachiropterans, including *Pteropus tonganus* on the island of Tonga (Harris & Baker 1959). Rosevear (1965) suggested that *Eidolon helvum* probably consumed *Erythrina* leaves in Uganda. Similarly, Cunningham van Someren (1972) reported that *Rousettus aegyptiacus* foraged at *Erythrina* trees, returning to its day roosts to consume the leaves. Thus, there is evidence that some bat species prefer *Erythrina* leaves over others.

WHY DO FRUIT BATS EAT LEAVES?—Since most fruits are low in protein (Table 2), many frugivorous vertebrates rely on alternative food sources to satisfy their protein requirements (Morton 1973, Thomas 1984, Stellar 1986). Although *Artibeus jamaicensis*

has been regarded as a fig (fruit) specialist by some investigators (*e.g.*, Jimbo & Schwassmann 1967, Morrison 1978), more recently this bat has been considered to be a fruit generalist (Gardner 1977, Bonaccorso 1979, Handley *et al.* 1991). This latter view is supported by studies of Morrison (1980) who concluded that captive *A. jamaicensis* could not obtain sufficient proteins from eating only *Ficus* fruits. Similarly, Herbst (1986) found that captive *Carollia perspicillata* was unable to meet its protein requirements unless its diet included fruits of the protein-rich *Piper amalago* (see Fleming 1988).

Given that most fruits are low in protein (Herrea 1987), bats should either selectively feed on fruits that are high in protein (Table 2), select alternate food items that are rich in protein, or modify their feeding tactics to increase protein consumption. In the latter context, Thomas (1984) suggested that Old World megachiropterans may over-consume and then "dump" carbohydrates in order to meet their protein requirements from otherwise protein-poor fruits. A similar conclusion was made by Stellar (1986) for *Pteropus poliocephalus*. However, leaves of several tree species offer potentially rich sources of dietary protein that would obviate the need for Old-World fruit-eating bats to over-consume fruits as suggested by Thomas (1984) and Stellar (1986). For example, the mean protein content of *E. poeppigiana* (~19% dry matter—Table 2) is similar to values reported for *E. excelsa* (17% dry matter) which serves as an important protein source for some neotropical primates (Choo *et al.* 1981). In fact, the dry-matter protein content of both species of *Erythrina* is considerably higher than values reported for leaves and fruits of many other plant species eaten by bats that have been analyzed for protein content. One exception is perhaps the leaves of *Ceiba pentandra* (Table 2). However, *Solanum* fruits also have a dry matter protein (13.4%) approaching levels observed for *Erythrina* leaves and also could provide an important protein source for some fruit-eating bats at times or in regions where this tree regularly produces fruit.

Some Old-World fruit-eating bats may resort to over-consumption of low-protein fruits (Thomas 1984, Stellar 1986), others may gain sufficient amounts of protein from ingesting pollen (Law 1992), and a few may ingest insects (Roberts & Seabrook 1989, Parry-Jones & Augee 1992). By contrast, echolocating New World fruit-eating bats are capable of capturing flying insects and other invertebrates as a source of protein (Fleming 1979). Although it has been suggested that *A. jamaicensis* includes some insects in its diet (Gardner 1977),

our observations of fecal splats (May–July) indicate that few insects are taken, and there is little evidence that pollen comprises a significant proportion of its diet. In Gardner's (1977) review of food habits of the Phyllostomidae, he noted that insects were infrequently included in the diet of *A. jamaicensis*, although none were mentioned by Handley *et al.* (1991) as dietary items from their field study in Panama. In deriving an energy and nutrient budget for *A. jamaicensis*, Morrison (1979) estimated that 0.86 g of insects containing 18 percent (wet mass) of protein would be needed to meet the daily protein requirement of this 45 g bat. This level of insect consumption would obviously require active pursuit of insects rather than fortuitous intake while eating fruit or other plant parts.

Alternatively, consumption of the soluble fraction of protein-rich leaves could provide the daily protein needs of *A. jamaicensis*. Cunningham van Someren (1972) extracted 1.58 g of liquid from a 5.8 g (fresh) *Erythrina* leaf. Assuming that *A. jamaicensis* could extract an equivalent amount from an *Erythrina* leaf containing 19 mg total N/100 mg protein (4.4-nitrogen-to-protein conversion factor—Milton & Dintzis 1981), the consumption of the liquid fraction from a fresh 3-g *Erythrina* leaf would yield 155 mg of protein. Based on an estimated daily protein demand of 307 mg for a 50 g *Artibeus* (Thomas 1984), and an assumed assimilation efficiency of 90 percent, two 3-g leaves would yield 278 mg of assimilated protein, which would almost satisfy its daily protein needs independent of quantities that may be present in ingested fruit.

Because of the relatively low energy value of leaves, and the potential energetic constraints that a diet high in fiber is likely to impose on flight, it is not surprising that true folivory (ingestion of whole leaves) is absent in bats (Kunz & Ingalls 1994). Although leaves potentially provide a super-abundant resource for phytophagous bats, the generally slow digestion of leaves (Eisenberg 1978, Waterman 1984, Hume 1989) and the need for a more robust gut to handle larger food loads probably would be enough to significantly reduce the efficiency of flight in bats (see Norberg & Rayner 1987). A regular diet of whole leaves would require specialized morphological and physiological adaptations (*e.g.*, robust dentition, a large cecum or rumen, and an elongated gut) that would most certainly increase wing-loading and the energetic costs of flight. Among folivorous birds, only the weakly-flighted hoatzin (*Opisthocomus hoatzin*) of South America (Grajal *et al.* 1989) and the kakapo (*Strigops habroptilus*), a flightless, nocturnal parrot of

New Zealand, have evolved specialized foreguts that promote leaf digestion (Gill 1990). Some folivorous bird species have evolved specializations of the hindgut to promote the digestion of leaves (Gasaway 1976, Buchsbaum *et al.* 1986).

Bats that feed on leaves appear to have overcome the problem associated with consuming a diet high in fiber, by extracting the leaf juices rather than ingesting the whole leaves. Cunningham van Someren (1972) observed that *R. aegyptiacus* "consumed" leaves by biting a chunk of leaf, rolling it back and forth on the palate, sucking the juices, and expelling the fibrous remains. This method of eating is similar to the description of fruit consumption reported for *A. jamaicensis* (Morrison 1978, Handley & Morrison 1991), a food-handling behavior that is also used when this and other species "consume" leaves. This description of food handling is also similar to that given by Lowry (1989) for how the liquid fraction of leaves is extracted by the megachiropteran *Pteropus alecto*.

Why should a fruit-eating microchiropteran such as *A. jamaicensis* eat leaves when it is indeed capable of capturing and eating insects as sources of protein or other nutrients? We believe that leaves may be eaten instead of insects as a source of protein, not because leaves are necessarily more abundant, but because they should have a higher yield of protein per unit foraging effort. Although bats must fly to obtain both leaves and insects, leaves are predictable in space and time and less energy should be required in their pursuit and capture. Alternatively, some leaves may be eaten by frugivorous bats as a source of important minerals. Studier and Wilson (1991) suggested that the consumption of fruit juices rather than an entire fruit may be an important source of dietary sodium. Perhaps folivory by leaf fractionation also provides an important source of dietary calcium to bats (see Barclay 1994).

New leaves of *Erythrina poeppigiana* are produced over a 9-month period (March through December) in Puerto Rico (Little *et al.* 1977). Although most *Erythrina* trees shed their leaves at the end of the rainy season, some retain their leaves well into the dry season, and some continue to produce new leaves especially if they do not flower during that year (A. Rodriguez-Duran, pers. comm.). Some leaves of *Erythrina* may be available to *A. jamaicensis* year-around, but our observations indicate that leaves of other tree species may be eaten when *Erythrina* leaves are less available. However, protein requirements of frugivorous bats may be relatively low during the dry season, since most nutrient-demanding periods of reproduction (late

pregnancy and lactation) coincide with the end of the dry season and the rainy season (May–December).

Our hypothesis that folivory by *A. jamaicensis* may be limited to adult males is supported by our observations that only mature males carried leaves into caves, and that small numbers of partially chewed leaves and rejected pellets were found mostly beneath harem roosts. *Artibeus jamaicensis* exhibits a type of social organization known as resource defense polygyny (Morrison 1979, Kunz *et al.* 1983, Kunz & McCracken 1995), in which harem males defend certain roost sites (*e.g.*, tree hollows, solution cavities in caves, leaf tents) from intrusions by other males. This type of social organization by *A. jamaicensis* appears to be accompanied by a foraging strategy where harem males principally forage in the vicinity of their harem roosts. Conversely, female *A. jamaicensis* often disperse from the area of their harem roosts and forage at greater distances and for longer times during the night (Morrison 1979, Morrison & Morrison 1981). Such gender-specific patterns of the nightly foraging have also been observed for *Carollia perspicillata* (Fleming 1988), *Phyllostomus hastatus* (McCracken & Bradbury 1981), and *Cynopterus sphinx* (Balasingh *et al.* 1995), in which harem males spend much of the night defending their roost sites.

If the nightly foraging activity of a harem male *A. jamaicensis* is concentrated in the vicinity of its harem roost, and it spends non-foraging time occupying and defending the harem roost, we could expect to find that most of the rejected food parts (partially chewed leaves, seeds, and fruit pulp) found beneath harem roosts are products of harem males. Conversely, if leaves and rejected plant parts are deposited in other areas, these could be attributed to females. Feeding roosts of female *A. jamaicensis* on Barro Colorado Island, Canal Zone, Panama, were often located in nearby trees different from those in which they roosted or took fruits. In Puerto Rico, where caves are abundant, entrance areas of some caves are commonly used as feeding roosts by *A. jamaicensis* (T. H. Kunz, pers. obs.). In both situations, it appears that feeding roosts may be chosen by females for their reduced accessibility to predators (see Handley & Morrison 1991).

Typically, roost defense by harem male *A. jamaicensis* includes regular surveillance throughout the night, interrupted by several brief foraging flights before returning to the roost (Morrison & Morrison 1981). By making such brief foraging forays to “capture” a leaf and returning the leaf to its roost where it is consumed, a harem male would be able

to maximize the amount of time allocated to roost defense, while at the same time minimize the amount of time it spends flying. By contrast, females frequently feed at greater distances from their day roost and usually do not return until after several hours of foraging (Morrison 1979, Morrison & Morrison 1981, Handley & Morrison 1991). Thus, it is unlikely that leaf eating among females would be observed unless they transported leaves to the harem roost following their last nightly foraging bout. Our data from mist netting indicate that female *A. jamaicensis* do not carry leaves back to harem roosts, although we cannot rule out that they do feed on leaves at feeding roosts at other locations. If leaves are eaten by female *A. jamaicensis* at feeding roosts located in a tree, it is quite likely that they would be overlooked, since rejected leaves and pellets are more difficult to distinguish on the forest floor than on the floor of a cave. Observations of leaves deposited beneath feeding roosts near the entrances to caves, but away from harem roosts, suggests that some female *A. jamaicensis* may use these sites in a similar manner to feeding roosts in trees. Evidence for folivory, based on partially eaten leaves and pellets found beneath harem and feeding roosts in caves, is more likely to be observed at such roosts than in forested regions.

Judging from our observations, we expect that females eat leaves to satisfy their protein intake, especially during the high nutrient demanding periods of pregnancy and lactation. As with males, search and handling time would be lessened by eating leaves, and the net return on their investment would be higher than if they fed on insects. The cost-benefit ratio for protein intake by folivory versus insectivory should be higher, since insectivory by bats usually involves active pursuit of mobile prey. We believe that a female *A. jamaicensis* could reduce its daily energy expenditure if it consumed leaves instead of insects during late pregnancy and lactation when energy and nutrient demands are expected to be the highest. Although the specific nutrient requirements for pregnant and lactating *A. jamaicensis* have not been determined, studies on some primates indicate that females increase their protein intake during lactation by consuming leaves (Gautier-Hion 1980).

Folivory in bats may have other consequences, especially in relation to reproduction. For example, in the African pteropodids, *Epomphorus walbergi* and *Rousettus aegyptiacus*, both species are known to extract liquid fractions from the leaves of *Balanites wilsoniana*. Leaves of this plant contain two types of steroidal saponin (diosgenin and ya-

mosgenin); epimeres of which are used in the synthetic manufacture of steroidal hormones (Sofoura & Hardman 1973). Similarly, plants of the genera *Erythrina* and *Solanum* both produce alkaloids (especially glycoalkaloids) of demonstrated toxicity to vertebrates. Since steroids are essential for hormone synthesis, the oral intake of these compounds by phytophagous bats may influence their reproductive activity (Wickler & Seibt 1964). Although *Erythrina* lacks the steroidal sapogenins (aglycones) found in *Balanites*, most members of the genus *Erythrina*, including *E. poeppigiana*, contain several secondary metabolites, including alkaloids (Telek & Martin 1983). Similar observations led Cunningham van Someren (1972) to suggest that *Erythrina* leaves may contain one or more metabolites (alkaloids) important for reproduction by *Rousettus aegyptiacus*. Of these compounds, beta-erythroidine has a cortisone like (muscle relaxant) effect on mammals (Hargreaves *et al.* 1974). Since steroidal alkaloids are known to be precursors of plant hormones (T. Swain, pers. comm.), these could be important in stimulating or inhibiting reproductive activity. Because steroid hormones such as androgens, gestagens, glucocorticoids, and mineralocorticoids play such a vital role in the lives of mammals, the ecological and behavioral implications of folivory in bats may be of considerable interest as a regulator of seasonal reproduction. Perhaps folivory by males may have evolved in response to the high cost of roost or harem defense (see above), as a consequence of being forced to feed on food sources that can be obtained nearby its roost site.

A potential disadvantage of folivory by bats is that leaves which are eaten may contain secondary metabolites, and many of these are known to act as feeding deterrents or inhibit protein digestion. Tannins in particular are known to deter protein digestion in mammals. However, perhaps one reason that leaves from such plants as *Erythrina* and *Albezia* are commonly eaten is that they are relatively low in condensed tannins and total phenols (Telek & Martin 1983). However, one of the most crucial problems for folivores is the phenol-protein interaction. Most plants contain polyphenol oxidases which catalyze the oxidation of *o*- and *p*-polyhydroxyphenols to the corresponding quinones. For example, polyphenol oxidases convert catechol to *o*-quinone which can then bind with protein. Even more important are the condensed tannins which bind proteins and form insoluble complex molecules. In fact, a high concentration of tannins in leaves can precipitate the entire protein content once it is eaten (Telek & Martin 1983).

Whether folivorous bats preferentially select leaves that are low in secondary metabolites which may deter consumption or inhibit protein digestion remains to be determined. Mature leaves often contain higher concentrations of secondary compounds than developing leaves (Telek & Martin 1983), although phytophagous bats appear to consume both mature and young leaves (and leaf buds) of certain species (Table 1). Our review points to a need for further studies to characterize the nutritional properties of both young and mature leaves eaten by phytophagous bats, to establish the pharmacological properties of secondary metabolites in bats, and to determine whether these compounds act as feeding deterrents or inhibitors of protein digestion or, alternatively, whether they act as precursors to steroidal hormones and thus function as cues to reproduction.

In summary, we propose six testable hypotheses relating to the folivorous habits of plant-visiting bats. These are: 1) Folivory is a regular part of the feeding repertoire of harem males that insures a protein-rich diet and that reduces the overall cost of harem defense; 2) Folivory is part of the feeding strategy of females that ensures a rich source of protein during the energetically and nutrient demanding periods of pregnancy and lactation; 3) Harem males sequester secondary metabolites from the liquid fraction of leaves that in turn promotes or stimulates reproductive activity; 4) Females sequester secondary metabolites as hormone precursors that in turn function as cues for the timing of reproduction; 5) Males and females preferentially select leaves that are low in secondary metabolites which at higher concentrations would act as feeding deterrents or inhibitors of protein digestion; and 6) Leaves provide an important source of micronutrients and vitamins that may not be available in fruit.

ACKNOWLEDGMENTS

This study was supported by grants from the Boston University Graduate School and The Lube Foundation, Inc. (THK), the American Society of Mammalogists, and the Theodore Roosevelt Memorial Fund (CAD). Logistic support in the field was provided to CAD by the Department of Natural Resources, Commonwealth of Puerto Rico and the U.S. Fish and Wildlife Service. We thank D. Marks, R. Buchsbaum, and T. Swain for analytical advice; Armando Rodriguez-Duran for field assistance and hospitality; H. R. Bhat, J. Balasingh, K. Parry-Jones, T. E. Lemke, and G. Wiles for making available unpublished observations on folivory in bats; and K. Lajtha, E. D. Pierson, G. Wiles, and W. Rainey for helpful comments on an earlier draft of this manuscript.

LITERATURE CITED

- BALASINGH, J., J. KOILRAJ, AND T. H. KUNZ. 1995. Tent construction by the short-nosed fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae), in southern India. *Ethology* (In press).
- BALASUBRAMANIAN, P. 1988. Short-nosed fruit bat (*Cynopterus sphinx* Vahl) feeding on the leaves of *Casia fistula* at Point Calimere Wildlife Sanctuary. *J. Bombay Nat. Hist. Soc.* 85: 183.
- BARCLAY, R. M. R. 1994. Constraints on reproduction by flying vertebrates: energy and calcium. *Am. Nat.* In press.
- BHAT, H. R. 1994. Observations on the food regimen and feeding behavior of *Cynopterus sphinx* Vahl (Chiroptera, Pteropodidae) at Pune, Indian. *Mammalia* In press.
- BONACCORSO, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. *Bull. Florida State Mus., Biol. Sci.* 24: 359-408.
- BUCHSBAUM, R., J. WILSON, AND I. VALIELA. 1986. Digestibility of plant constituents by Canada geese and Atlantic brant. *Ecology* 67: 386-393.
- CALVERT, J. P. 1985. Food selection by western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia* 65: 236-246.
- CARROLL, J. B. 1983-1984. The conservation and wild status of the Rodrigues fruit bat *Pteropus rodricensis*. *Myotis* 21-22: 148-154.
- CHOO, G. M., P. G. WATERMAN, D. B. MCKEY, AND J. S. GARTLAN. 1981. A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist herbivores. *Oecologia* 49: 170-178.
- COOK, J. A. 1979. The feeding ecology of the Seychelles fruit bat *Pteropus seychellensis*. In P. A. Racey (Ed.). *Aberdeen University Expedition to the Seychelles*. 1977. Dept. Zool., Univ. Aberdeen, Aberdeen.
- CUNNINGHAM VAN SOMEREN, G. R. 1972. Some fruit bats eat leaves. *E. Afr. Nat. Hist. Soc. Bull.* 2: 24-25.
- EISENBERG, J. F. 1978. The evolution of arboreal folivores in the class Mammalia. In G. Montgomery (Ed.). *The ecology of arboreal folivores*, pp. 135-152. Smithsonian Institution Press, Washington, D.C.
- FALANRUW, M. V. C. 1988. On the status, reproductive biology and management of fruit bats on Yap. *Micronesica* 21: 39-51.
- FLEMING, T. H. 1979. Tropical frugivores compete for food? *Amer. Zool.* 19: 1157-1172.
- . 1988. *The short-tailed fruit bat: a study of plant-animal interactions*. Univ. Chicago Press, Chicago.
- FORMAN, G. L. 1990. Comparative macro- and microanatomy of stomach of MacroGLOSSINE bats (Megachiroptera: Pteropodidae). *J. Mammal.* 71: 555-564.
- , C. J. PHILLIPS, AND C. S. ROUK. 1979. Alimentary tract. In R. J. Baker, J. K. Jones, Jr., and D. C. Carter (Eds.). *Biology of bats of the New World family Phyllostomatidae*, Part III, pp. 205-228. Texas Tech Univ. Press, Lubbock.
- FOSTER, M. S., AND R. M. TIMM. 1976. Tent-making by *Artibeus jamaicensis* (Chiroptera: Phyllostomatidae) with comments on plants used by bats for tents. *Biotropica* 8: 265-269.
- FREELAND, W. J., AND D. JANZEN. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *Am. Nat.* 108: 269-289.
- FUNAKOSHI, K. 1989. Northernmost populations of the flying fox. *Shizen Aigo* 16: 1-6. (in Japanese).
- FUNMILAYO, O. 1979. Ecology of the straw-colored fruit bat in Nigeria. *Rev. Zool. Afr.* 93: 589-600.
- GARDNER, A. L. 1977. Feeding habits. In R. J. Baker, J. K. Jones, Jr., and D. C. Carter (Eds.). *Biology of bats of the New World family Phyllostomatidae*, Part II, pp. 293-350. *Spec. Publ. Mus. Texas Tech Univ.*, Lubbock.
- GASAWAY, W. C. 1976. Seasonal variation in diet, volatile fatty acid production, and size of the cecum of rock ptarmigan. *Comp. Biochem. Physiol.* 54A: 179-182.
- GAUTIER-HION, A. 1980. Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkey. *J. Anim. Ecol.* 49: 237-269.
- GILL, F. B. 1990. *Ornithology*. W. H. Freeman and Company, New York.
- GOODWIN, R. E. 1970. The ecology of Jamaican bats. *J. Mammal.* 51: 571-579.
- , AND A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago. *Bull. Amer. Mus. Nat. Hist.* 122: 187-302.
- GRAJL A., S. D. STRAHL, R. PARRA, M. G. DOMINQUEZ, AND A. NEHER. 1989. Foregut fermentation in the hoatzin, a neotropical leaf-eating bird. *Science* 245: 1236-1238.
- GREENHALL, A. M. 1957. Food preference of Trinidad fruit bats. *J. Mammal.* 38: 409.
- HANDLEY, C. O., JR., AND D. W. MORRISON. 1991. Foraging behavior. In C. O. Handley, Jr., D. E. Wilson, and A. L. Gardner (Eds.). *Demography and natural history of the common fruit bat, Artibeus jamaicensis*, on Barro Colorado Island, Panama, pp. 137-140. *Smithsonian Contributions in Zoology*, No. 511, Washington, D.C.
- , A. L. GARDNER, AND D. E. WILSON. 1991. Food habits. In C. O. Handley, Jr., D. E. Wilson, and A. L. Gardner (Eds.). *Demography and natural history of the common fruit bat, Artibeus jamaicensis*, on Barro Colorado Island, Panama, pp. 141-146. *Smithsonian Contributions in Zoology*, No. 511, Washington, D.C.
- HLADIK, C. M., A. HLADIK, J. BOUSETT, P. VALDEBOUZE, G. VIROBEN, AND J. BELORT-LAVAL. 1971. Les régimes alimentaire de primates de l'île de Barro Colorado (Panama). *Fol. Primatol.* 16: 95-122.
- HARRIS, B. J., AND H. G. BAKER. 1959. Pollination of flowers by bats in Ghana. *Niger. Fld.* 24: 151-159.

- HARGREAVES, T. T., R. D. JOHNSON, D. S. MILLINGTON, M. H. MONDAL, W. BEAVERS, L. BECKER, C. YOUNG, AND J. L. RINEHART, JR. 1974. Alkaloids of the American species of *Erythrina*. *Lloydia* 37: 589-580.
- HERBST, L. H. 1986. The role of nitrogen from fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. *Biotropica* 18: 39-44.
- . 1988. Methods of nutritional ecology of plant visiting bats. In T. H. Kunz (Ed.). *Ecological and behavioral methods for the study of bats*, pp. 23-246. Smithsonian Institution Press, Washington, D.C.
- HERREA, C. M. 1987. Vertebrate dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecol. Monogr.* 57: 305-331.
- HUME, I. D. 1989. Optimal digestive strategies in mammalian herbivores. *Physiol. Zool.* 62: 1145-1163.
- IRVINE, F. R. 1961. *Woody plants of Ghana*. Oxford University Press, London.
- JANZEN, H., AND M. EISENTRAUT. 1945. *Biologie der Flederhunde (Megachiroptera)*. *Biol. Gen.* 18: 327-435.
- JIMBO, S., AND H. O. SCHWASSMANN. 1967. Feeding behavior and the daily emergence pattern of *Artibeus jamaicensis* Leach (Chiroptera: Phyllostomatidae). *Atas Simp. Biota Amaz.* 5: 239-253.
- KITCHENER, D. J., A. GUNELL, AND MAHARDATUNKAMSI. 1990. Aspects of the feeding biology of fruit bats (Pteropodidae) on Lombok Island, Nusa Tenggara, Indonesia. *Mammalia* 54: 561-578.
- KLITE, P. D.. 1965. Intestinal bacterial flora and transit time of three neotropical bat species. *J. Bacteriol.* 90: 375-379.
- KUNZ, T. H., AND K. A. INGALLS. 1994. Folivory in bats: an adaptation derived from frugivory. *Funct. Ecol.* 8: 665-668.
- , AND G. F. McCRACKEN. 1995. Tents and harems: apparent defense of foliage by tent-making bats. *J. Trop. Ecol.* In press.
- , P. V. AUGUST, AND C. D. BURNETT. 1983. Harem social organization in cave roosting *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica* 15: 133-138.
- , M. S. FUJITA, A. P. BROOKE, AND G. F. McCRACKEN. 1994. Convergence in tent architecture and tent-making behavior among neotropical and paleotropical bats. *J. Mammal. Evol.* In press.
- LAW, B. S. 1992. Physiological factors affecting pollen use by Queensland blossom bats (*Syconycteris australis*). *Funct. Ecol.* 6: 257-264.
- LEWIS, R. E., AND D. L. HARRISON. 1962. Notes on bats from the Republic of Lebanon. *Proc. Zool. Soc. Lond.* 138: 473-486.
- LITTLE, E. L., JR., F. H. MARERO, AND J. MARERO. 1977. *Arboles comunes de Puerto Rico y las Islas Virgenes*. Editorial Universitaria, Universitat de Puerto Rico, Rio Piedras.
- LOWRY, J. B. 1989. Green-leaf fractionation by fruit bats: is this feeding behaviour a unique nutritional strategy for herbivores? *Aust. Wildl. Res.* 16: 203-206.
- MAKIN, D., AND H. MENDELSON. 1986. Israel wipes out its bats. *Ecologist* 6: 46-47.
- MALAGNOUX, J., AND J. C. GAUTIN. 1976. Un ennemi des plantations D'Araucariaen Côte D'Ivoire. *Rev. Bois et For. Trop.* 165: 35-38.
- MARKS, D. L., R. BUCHSBAUM, AND T. SWAIN. 1985. Measurements of total protein in plant samples in the presence of tannins. *Anal. Biochem.* 147: 136-143.
- MARSHALL, A. F. 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zool. J. Linn. Soc.* 83: 351-369.
- MARUYAMA, K. 1980. An ecological study of *Pteropus dasymallus inopinatus* in captivity. Unpublished Thesis, College of Science and Engineering, Univ. Ryukus, Japan (in Japanese).
- MCCRACKEN, G. F., AND J. W. BRADBURY. 1981. Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behav. Ecol. Sociobiol.* 8: 11-34.
- MICKLEBURGH, S. P., P. A. RACEY, AND A. M. HUTSON. 1992. *Old-world fruit bats: an action plan for the family Pteropodidae*. IUCN Publ. Unit, Information Press, Oxford.
- MILTON, K. 1981. Food choice and digestive strategies for two sympatric primate species. *Am. Nat.* 117: 496-505.
- , AND Y. DINTZIS, F. R. 1981. Nitrogen-to-protein conversion factors for tropical plant samples. *Biotropica* 13(3): 177-181.
- MORRISON, D. W. 1978. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* 59: 716-723.
- . 1979. Apparent male defense of tree hollows in the fruit bat *Artibeus jamaicensis*. *J. Mammal.* 60: 11-15.
- . 1980. Efficiency of food utilization by fruit bats. *Oecologia* 45: 270-273.
- , AND S. H. MORRISON. 1981. Economics of harem maintenance by a neotropical bat. *Ecology* 62: 864-866.
- , AND C. O. HANDLEY, JR. 1991. Roosting behavior. In C. O. Handley, Jr., D. E. Wilson, and A. L. Gardner (Eds.). *Demography and natural history of the common fruit bat, Artibeus jamaicensis*, on Barro Colorado Island, pp. 131-136. Smithsonian Contributions in Zoology, No. 511, Washington, D.C.
- MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *Am. Nat.* 107: 8-22.
- NELSON, J. E. 1965. Behavior of Australian Pteropodidae (Megachiroptera). *Anim. Behav.* 8: 544-557.
- NORBERG, U. M. 1990. *Vertebrate flight*. Springer-Verlag, Berlin.
- , AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing

- adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* 316: 335–427.
- OATES, J. F., P. G. WATERMAN, AND G. M. CHOO. 1980. Food selection by South Indian leaf-monkey, *Presbytis johnii* in relation to leaf chemistry. *Oecologia* 45: 45–56.
- OKON, E. E. 1977. Functional anatomy of the alimentary canal in the fruit bat *Eidolon helvum* and the insect *Tadarida nigeriae*. *Acta Zool. (Stockholm)* 58: 83–93.
- PAKARNSEREE, L. 1986. Food habits of Thai bats: studies on stomach contents of fruit-eating and insectivorous bats in Thailand (Mammalia: Megachiroptera). *Cour. Forsch. Inst. (Senckenberg)* 87: 73–89.
- PARRY-JONES, K., AND M. L. AUGEE. 1991a. Food selection by grey-headed flying foxes (*Pteropus poliocephalus*) occupying a summer colony site near Gosford, New South Wales. *Wildl. Res.* 18: 111–124.
- , AND ———. 1991b. The diet of flying foxes in the Sydney and Gosford areas of New South Wales, based on sighting reports 1986–1990. *Aust. Zool.* 27: 49–54.
- , AND ———. 1992. Insects in flying-fox diets. *Bat Res. News* 33: 9–11.
- RHODES, D. F., AND R. G. OATES. 1976. Toward a general theory of plant antiherbivore chemistry. In J. W. Dalling and R. L. Mansell (Eds.). *Biochemical interactions between plants and insects*, pp. 168–312. Plenum Press, New York.
- RICHARDS, G., AND P. PROVIC. 1984. Folivory in *Pteropus*. *Aust. Bat. Res.* 20: 13–14.
- RICHARDSON, K. C., R. B. STUEBING, AND H. K. NORMAN. 1987. Alimentary tract morphology and digesta transit of some Malaysian chiropterans. *Indo-Malay. Zool.* 4: 399–412.
- ROBERTS, P., AND W. A. SEABROOK. 1989. A relationship between black rats (*Rattus rattus*), Seychelle fruit bats (*Pteropus seychellensis aldabrensis*) and the coccid (*Icerya seychellarum*) (Insecta, Homoptera) on Aldabra Atoll, Seychelles. *J. Zool. (Lond.)* 218: 332–334.
- ROSEVEAR, D. R. 1965. The bats of West Africa. British Museum (Nat. Hist.), London.
- SILVA-TABOADA, G. 1979. Los murcielagos de Cuba. Academia de Ciencias de Cuba, Habana, Cuba.
- SOFOURA, E. A., AND R. HARDMAN. 1973. Steroids, phthalyl esters and hydrocarbons from *Balanites wilsoniana* stem bark. *Phytochemistry* 12: 403–406.
- STELLAR, D. C. 1986. The dietary energy and nitrogen requirements of the grey-headed flying fox, *Pteropus poliocephalus* (Temminck) (Megachiroptera). *Aust. J. Zool.* 34: 339–349.
- STUDIER, E. H., AND D. E. WILSON. 1991. Physiology. In C. O. Handley, Jr., D. E. Wilson, and A. L. Gardner (Eds.). *Demography and natural history of the common fruit bat, Artibeus jamaicensis*, on Barro Colorado Island, pp. 9–17. Smithsonian Contributions in Zoology, No. 511, Washington, D.C.
- TELEK, L., AND F. W. MARTIN. 1983. Tropical plants for leaf protein concentrates. In L. Telek and H. D. Graham (Eds.). *Leaf protein concentrates*, pp. 81–116. AVI Publishing Company, Inc., Westport, Connecticut.
- TEDMAN, R. A., AND L. S. HALL. 1985. The morphology of the gastrointestinal tract and food transit time in the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera). *Aust. J. Zool.* 33: 625–640.
- THOMAS, D. W. 1984. Fruit intake and energy budgets of frugivorous bats. *Physiol. Zool.* 57: 457–467.
- TIMM, R. M. 1987. Tent construction by bats of the genera *Artibeus* and *Uroderma*. In B. Patterson and R. M. Timm (Eds.). *Studies in neotropical mammalogy: essays in honor of Philip Hershkovitz*, pp. 187–212. Fieldiana: Zool., New Ser., No. 39.
- TUTTLE, M. D. 1968. Feeding habits of *Artibeus jamaicensis*. *J. Mammal.* 49: 787.
- VAN DER PIJL, L. 1957. The dispersal of plants by bats (Chiropterochory). *Acta Bot. Neerl.* 6: 291–315.
- WATERMAN, P. G. 1984. Food acquisition and processing by primates as a function of plant chemistry. In D. J. Chivers, B. A. Wood, and S. Bilsborough (eds.). *Food acquisition and processing by primates*, pp. 177–211. Plenum Press, New York.
- WICKLER, W., AND U. SEIBT. 1964. Field studies of the African fruit bat, *Epomophorus wahlbergi* (Sundovall), with special reference to male calling. *Z. Tierpsychol.* 40: 345–376.
- WILES, G. J. 1987. The status of fruit bats on Guam. *Pac. Sci.* 41: 148–157.
- , J. ENGBRING AND M. V. C. FALANRUW. 1991. Population status and natural history of *Pteropus mariannus* on Ulithi Atoll, Caroline Islands. *Pac. Sci.* 29: 131–138.
- , AND M. S. FUJITA. 1992. The food plants and economic importance of flying foxes on Pacific Islands. In D. W. Wilson and G. Graham (Eds.). *Pacific island flying foxes: proceedings of an international conference*, pp. 24–35. U.S. Dept. Int. Biol. Rept. 90 (23), Washington, D.C.
- WILSON, D. E. 1971. Food habits of *Micronycteris hirsuta* (Chiroptera: Phyllostomidae). *Mammalia* 35: 107–110.
- ZORTEA, M. 1994. Folivory in *Platyrrhinus (Vampyrops) lineatus*. *Bat Res. News* 34: 59–60.
- , AND S. L. MENDES. 1993. Folivory in the big fruit-eating bat, *Artibeus lituratus* (Chiroptera: Phyllostomidae) in eastern Brazil. *J. Trop. Ecol.* 9: 117–120.