

## Food habits of some Costa Rican bats

by

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**ABSTRACT:** Dietary habits of 42 species of Costa Rican bats were studied by examination of feces, by stomach analysis and by identification of pollen grains adhering to the fur. Food items were identified to a finer level than offered in previous literature and not merely as "plant material", "insects" or "vertebrate food". Although the sample size for some species prohibits generalizations, the analysis reveals that many genera, supposed to be nectarivorous, eat only insects, primarily Lepidoptera, during April, May and June and that although there may be some overlap in particular food items in the diets of closely related bats, the major items sought by each bat are different. Generic competition, and in some cases, specific competition for food is low.

Because bats are of considerable usefulness in controlling insects, in pollination, and in seed dispersal, a plea is made for bat conservation by using the technique of guano analysis rather than sacrificing bats for stomach analysis. The former technique gives equivalent results and proves easier for the investigator.

It is generally supposed that bats were, at their origin, insectivorous. Many of the microchiroptera, especially temperate genera, have retained this habit through present time. Other bats, notably tropical forms, have derived different feeding habits with corresponding adaptation of the teeth, wings and digestive apparatus.

Bats are an important component of the tropical fauna. In some areas they constitute nearly one-half of the mammalian species (FLEMING, HOOPER and WILSON, 7), yet little is known about their specific food preferences. The information that the literature offers on dietary habits of tropical bats is often speculative or anecdotal. The few field studies of bat diets have, for the most part, failed to identify ingested items beyond the grossest classification (FLEMING,

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HOOPER and WILSON 7; WILSON, 20; CARVALHO, 3; GOODWIN and GREENHALL, 8).

More detailed information on feeding is necessary for a variety of reasons. In recent years, a number of ecologists have been interested in the concept of niche partitioning. It is hoped that comparative studies of diet may provide a measure of species overlap or diversity. Several papers on the structure of bat communities (FLEMING, HOOPER, and WILSON, 7; McNAB, 14; TAMSITT, 17), which come to conflicting conclusions about overlap, may be criticized as presenting food categories which are too broad to allow statements about niche partitioning.

Dietary data are likewise of importance in behavioral studies. Recent work on bat echolocation ability indicates that certain species can discriminate qualities of laboratory targets differing in pattern by only  $800\mu$  (J. Simmons and N. Suga, personal communication). These workers and others are interested in the bat's use of this ability in the field to select certain prey items. A primary step in obtaining this knowledge is to determine whether bats have food preferences of a finer degree than simply fruit or insects in general.

Uneven sample sizes among genera, together with a limited temporal scope do not allow this paper to be a definite statement on food partitioning. Rather it is intended as a reference for community ecologists and bat biologists. However, dietary items for most genera are identified to finer taxonomic units than those in previous papers; this allows some speculation on niche width in tropical bats. In addition, dates are provided for animals captured; for those genera with larger sample sizes seasonal dietary changes may be seen.

## MATERIAL AND METHODS

During a three month period in Costa Rica (April-June, 1971), the feeding habits of 42 species of bats were investigated. Data were obtained from several sources. For the most part, guano was collected from freshly captured animals. Since most bats defecate while being removed from mist nets, it is a simple matter to collect this material on a slide.

If the captured animals had full stomachs (as distinguished from embryos by palpation) but failed to defecate, they were killed and gastrointestinal tracts were removed immediately.

Food materials obtained by these two techniques were examined on glycerin slides or in petri dishes. Pollen, fruit sclereids, seeds, chitin fragments and vertebrate integumentary structures were identified by consulting standard texts or by comparison with an extensive reference collection made by the authors during the study. In cases where several types of food were found in an individual bat stomach or fecal pellet, the approximate percentages of each type were estimated by noting the amount of area covered on a grided slide or petri dish.

Since the taxonomically identifiable characters of the finely masticated food items are not subject to digestive breakdown (pollen exine patterns, scleroids, chitin patterns), guano sampling proves the more efficient means of handling dietary analyses. Stomach contents are less condensed, and such a technique runs the risk of sacrificing gravid bats or bats with empty stomachs. FLEMING, HOOPER and WILSON (7) indicate that they obtained "disappointingly little information" since 80% of the 2,176 Panamanian bats they killed had empty stomachs.

In addition to the above techniques, swabs were taken of bats' fur using bits of jelly made from Knox gelatin and safranin O. The bits were passed over the bats with a forceps, placed between glass slides and coverslips and held over an alcohol flame. This procedure stained and mounted any pollen grains or moth scales adhering to the fur.

To reduce bias, nets were placed from ground level to approximately 80 feet in the air (HUMPHREY, BRIDGE and LOVEJOY, 10) and checked frequently throughout the night.

## RESULTS AND DISCUSSION

Data on preferred foods of the family Noctilionidae in Costa Rica are shown in Table 1. Although the sample size is small, several interesting items may be noted. FLEMING, HOOPER and WILSON (7) indicated that the *N. labialis* they sampled were entirely insectivorous, as did DUKE in his mammalian dietary (5). Both of these works stated that *N. leporinus* consumed both fish and insects. Our data show *N. labialis* feeding on plant material and insects. During the peak fruiting of the moraceous tree *Brosimum*, several bats appeared to feed entirely from this source. DOBSON (4) indicated that this species consumed fruit in addition to other foods. He described specimens from British Guiana whose stomachs contained seeds from the berry *Morus*. The difference in diets seen in our specimens and those of FLEMING, HOOPER and WILSON (7) may represent seasonal differences. Dates of capture for their *Noctilio* are not given.

TABLE 1

*Food habits of Costa Rican Noctilionid bats (Noctilionidae)\**

Species	Date (1971)	Location	N	Food
<i>Noctilio labialis</i>	April	Taboga	2	Mixed <i>Ceiba</i> (Bombacaceae) pollen and Lepidoptera 1 Fish parts and scales 1
	June	Taboga	4	<i>Brosimum</i> (Moraceae) 3 Mixed <i>Brosimum</i> and unknown insect 1
<i>Noctilio leporinus</i>	April	Taboga	2	Fish parts and scales 2

\* N—Total specimens examined. Numbers following food indicate specimens feeding on the item.

VILLA (19), in giving general characteristics of the family said the bats are ichthyophagous but would also eat insects and fruit. Speaking of *N. leporinus* he said "We saw them use the interfemoral membrane to trap moths which evidently constitute a major volume of their diet".

*N. leporinus* is evidently not alone in his piscivorous habits. One specimen of the smaller congener from Taboga also contained fish scales. This is not entirely surprising since it is postulated that the fishing habit developed historically from insectivory (picking insects off water surfaces). The separation of piscivory and insectivory is also incomplete in *Myotis daubentoni* (BROSSET and DEBOUTVILLE, 2). Further work on the particular types of insects fed upon by the smaller species, or field observations of their hunting strategies might reveal a relationship with bodies of water.

Table 2 provides data for the mormoopid bats. The family was primarily insectivorous during the months sampled. One individual captured had been feeding on plant material however. *Pteronotus parnellii* strongly preferred beetles and moths in both localities. Beetles were not included in the diets of *P. davyi* or *P. suapurensis*, although the latter genus ingests moths. There is a suggestion of food partitioning between *P. parnellii* and *P. suapurensis* on the Osa peninsula in May, with the former preferring Coleoptera and Lepidoptera, and Orthoptera the latter.

TABLE 2

*Food habits of Costa Rican Mormoopid bats (Mormoopidae)*

Species	Date (1971)	Location	N	Food
<i>Pteronotus parnellii</i>	May	San Vito	2	Mixed Coleoptera (40%), Lepidoptera (30%), Diptera, Acrididae 2
	May	Osa	2	Mixed Coleoptera (40%), Lepidoptera (20%), Hymenoptera, Diptera, Acrididae 2
<i>Pteronotus davyi</i>	June	Taboga	1	Lepidoptera 1
<i>Pteronotus suapurensis</i>	May	Osa	4	Orthoptera 3 Mixed fruit, Lepidoptera, Legume pollen 1
	June	Taboga	2	Lepidoptera 2

VILLA (19) found that Mantidae and Acrididae were ingested by the genus *Pteronotus* but said "It is unknown whether they compete with other insectivorous bats... or whether they prefer some special type of insect". Echolocation parameters and auditory tuning for different species within the genus are quite distinct (J. Simmons, personal communication; POLLACK and HENSON, 15) and may possibly reflect different hunting strategies. Likewise, body weights and rostral measurements of the large species may be several times greater than those of smaller forms such as *P. psilotus* and may parallel dietary specialization.

Phyllostomatid subfamilies and their preferred food items are presented in Table 3. Among the phyllostomatines, 3 species of the genus *Micronycteris* were insectivorous and 1 frugivorous. Sample sizes are too small to allow generalization. FLEMING, HOOPER and WILSON (7) stated that *Micronycteris* in their sample were insectivorous. WILSON (20) found a seasonal change from insects to fruit in the diet of *M. hirsuta*. GOODWIN and GREENHALL (8) reported a mixed diet for *M. brachyotis* as well. These authors indicated that *Lonchorhina aurita* from Trinidad were exclusively insectivorous. The individual examined in this study did not differ from their data. Goodwin and Greenhall called *Trachops cirrhosus* the "lizard-eating bat" because of the remains of a gecko found in the stomach of one bat. The four Costa Rican individuals in our sample fed heavily on moths. The bat hair that comprised the rest of the stomach contents seemed too abundant to have been ingested during grooming. It is possible that *Trachops* were preying on other bats, but no flesh or bones were found in the guts.

The two *Tonatia sylvicola* were associated with plants in April. GOODWIN and GREENHALL (8) listed a fruit diet for other species in the genus *Tonatia*, but did not report on *T. sylvicola*.

Although McNAB (13) reported the entire genus *Phyllostomus* as feeding on meat and fruit, and placed *P. discolor* in the "carnivorous" cell of his niche matrix (14), our data of *P. discolor* show no evidence of carnivory. GOODWIN and GREENHALL (8) stated that the species "is a fruit-eating bat... it will not eat flesh...". It is conceivable that McNab had a different temporal sample. The *P. discolor* we investigated showed mixed feeding, consuming fruit and insects.

The larger species in the genus, *P. bastatus*, likewise ate fruit and insects. *Cecropia* (Moraceae) and *Piper* (Piperaceae) were favored fruits. The former was never found in materials taken from the smaller species. Both species took large numbers of Coleoptera, though it was not determined whether there was finer partitioning of this insect order between the two bats. Although many sources have related carnivorous habits of *P. bastatus* (ALLEN, 1; PRAKASH, 16; GOODWIN and GREENHALL, 8), no evidence of vertebrate items was found in our specimens.

Individuals of the genus *Phyllostomus* were often found with mixed materials in the stomach or guano. This was not a common phenomenon in other bats. Whereas the total sample of another species might indicate a mixed diet for the species, individuals usually contained a single food item.

In April in Taboga, one *Vampyrum spectrum* female was netted. The bat had apparently not fed the night of its capture. During two months in captivity this single specimen ate 3 *Vampyrops helleri*, 10 *Sturnira lilium*, 7 *Glossophaga soricina*, 2 *Vampyressa pusilla*, 5 *Carollia castanea*, 20 *Carollia perspicillata*, 1 white tailed pigeon, 1 ruddy ground dove and 10 variable seedeaters. The bat devoured her prey in a stereotyped fashion, clipping off and expelling the wings and head. She was often released in a large room to fly and feed on

TABLE 3

*Food habits of Costa Rican Phyllostomid bats (Phyllostomatidae)*

Species	Date	Location	N	Food
	1971			
Subfamily Phyllostomatinae				
<i>Micronycteris brachyotis</i>	May	Osa	1	Mixed Hymenoptera, Coleoptera, unknown insect 1
<i>Micronycteris hirsuta</i>	May	San Vito	1	Lepidoptera 1
<i>Micronycteris megalotis</i>	June	Taboga	1	Unknown green fruit 1
<i>Micronycteris schmidtorum</i>	May	Osa	2	Lepidoptera 2
<i>Lonchorhina aurita</i>	May	San Vito	1	Lepidoptera 1
<i>Trachops cirrhosus</i>	April	Taboga	2	Mixed Lepidoptera and bat hair 2
	May	Osa	2	Mixed Lepidoptera and bat hair 2
<i>Tonatia sylvicola</i>	April	Taboga	2	<i>Stemmadenia</i> (Apocynaceae) 1 Legume pollen and unknown 1
<i>Phyllostomus discolor</i>	April	Taboga	5	<i>Hymenaea</i> (Leguminosae) pollen 2 <i>Ceiba</i> (Bombacaceae) pollen 1 Mixed Coleoptera and Hymenoptera 2
	May	San Vito	6	<i>Piper</i> (Piperaceae) 1 <i>Acnistus</i> (Solanaceae) 1 Unknown fruit 1 Coleoptera 1 Mixed <i>Piper</i> and Diptera 1 Mixed Hymenoptera, Lepidoptera, and Banana 1
	May	Osa	1	Plant material with vessels (pedicel or young fruit) 1
<i>Phyllostomus hastatus</i>	May	San Vito	5	<i>Cecropia</i> (Moraceae) 2 Mixed <i>Piper</i> and Coleoptera 1 Mixed <i>Piper</i> and Diptera 1 Coleoptera 1
	May	Osa	8	<i>Cecropia</i> 1 Coleoptera 1 Unknown insect 1 Mixed <i>Cecropia</i> and Lepidoptera 2 Mixed Hemiptera and Lepidoptera 1 Mixed Coleoptera and Culicidae 1
Subfamily Glossophaginae				
<i>Glossophaga commissarisi</i>	May	San Vito	5	Lepidoptera 2 Nectar and <i>Musa</i> (Musaceae) pollen 1 <i>Acnistus</i> 2
	May	Osa	2	Lepidoptera 1 Nectar and <i>Mucuna</i> (Leguminosae) pollen 1

TABLE 3 (cont.)

Species	Date (1971)	Location	N	Food		
<i>Glossophaga soricina</i>	April	Taboga	8	Lepidoptera 3 <i>Muntingia</i> (Elaeocarpaceae) 1 Nectar and <i>Inga</i> (Leguminosae) pollen 2 Nectar and <i>Hymenaea</i> pollen 1 Nectar and bombacaceous pollen 1		
	May	Osa	13	Lepidoptera 10 Nectar and <i>Musa</i> pollen 3		
	May	San Vito	30	Lepidoptera 11 Nectar and <i>Mucuna</i> pollen 5 Nectar and <i>Pitcairnia</i> (Bromeliaceae) pollen 1 <b>Banana</b> 1 <b>Acnistus</b> 12		
	June	Taboga	11	<i>Muntingia</i> 2 Melastomaceous fruit 1 Unknown fruit 1 Nectar and <i>Crescentia</i> (Bombacaceae) pollen 7		
<i>Lonchophylla concava</i>	May	San Vito	2	Nectar and <i>Mucuna</i> pollen 1 Lepidoptera 1		
	May	Osa	4	Nectar and <i>Musa</i> pollen 2 Lepidoptera 2		
<i>Lonchophylla robusta</i>	May	San Vito	1	Lepidoptera 1		
	May	Osa	2	Mixed Lepidoptera and Streblidae 1 Mixed Lepidoptera and Coleoptera 1		
<i>Anoura cultrata</i>	May	San Vito	5	Lepidoptera 5		
<i>Anoura geoffroyi</i>	May	San Vito	1	Lepidoptera 1		
<i>Hylonycteris underwoodi</i>	May	San Vito	1	Lepidoptera 1		
Subfamily Carollinae						
<i>Carollia castanea</i>	May	Osa	8	<i>Piper auritum</i> 3 Other <i>Piper</i> 5		
	April	Taboga	14	<i>Piper</i> 7 <i>Cecropia</i> 4 <i>Heisteria</i> (Olacaceae) 1 Coleoptera 1 <i>Licania</i> (Chrysobalanaceae) 1		
May				Osa	8	<i>Cecropia</i> 5 <i>Piper</i> 2 Unknown insect 1
May				San Vito	6	<i>Piper</i> 4 Large-seeded solanaceous fruit 1 <i>Acnistus</i> 1
June				Taboga	7	<i>Solanum</i> 4 <i>Piper</i> 1 <i>Mangifera</i> (Anacardiaceae) 2

TABLE 3 (cont.)

Species	Date (1971)	Location	N	Food
Subfamily Sturnirinae				
<i>Sturnira lilium</i>	April	Taboga	13	<i>Piper</i> 3 Melastomaceous fruit 2 Large-seeded solanaceous fruit 2 <i>Licania</i> 2 <i>Muntingia</i> 2 <i>Ceiba</i> pollen 1 Mixed <i>Muntingia</i> , <i>Licania</i> , Lepidoptera 1
	May	San Vito	10	<i>Acnistus</i> 10
	June	Taboga	2	<i>Solanum</i> (Solanaceae) 2
<i>Sturnira mordax</i>	May	San Vito	10	<i>Ceotropogon</i> (Campanulaceae) 3 <i>Anthurium</i> (Araceae) 1 Banana 1 <i>Cecropia</i> 2 Unknown fruit 3
<i>Sturnira ludovici</i>	May	San Vito	1	Unknown fruit 1
Subfamily Stenodermatinae				
<i>Vampyrops helleri</i>	May	San Vito	10	<i>Acnistus</i> 8 Mixed <i>Cecropia</i> and Lepidoptera 2
<i>Vampyrops vittatus</i>	May	San Vito	2	<i>Cecropia</i> 1 <i>Acnistus</i> 1
<i>Uroderma bilobatum</i>	April	Taboga	1	Unknown green fruit 1
	June	Taboga	1	<i>Brosimum</i> 1
<i>Artibeus jamaicensis</i>	April	Taboga	10	<i>Licania</i> 3 <i>Genipa</i> (Rubiaceae) 1 <i>Muntingia</i> 2 <i>Hymenaea</i> pollen 2 <i>Ceiba</i> pollen 1 <i>Bombax</i> (Bombacaceae) pollen 1
	May	San Vito	1	Melastomaceous fruit 1
	June	Taboga	30	<i>Brosimum</i> 24 <i>Ficus</i> (Moraceae) 2 <i>Cecropia</i> 1 Unknown fruit 2 Mixed Coleoptera and unknown fruit 1
<i>Artibeus lituratus</i>	May	San Vito	1	Large-seeded <i>Piper</i> 1
<i>Artibeus watsoni</i>	May	Osa	2	<i>Cecropia</i> 2
<i>Artibeus toltecus</i>	May	San Vito	6	<i>Cecropia</i> 6
Small <i>Artibeus</i> sp.	May	San Vito	6	<i>Cecropia</i> 6
<i>Vampyressa pusilla</i>	May	San Vito	5	<i>Acnistus</i> 5

smaller bats released for the purpose. We noted with interest the apparent unsophistication of the smaller species with regard to their predator. Often the small bats would alight next to the *Vampyrum* and seek to cluster with her. They were promptly swept up in her wings and disposed of in the usual manner. Bananas and other fruits were offered to the *V. spectrum* for the duration of her captivity and always rejected. VILLA (19) assigns primarily frugivorous tendencies to this species.

Within the subfamily Glossophaginae the bats did not act in strict accord with previous notions. It has been commonly supposed that all the genera in the group feed primarily on nectar (1, 19). Table 3 indicates that the genus *Glossophaga*, a less specialized member of the subfamily, fed upon insects in addition to nectar and pollen. In all cases the insects eaten were Lepidoptera. Several bats of both species (*G. commissarisi* and *G. soricina*) had the dorso-caudal region of the body covered with *Mucuna* pollen (Leguminosae). Herbert Baker (personal communication) suggests that the bat throws itself off the flowers in a backwards flip to take flight and thus gets the tail region coated with pollen. When *Musa* pollen was seen on bat fur it was always most concentrated on the neck and head.

Many of the San Vito phyllostomatids, including *Glossophaga*, fed heavily upon the small fruits of the solanaceous tree *Acnistus*. A grove of these trees was cultivated at the finca of Robert Wilson and was probably the source of this fruit for many opportunistic vertebrates.

The small sample size of *G. commissarisi* does not permit a partitioning comparison with the congener. What can be seen from the *Glossophaga* data is that *G. soricina* switched from a mixed insect-plant material diet to one more strictly associated with plants as the rainy season began.

The two species of *Lonchophylla* distinguished themselves in that *L. concava* ate a mixed insect-nectar and pollen diet whereas *L. robusta* ate only insects. Although moths were again preferred items, this bat took some beetles.

*Anoura cultrata* and *A. geoffroyi* fed solely on moths during the one month in which they were captured, as did one of the two *Hylonycteris*.

The high percentage of Lepidoptera in the diets of the glossophagine "nectar bats", found as well by FLEMING, HOOPER and WILSON (7), is very interesting and indicates the need for work in other months at other localities on the diets and energy budgets of these bats. Recent work on pollinating bats (HOWELL, 9) indicates that the syndrome of chiropterophily is more closely adhered to in areas where broad food sources may be less abundant and competition may be more severe (subtropical or temperate zones).

Three of the glossophagine genera studied here are, in terms of dentition, relatively less specialized members of the subfamily. *Glossophaga*, *Anoura*, and *Lonchophylla* reflect the primitive insectivorous condition by retaining a greater number of teeth and showing more of the W ectoloph pattern than do other more specialized glossophagines. *Leptoncyteris*, *Choeronycteris* and *Musonycteris*

appear more adapted to a nectar diet by diminution of teeth and elongation of the rostrum. The latter bats have been found rarely, if ever, in Costa Rica, but do occur commonly (with the exception of *Musonycteris*) farther north into Arizona.

Bats of the genus *Carollia* which we studied in Costa Rica showed a more dramatic food preference than other genera. Over 50% of the bats examined showed evidence of a diet of pure *Piper* (Piperaceae). All individuals of *C. castanea* fed on this plant. *C. perspicillata* included other fruits and some insects in their diet but also relied heavily on *Piper*. Extensive stands of this plant were in evidence at all localities. A growth form whereby the fruits are exerted from the main vegetative area is similar to that in the chiropterochorous plants discussed by VAN DER PIJL (18). An ultrasonic "bat detector" aimed above the canopy of *Piper*, level with the exerted fruit spikes revealed a veritable din of chirps every night.

TABLE 4

*Food habits of Costa Rican Thyropterid bats (Thyropteridae)*

Species	Date (1971)	Location	N	Food
<i>Thyroptera tricolor</i>	May	Osa	1	Lepidoptera 1

We sampled 28 species of tropical bats commonly reported to be frugivorous. Of these, only a few include *Piper* in their diet. Generic partitioning between frugivorous bats is evidenced not so much by the utilization of discrete food items as by different curve "convexity" on the scale of possible food items. There is reason to believe *C. castanea* and *C. perspicillata* show specific food partitioning at least in the three months sampled. The one species relies solely on *Piper*, the other on a mixed diet, with *Cecropia* playing an important role.

*Cecropia*, another plant whose growth form and fruiting pattern indicate chiropterochory, was also fed upon by *Vampyrops* and *Artibeus*. The site bias for cultivated *Acnistus* which is evident for many San Vito bats may have obscured any partitioning that could be seen among the phyllostomatids captured there. It should be pointed out, however, that not all the frugivores taken at San Vito fed on the abundant *Acnistus* fruits. No bats of the common genus *Artibeus* ate it, yet all individuals of *Vampyressa pusilla* and *Sturnira lilium* from San Vito ate entirely *Acnistus*. Although it is risky to talk about specific diet partitioning when including a semi-artificial food source, it is notable that another species of *Sturnira*, *S. mordax*, never ate *Acnistus*. Sample sizes for the two species were equal.

Among the families Thyropteridae, Vespertilionidae and Molossidae (Tables 4-6) there is little specialization seen. It is entirely possible that a finer breakdown of insect taxonomic units or a bat-insect stratification study would

bring partitioning to light. Stereoscan photos of an insect reference collection compared with photos of guano from captive bats offered these insects give clearly useful data (FENTON, COUTTS, and WORREL, 6) and suggest a technique whereby partitioning may be studied in the field.

TABLE 5

*Food habits of Costa Rican Vespertilionid bats (Vespertilionidae)*

Species	Date (1971)	Location	N	Food
<i>Myotis nigricans</i>	May	Osa	1	Lepidoptera 1
<i>Myotis</i> sp.	May	Osa	3	Coleoptera 1 Orthoptera 1 Mixed Coleoptera, Lepidoptera, Diptera 1
<i>Rhogeessa tumida</i>	April	Taboga	1	Mixed Lepidoptera, Coleoptera <i>Piper</i> 1
	June	Taboga	3	Coleoptera 1 Mixed Lepidoptera, Coleoptera, Orthoptera 1 Mixed Hymenoptera, Lepidoptera, Coleoptera 1
<i>Eptesicus andinus</i>	May	Osa	2	Lepidoptera 1 Mixed Lepidoptera, Coleoptera 1

Because only a light microscope was available to the authors, insects could be identified no further than order or family. The only trend apparent with this technique was the molossid exclusion of Lepidoptera which was in direct contrast with other insectivores.

TABLE 6

*Food habits of Costa Rican Molossid bats (Molossidae)*

Species	Date (1971)	Location	N	Food
<i>Molossus ater</i>	May	Osa	1	Mixed Coleoptera, Orthoptera, Hymenoptera 1
<i>Molossus major</i>	April	Taboga	1	Coleoptera 1
	June	Taboga	9	Coleoptera 8 Diptera 1

## CONCLUSIONS

These data suggest that certain bats of a particular dietary category (frugivory, insectivory, nectarivory, etc.) may concentrate on selected food items differing from those fed upon by related bats.

This is not to say that each bat taxon chooses a singular and discrete taxon of plant or insect, but rather that food sources are a continuum and many bat genera appear to concentrate upon certain items along this continuum, paying little or no attention to others. This selection should be seen as a permutation of a normal curve, where the particular degree of skew for one bat contrasted to that of another, indicates partitioning.

Of course, there are data here that show no distinction in the diets of related bats, but until more thorough studies have been done, this cannot be taken to mean the bats do not partition. Large dietary groupings such as fruit or insects which have been used by others to conclude no niche specificity have been broken down into finer units here and seem to indicate some specificity. The same can be expected in future work which will analyze our categories more thoroughly, for instance breaking down the orders of insects or the genera of fruit. ALLEN (1) cites a number of older studies on Old World Chiroptera which indicate that bats had preyed upon certain types of insects that were not particularly numerous in the local fauna, to the exclusion of more common types.

Using gross food categories, even combined with measurements of bat forearms or rostrum to construct niche matrices can only shelter future studies from rigorous thought. HUTCHINSON (11) introduced ratios of feeding apparatus only as an objective measure of difference between similar species, and indicated that, in themselves, they were not a measure of specialization. The phenomenon of the lessening of these ratios in the tropics, found by KLOPFER and MACARTHUR (12) for birds and by TAMSITT (17) for bats, does not in itself indicate lack of feeding specialization. For instance, the range of the forearm lengths for *Carollia castanea*, *C. perspicillata*, *Artibeus toltecus* and *Sturnira lilium* could well place all these bats in a single category of FLEMING, HOOPER and WILSON (7)—they all eat fruit. Yet they do appear to partition in terms of the convexity of their choices.

To reiterate, competition can scarcely be understood without a good look at the things for which bats are competing. If, after a thorough study of bat diets, it appears that certain taxa exhibit overlap, we must bring together information on microhabitat requirements, height stratification, and temporal patterns before conclusions are drawn. Assigning numbers to speculations of what bats are supposed to do can only result in misinformation about the efficiency of natural selection.

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