THERMOREGULATION

JOHN J. MCNAMUS

There is a substantial literature on mammalian thermoregulation, and several comprehensive reviews are available for different orders of mammals (Whittow, 1971). Excellent surveys of existing literature on temperature regulation in bats were prepared by Stotes and Wiebers (1965), McNab (1969), and Lyman (1970) and these should be consulted for general coverage of the Chiroptera. Also, because many species of bats enter torpor, the order is frequently discussed in context with the evolution and adaptive significance of heterothermy (Hudson, 1973; Whittow, 1973). Most earlier papers on bat metabolism and thermoregulation dealt with temperate zone microchiropterans (Hock, 1951; Reeder and Cowles, 1951) or tropical megachiropterans (Burbank and Young, 1934; Bartholomew et al., 1964). A rough pattern emerged from these studies, which contrasted the relatively precise homeothermy achieved by the large, frugivorous megachiropterans with the pronounced thermolability and capacity for torpor shown by the smaller, insectivorous species that inhabit areas with more rigorous thermal environments. Within the past decade, many additional species of tropical microchiropterans have been examined. Most of these have proved to be intermediate in their temperature regulation and, collectively, they illustrate the continuum of thermoregulatory strategies that exists within the order Chiroptera. These recent works include data on temperature relation in more than two dozen members of the Phyllostomatidae, and the scope of this chapter will be restricted principally to a summary of this information. Some attempt will be made to place what is known of thermoregulation in phyllostomatids in evolutionary perspective and to suggest possible directions for future studies on New World leaf-nosed bats.

STATUS OF THERMOREGULATION BY PHYLLOSTOMATIDS

Problems of Measurement

Even the most casual survey of the literature indicates that within the Chiroptera there is an extraordinarily wide variation in the quality of temperature control. This variability makes generalizations regarding thermoregulatory strategy difficult and forces a careful analysis of the sources that contribute to wide differences in results, even at the species level. Lyman (1970) has enumerated some of the more important factors that should be considered in assessing temperature regulation in bats: 1) phylogenetic antiquity of the order; 2) high species diversity; 3) broad geographic distribution; 4) wide differences in habitat preference, feeding habits, and daily and seasonal levels of activity; 5) preponderance of smaller size classes; 6) high surface area to volume ratios; 7) capacity for energetically costly sustained flight; and 8) peculiarities of behavior and habitat requirements in the wild that often make it difficult to simulate ecologically realistic
conditions for testing the thermoregulatory capacity of captive animals. Thus, it is not surprising that various investigators have employed quite different methods and criteria for assessing temperature control in bats. All of the above constraints apply to the literature of the Phyllostomidae and these should be noted when the following comparisons are made. A tabular summary of recent work on phyllostomatid thermoregulation is given (Table 1).

**Effect of Body Weight on Basal Heat Production**

In general, maintenance of a differential between body temperature and reduced ambient temperatures requires the generation of metabolic heat at levels just equal to the rate at which heat is lost from the body. Because heat production occurs within the volume of the body and heat loss is primarily a surface phenomenon, the ratio between surface area and body volume is important in establishing the level at which heat production and heat loss are balanced. Smaller animals, in which the surface area is high in relation to body mass, will have proportionally higher rates of heat loss and heat production than would be found in larger species. The predictive relationship between weight-specific metabolic rate (heat production per unit weight per unit time) and body weight takes the general form $M = kW^b$, where $M$ is weight specific heat production, $W$ is body weight, and $k$ and $b$ are constants. When heat production for many species of mammals at thermoneutrality is calculated as milliliters of oxygen per gram per hour ($ml.\ 0_2g/hr$), the constants $k$ and $b$ take the values 3.8 and -0.27, such that $M = 3.8W^{-0.27}$ (Brody, 1945; Kleiber, 1961).

McNab (1969) compared the basal metabolic rates of 23 species of New World leaf-nosed bats to the rates predicted for mammals within the weight range of nine to 97 grams (Fig. 1). As in other bats, the basal metabolic rates of phyllostomids are inversely related to body size, and, for most species, the measured rates of heat production tend to be higher than those predicted by body weight. This is expected in view of the high surface area to volume relations caused by the presence of wings, large ears, and associated membranes.

The level at which body temperature is maintained is dependent on the ratio of heat production to heat loss and appears to be weight dependent (McNab, 1969, 1970). Smaller species of bats tend to have lower body temperatures than do larger species and this generalization seems to hold true for those phyllostomids for which body temperatures have been recorded (Fig. 2). It is obvious, however, that smaller species of leaf-nosed bats show considerable variation in resting body temperatures and in many instances it is not clear whether this is the result of species differences or a reflection of such confounding variables as differences in physiological state, nutritional status, activity level, or methods of body temperature measurement (Lyman, 1970; Studier and Wilson, 1970). Nevertheless, because heat loss depends directly on the differential between internal and external temperature, even slight reductions in the set-point temperature by smaller phyllostomatids are advantageous in that they decrease the levels at which heat must be produced for maintenance of homeothermy.
Effect of Diet on Basal Heat Production

Phyllostomatids can be placed in categories based on their feeding habits—fruit and nectar feeders, larger carnivorous feeders, insect feeders, and blood feeders (McNab, 1969, 1970). Excepting the sanguivores and perhaps some of the most specialized nectar feeders, it is likely that insects are taken to varying degrees by all leaf-nosed bats, but the preceding categories will be used as approximate indices of the bulk of the diet.

*Frugivorous.*—The leaf-nosed bats as a group are principally fruit eaters and this dietary commodity apparently has exerted a strong influence on temperature regulation in the family. McNab (1969) argued persuasively the notion, that seasonal availability of fruit and nectar in Neotropical areas has allowed frugivorous phyllostomatids the luxury of elevated metabolic rates (Fig. 1) and has made nonessential the diurnal and seasonal torpor characteristic of temperate-zone insect feeders, the food supply of which is subject to severe daily and seasonal fluctuation. Arata and Jones (1967) posed a similar hypothesis and extended the reasoning to include tropical insect feeders. Despite a high degree of variation, resting body temperatures of frugivorous leaf-nosed bats (Fig. 2) tend to be held at relatively high levels, approximately 5 to 10°C higher than those of insectivorous species of comparable size (McNab, 1969: fig. 31; Lyman, 1970: table 1). It seems reasonable that this could be achieved only if energy sources were readily available to support the high levels of heat generation needed for such homeothermy.

*Carnivorous.*—The meat-eating phyllostomatids (*Toniatta bidens, Phyllostomus discolor, P. hastatus, P. elongatus, Chrotoperus auritus*) appear to approximate or slightly exceed the basal metabolic rates predicted by weight. They also are among the largest of the phyllostomatids. Practically nothing is known about the diet of carnivorous bats in the wild, but I presume that vertebrates comprise its bulk. Considering the relative stability of vertebrate populations in tropical areas, compared to the more pronounced fluctuations in abundance and availability of populations in temperate zones, one can speculate that larger carnivorous phyllostomatids have adjusted their energy expenditures in response to food reserves that remain relatively fixed in supply throughout the year. Availability of food and large body size contribute to their fairly precise control of body temperature. However, the carnivorous species of leaf-nosed bats apparently depend on food supplies that, while temporarily available, may be spatially distributed in a way that cannot support second-level consumers. McNab (1971) observed that carnivorous species are the first to disappear from bat faunas on tropical islands with depauperate vertebrate communities.

*Insectivorous.*—Although Arata and Jones (1967) postulated that tropical insect feeders may resemble fruit and nectar feeders in thermal ecology, McNab's (1969) study suggested that they are quite different. Tropical insect feeders more closely resemble temperate zone taxa in their proclivity to relax thermoregulatory control when at rest and in their tendency to have lower basal metabolic rates. This apparently results from the fact that insectivorous species tend generally to be smaller and gain considerable metabolic savings by reducing body temperature-
ambient temperature differentials. In addition, for many tropical areas, the presumption of a constant level of availability of insect foods is unfounded; tropical insect populations may respond seasonally to rainfall in a fashion similar to the response of temperate zone insects to seasonal temperature changes (Janzen and Schoener, 1968). Thus, tropical insect feeders do not utilize a dietary item in constant supply and cannot afford the luxury of the elevated metabolic rates seen in frugivorous species. Of the phylllostomatids studied, metabolic data are available for only one insectivorous species, *Tonatia sylvicola* (Fig. 1). It appears to conform to the pattern seen in other tropical insect feeders.

*Sanguivorous.*—Because of their unique feeding habits, vampire bats have attracted the attention of several investigators, and details of the thermoregulation and bioenergetics of one species, *Desmodus rotundus*, are as well known as for any bat. Early observations (Wimsatt, 1962) indicated that despite its moderate size (30 grams), *Desmodus rotundus* was surprisingly ineffective at controlling body temperature. At rest, body temperatures of vampire bats fell close to ambient temperatures (even at environmental temperatures as high as 33°C, Lyman and Wimsatt, 1966), and responses of individuals to reduced ambient temperatures varied markedly. McNab (1969, 1973) provided data for *Diademus youngii* and *Diphylla ecaudata*, as well as for *Desmodus rotundus*, and both basal metabolic rates and body temperatures tended to be low in these species (Figs. 1, 2).

The effect of diet on the thermal economy of desmodontines was considered extensively by McNab (1969, 1973) and the following is a summary of his findings. The use of mammalian or avian blood by a vampire bat requires transporting all or part of the blood meal in flight. The size of the meal that can be ingested, therefore, is limited by the ability of the bat to carry it back to the roost (Crespo et al., 1970). Furthermore, whole blood has a relatively low caloric density
and, although some concentration of the meal may occur prior to flight (by urination while feeding—McFarland and Wimsatt, 1969), vampires appear to be limited by the amount of energy they can acquire and process per foraging flight. Such limitations on energy intake would presumably be most severe for females near the end of pregnancy when load-lifting capacity is lowered and absolute energy needs are greatest. The conclusion drawn, then, is that the type of food employed by vampire bats forces them to conserve energy at times other than flight by relaxing control of body temperature while at rest and by sustaining relatively lowered rates of basal metabolism.

Resistance to Hyperthermia

With the exception of a few species, high temperature tolerance has not been studied systematically in leaf-nosed bats. The temperate zone species *Macrotus californicus* responded to increasing ambient temperatures (*T*<sub>a</sub>) by initiating a series of slow wing-flapping movements when body temperature (*T*<sub>b</sub>) reached 32.6°C (Reeder and Cowles, 1951). At *T*<sub>b</sub> 34.7°C, wing movements increased in frequency and at *T*<sub>b</sub> 38.7°C constant fanning occurred; after 26 minutes, *T*<sub>b</sub> was held at 39.0°C in a *T*<sub>a</sub> of 40.6°C. Wimsatt (1962) reported *Desmodus rotundus* to have surprisingly little tolerance of even moderately high air temperatures and suggested that the critical tolerance level was within the *T*<sub>a</sub> range of 27 to 30°C. In controlled experiments, Lyman and Wimsatt (1966) found this same species unable to tolerate *T*<sub>a</sub> s of 33 to 34°C for more than two hours. No wing fanning or salivation responses were noted.

Unpublished observations (McManus and Nellis) on *Artibeus jamaicensis* indicated that individuals of this species can tolerate *T*<sub>a</sub> 40°C for up to five
TABLE 1.—Thermoregulation data for various phyllostomatid bats. $M_b$ is basal metabolic rate expressed as ml. O$_2$/g/hr. $C$ is thermal conductance given as ml. O$_2$/g/hr/°C. All temperatures are in degrees centigrade.

<table>
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<th>Weight in g (N)</th>
<th>$T_b$</th>
<th>$M_b$</th>
<th>$C$</th>
<th>$T_a 20^\circ$</th>
<th>$T_a 15^\circ$</th>
<th>$T_a 10^\circ$</th>
<th>Upper $T_b$</th>
<th>Lower $T_a$</th>
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<th>Remarks</th>
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*Where weights were not given they were taken from Walker et al. (1968).

**Tb rounded to the nearest 0.5°C; most were read from graphs.

hours, but die within two hours at $T_a$ 45°. Lethal body temperature is near 43°C. Carpenter and Graham (1967) found that $A. hirsutus$ begins panting vigorously at $T_a$ 38°C and suggested that these bats probably cannot survive higher ambient temperatures. The same authors reported that $Leptonycteris sanborni$ maintained a body temperature between 39.2 and 41.5°C after a four-hour exposure to 41.5°. Although $Leptonycteris$ was quite efficient at resisting hyperthermia, no conspicuous thermoregulatory behaviors such as wing fanning or salivation occurred. The lethal body temperatures listed in Table 1 usually were recorded after accidental deaths during oxygen uptake tests. Collectively, they resemble those of other mammals, although lethal $T_b$ values for $Carollia perspicillata$ and $Rhinophylla pumilio$ are suspect because death probably resulted from causes other than hyperthermia. Levels of ambient temperature tolerated by phyllostomatids tend to be high, but not exceptional. This probably reflects the moderating nature of most roost sites and the nocturnal habits of the animals.

**Resistance to Hypothermia**

As a rule, leaf-nosed bats show little tendency to experience large reductions in body temperature when exposed to low ambient temperatures for short periods (Table 1). As exposure time increases, however, body temperatures vary erratically, particularly at ambient temperatures outside the normal range of temperature encountered in the wild. Additionally, the length of time between capture and testing appears to confuse the issue (McNab, 1969; Studier and Wilson, 1970) and nutritional status undoubtedly influences the magnitude of $T_b-T_a$ differentials sustained. In several species, exposure to low ambient temperatures causes a drop in body temperature, but to some relatively constant level above the ambient temperature. Studier and Wilson (1970) computed regression formulas to describe the relation between $T_b$ and $T_a$ for two species at various ambient temperatures. Between $T_a$ 33.2 and 8.0°C, $Artibeus jamaicensis$ gave the response $T_b = 8.8 + 0.9333 \ T_a$ whereas between $T_a$ 33.1 and 7.8°C, $Vampyromes caracoloi$ showed $T_b = 12.0 + 0.813 \ T_a$. McNab and Nelis (1972) found $A. jamaicensis$ able to maintain $T_b$ above 35° after six hours at 10°C and one individual was able to keep $T_b$ above 18° for at least 14 hours at 10°.

$Brachyphylla cavernarum$ held $T_b$ above 25° after 24 hours at 10°. There are no known species of phyllostomatids that naturally enter deep torpor—even those species, such as $Macroptychus californicus$ or $Leptonycteris sanborni$, which are native to, or regularly enter, temperate areas, Carpenter and Graham (1967) observed that $Leptonycteris sanborni$ and $Artibeus hirsutus$ were able to regulate body temperature within levels of precision equivalent to those of other small mammals of comparable size, and McNab’s (1969) study extended this pattern to many other species.

An interesting observation made by McNab (1969) on $Phyllostomus discolor$, $Tonatia bidens$, and $Chrotoglossus auritus$ was that these species may show a temporary relaxation of temperature control at moderately reduced ambient temperatures (approximately similar to those of their roost sites), yet are capable
of more effective thermoregulation at lower temperatures. The implication is that temporary hypothermia may be "intentionally" tolerated and serves to decrease the differential between ambient and core temperature. Such a strategy would reduce energy requirements during periods of inactivity and may explain in part the rather pronounced diurnal variation in resting body temperatures noted by Morrison and McNab (1967). Nevertheless, the overriding tendency among the majority of leaf-nosed bats examined is to maintain body temperature at a roughly constant level when exposed to moderately low ambient temperatures. When forced to withstand temperatures well below those normally encountered, responses vary markedly, with larger species tending to conserve body heat more effectively than smaller kinds (Table 1). Compared to temperate zone microchiropterans that regularly enter deep torpor, the lower lethal minima for phyllostomatids appear to be higher by 10°C or more.

Social Thermoregulation

With one exception, the energetic significance of clustering as a means of behavioral thermoregulation has been neglected in New World leaf-nosed bats. In torpid microchiropterans from temperate areas, clustering is regarded as a means of reducing variations in body temperature by decreasing the exposed surface area of any individual in a cluster. In contrast to the result of such behavior in strict homeotherms (Tertil, 1972, and references therein), clustering in hibernating bats is not intended to conserve heat, but rather to keep body temperature low and to avoid temporary increases in ambient temperature (Twente, 1955). Such behavior promotes the most prudent use of stored fats during hibernation by keeping metabolic rate low (Hcck, 1951; McManus and Esher, 1971). Apparently a similar strategy is employed by at least one species of phyllostomatid, Phyllostomus discolor. McNab (1969) found that clustering at 20°C resulted in a drop in both mean body temperature and mean resting metabolic rate of bats in a cluster as compared to that of single individuals. Whether such behavior is widespread among leaf-nosed bats is unknown. Additionally, the object of social thermoregulation in species with more precise thermoregulatory control than P. discolor (see preceding section) may in fact be heat conservation rather than maintenance of reduced body temperatures. Finally, for species of bats that regularly form clusters while roosting, the testing of an individual in a metabolism experiment is an abnormal situation and may contribute greatly to variation in physiological performance. I suspect that this area would yield interesting results with further study.

Torpor

Deep torpor and seasonal hibernation are found only in the families Vespertilionidae, Rhinolophidae, and to a lesser extent in the Molossidae. Viewing this as one extreme condition and precise endothermy as the other, phyllostomatids appear to occupy a broad portion of the spectrum. Hudson (1973) regarded the ability of Neotropical bats to tolerate low body temperatures as "an ancestral phenotype (as well as genotype) which could easily be modified to give the 'deep"
or 'true' hibernator. Under tropical conditions, such a thermoregulatory performance represents a solution for which there is no problem." A similar thesis was advanced by Studier and Wilson (1970) who suggested the possibility that the thermolability of tropical bats may be nonadaptive. Although this may be true for frugivorous and perhaps carnivorous bats, the facultative capacity to experience and tolerate slight reductions in body temperature during periods of inactivity is clearly advantageous for small insect feeders and sanguivores.

CONCLUSIONS

The family Phyllostomidae presents a varied mosaic of thermoregulatory strategies, but the problems of measurement, coupled with natural variation in levels of temperature control among species, make broad generalizations difficult. Perhaps the easiest way to summarize this review is to indicate those parameters that appear to have influenced the development of thermoregulation in leaf-nosed bats.

Body size appears to affect resting rates of metabolism and resistance to hypothermia in much the same way as it does in other mammals. Qualitatively, smaller species have higher basal metabolic rates and poorer temperature control at reduced temperatures than do larger species. Quantitatively, the peculiar surface area to volume ratios unique to bats cause the levels of metabolism to be higher in general than those of other mammals of comparable weight. This disparity is most obvious in small and intermediate-sized phyllostomatids.

Diet and trophic position seem to be of particular importance in determining thermoregulatory performance. First-level consumers feeding on spatially and temporally available foods such as fruits and nectar achieve higher basal rates of metabolism than do most second-level consumers. Carnivorous species have fairly precise thermoregulation, but this is associated with their generally larger body size. Insect feeders and blood feeders, for which food supplies are temporally or logistically limited, or both, seem to have developed either a more relaxed pattern of temperature control or have reduced the set-point at which metabolism proceeds. One glaring insufficiency in our knowledge of thermoregulation in leaf-nosed bats (and most other bats) is the paucity of data on food intake under natural conditions or in the laboratory. Associated with this is the scarcity of field temperatures for bat roost sites upon which any type of bioenergetic analysis must depend.

Social aggregation is suspiciously well developed in several species of leaf-nosed bats and, along with such obvious factors as availability of roost sites and synchronization of reproductive activities, the thermoregulatory significance of such behavior merits investigation. The climatic history of New World leaf-nosed bats during their evolution seems to have allowed considerable latitude in the degree of temperature control. Thermal stresses comparable to those encountered in temperate regions have not been present in sufficient strength to force the development of precise homeothermy, nor have they caused the adoption of "deep torpor" capabilities typical of bats at higher latitudes. One broad generalization that can be made with respect to the family Phyllostomidae is that they are extremely diversified in details of their temperature control.
ACKNOWLEDGMENTS

I am indebted to Diane Ruffino for typing several drafts of this manuscript. Many of the ideas incorporated into this review are based on the studies of Brian McNab, and I urge a perusal of his papers for fuller treatments of several aspects of bat energetics included herein.

LITERATURE CITED


[Editors' note: John J. McManus died on 22 August 1975 without having an opportunity to read galley proofs or correct any errors inadvertently incorporated, or overlooked, in his contribution to this volume.]
FEEDING HABITS

ALFRED L. GARDNER

There is something fascinating about science. One gets such wholesale returns of conjecture out of such a trifling investment of fact.

Mark Twain

With few exceptions, knowledge of bat food habits, like that of many other aspects of chiropteran biology, is superficial or wanting. Nevertheless, the study of bats has occasionally been stimulated because of the interest generated by their unusual or economically important food habits: the sanguineous diets of vampires, flower-feeding habits of glossophagines, and the carnivory of some phyllostomatines.

General knowledge of food habits was used in some of the early classifications of bats. Gray (1821: 299) divided his suborder Chiroptera into two orders, the Frugivora and the Insectivora. Along the same lines, Koch (1866-1868: 298) erected the two suborders Carnophagen and Entomophagen, and Gill (1874, 1886) separated the Chiroptera into the suborders Animalivora and Frugivora (again representing major differences in food habits). In these examples, the Insectivora, Entomophagen, or Animalivora included all of the known forms of the Phyllostomatidae. The Frugivora, Carnophagen, or Frugivora are equivalent to the Old World fruit bats, the Megachiroptera.

Other names applied to members of the Phyllostomatidae reflect known or alleged feeding habits. The generic names Vampyrum, Vampyrus, Vampyrodes, and Vampyressa refer to the alleged blood-feeding habits of vampires. Diemenus means blood-stained, an appropriate name for a true vampire. Glossophaga literally means to eat with the tongue. Lichonycteris means a bat that licks, also in reference to using the tongue when feeding. Musonycteris implies an association with banana plants. The name Anoura werckleae was employed to reflect the feeding relationship of this bat with the plant Wercklea lutea. The trivial name mordax refers to biting (Lonchophylla mordax and Sturnira mordax).

Common names often refer to presumed food habits as well. Some of these are the “Cuban Fruit-eating Bat” (Brachyphylla nana), the “Hairy Fruit-eating Bat” (Artibeus hirsutus), and the “Cuban Flower Bat” (Phyllonycteris poeyi). A few names suggest diets when, in fact, the foods consumed are not known (for instance, the “Red Fig-eating Bat,” Stenoderma rufum; the “Brown Flower Bat,” Erophylla bombifrons).

My principle objective in surveying the food habits of the Phyllostomatidae was to bring together most of the available published information on the diets of these bats in a form that not only will provide an accessible information source, but also will encourage future investigations on this aspect of bat biology. I have reviewed most of the accessible literature with disappointing results. With few exceptions, very little has been recorded on the diets of these animals, and much
of this is superficial and noninformative. The information presented in the species accounts deals almost exclusively with the diets of free-living bats as reported in the literature. A few personal observations on food habits as well as some literature references on foods consumed in captivity have been included when considered pertinent, although the chapter, Care in Captivity, by Greenhall adequately covers the latter subject. Inferences on diets as suggested by dental and alimentary tract anatomy are equally restricted because the chapters, Oral Biology, by Phillips et al., and Gastro-intestinal Morphology, by Forman and Rouk, provide ample information on these aspects as well. The diet for each species follows the scientific name in the food habits accounts below.

Table 1 is a list of those plant genera and species for which parts have been reported as foods consumed by phyllostomatid bats.

PROBLEMS IN DETERMINING FOOD HABITS

If we could observe and record the variety and quantity of foods as they are gathered and consumed by bats, the determination of diets would be a relatively simple matter. Because this usually is not possible, the examination of feces or digestive tract contents would appear to be the next best method. However, the comminuted remains of insects and small vertebrates are usually difficult to identify; a problem intensified by the habit of many bats to discard the harder, and often the only diagnostic, parts of their prey. For example, the abdomens of lepidopterans and other large insects are often the only parts consumed, the other parts being discarded. The taxonomy of many of the insects consumed by bats is little known and reference collections of insects from areas where the bats were collected are usually not available. Therefore, the determination of the insect order or family may be the only identification possible from fecal or stomach contents. Masticated remains of fruits found in stomachs are almost impossible to identify if associated seeds are not present. Seeds found in stomach contents and feces also are difficult to identify, particularly without the aid of a comprehensive reference collection of seeds. Nevertheless, fruits are often emphasized when diets are reported because when seeds are available, they are usually easier to identify than insects. This is especially true when the fruits come from locally conspicuous and well-known plants.

Some items such as seeds, fruit, or bits of sand or gravel found in the stomachs of omnivorous and carnivorous bats can be misleading because they may have been consumed by an animal before it was ingested by the bat itself. Stomach content analyses also can be deceptive if the bats are maintained alive together in small cages or cloth bags subsequent to their capture. Fighting and cannibalism among bats held under these conditions is common, and finding blood or the remains of bats in the stomachs of these bats should not be considered as indicative of normal diets unless, of course, the bats are vampires or species with known carnivorous habits.

Detailed analyses of stomach contents can be very informative. The excellent study by Alvarez and Gonzalez Q. (1970) demonstrated that analyses of the digestive tracts of pollinivorous species not only indicate what flowers are being
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Table 1.—Continued.
TABLE 1.—Continued.

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visited but can provide evidence on the movements of populations, seasonal changes in diets, and competition for the same foods by sympatric species. The recovery and identification of pollen grains from the fur of bats may indicate the flowers visited as well (Heithaus et al., 1975; Howell and Burch, 1974). Analyses of blood meals in the stomachs of vampires have indicated if mammals, birds, or both were the prey (Villa-R. et al., 1969).

When names of the food items of bats are reported (Greenhall, 1956; Goodwin and Greenhall, 1961; Wilson, 1971; Vázquez-Yáñez et al., 1975), they most often are based on identifications of dropped or discarded parts of plants, insects, or vertebrates found associated with bat roosts. Here the problem is to associate the remains with the bats that left them. Correctly associating food remains is difficult if the roost sites where the remains were recovered are used by one or more species during the day and by yet other species at night.

Observing, photographing, or collecting bats as they feed on flowers or fruit are ways to associate species with the foods they eat. Another way is to identify items the bats are carrying when captured in mist nets. Among the Phyllostomatidae, the commonest food items found in nets are fruits; however, Valdez and LaVal (1971) recovered an Anolis lemurinus after it had been carried into a net by a Trachops cirrhosus.
FOOD HABITS

The Phyllostomidae display a wide variety of food preferences, and relatively few species are restricted to a specific dietary regime. Only piscivory, among the types of chiropteran food habits, has not been found in the New World leaf-nosed bats.

The majority of the Phyllostominae are omnivores; however, some have strong tendencies toward carnivory. The only true insectivore in the subfamily (and family) may be Macrophylium macrophyllum. Vampyrum spectrum and Chiropterus auritus, both principally carnivorous, prey upon a variety of small vertebrates, including bats. Fruits and flowers are important components in the diets of many phyllostomatines, and some species, such as Phyllostomus hastatus, serve an important function in flower pollination (chiropterogamy) and plant dispersal (chiropterochory). Most phyllostomatines have the ability for hovering flight and, as suggested by their relatively large ears and eyes, probably are able to detect and capture prey on the ground or from foliage, tree trunks, and other surfaces.

The diets of the Glossophaginae include pollen, nectar, and, occasionally, parts of the corolla of flowers. As specialized flower feeders, these bats, too, play an important role in chiropterogamy. The majority is known to consume a variety of fruits, and some are suspected to pursue actively insects in addition to eating those captured at flowers. Windborne pollen (Alnus and Pinus, see Alvarez and Gonzalez, 1970) has been found in the stomachs of Glossophaga, Leptonycteris, Choeronycteris, and Anoura. These pollen grains probably were ingested from flowers and watering places where they settled (on pools of water, in bromeliads, and in cavities or depressions in trees).

The Caroliinae and Stenoderminae perhaps are best considered as frugivorous and some species indeed may be obligate frugivores (for example, Pygoderma, Amertrida, and Centurio). Many, however, also consume flower parts, pollen, nectar, and insects, particularly the Caroliinae, which are known to consume quantities of insects (Fleming et al., 1972). Stenodermines undoubtedly consume insects in the course of eating fruit because many fruits contain insect larvae. Frugivorous bats, as pointed out by Ayala and D’Alessandro (1973) and Forman (1973), probably must consume large amounts of fruit because adequate proteins, fats, and minerals are not abundant in this food. Several bats have been caught in fruit-baited traps placed on the ground and their capture supports the observations of Jimbo and Schwassmann (1967) that bats will feed on ripe fruit that has fallen to the ground. Aribeus has been reported to capture insects (Tuttle, 1968) and eat nestling birds (Ruschi, 1953); other stenodermines may prove to be insectivorous or carnivorous.

The Phyllonycterinae are an assemblage of fruit, pollen, nectar, and insect-eating species restricted in distribution to the Antilles. The limited information available on their food habits indicates a preference for pollen and insects, although soft fruits are eaten as well.

The Desmodontinae are obligate sanguivores and, within the Phyllostomidae, have the most specialized dietary requirements. Insects and bits of flesh have
been found in the stomachs of *Desmodus rotundus* (Arata et al., 1967; Greenhall, 1972). These items, however, were most likely ingested during bite site preparation or when feeding on the host. The ectoparasite reported by Arata et al. (1967) in a *Desmodus* stomach probably was consumed during grooming activities. *Diaemus* and, to a lesser extent, *Diphylla* show a preference for bird blood. *Desmodus* preys on birds as well, but apparently prefers mammalian blood.

Population densities of vampires probably have increased owing to the readily available food source supplied by domestic livestock. Before the availability of livestock and the widespread use of mosquito netting, vampires (particularly *Desmodus*) may have depended on human populations as a major food source. Cashinahua Indians living at Balta, Departamento de Loreto, Perú, an area with very few *Desmodus* and no domestic livestock, like mosquito netting as much for keeping away vampires as for protecting against insects. These people have been using mosquito netting for relatively few years and clearly remember having been bitten by bats in the past.

**Subfamily Phyllostomatinae**

**Genus Micronycteris** Gray

*Micronycteris megalotis*

A variety of insects and fruits.

Gaumer (1917), observing that *M. megalotis* flew slowly and near the ground in Yucatán, México, surmised that they ate insects caught close to the ground. Ruschi (1953d) mentioned insects and the fruits of *Musa paradisiaca*, *Psidium guajava*, *Jambosa vulgaris*, *Cecropia sp.*, *Eriobotrya japonica*, and *Solanum paniculatum* as part of the diet of Brazilian *M. megalotis*. Guavas (*Psidium guajava*) were also reported as a food item of this species in San Luis Potosí, México, by Dalquest (1953), who believed that they probably feed on many kinds of fruit. He found them feeding on small guavas, which they plucked and carried off to a nearby tree to eat, often dropping and losing much fruit in the process. Goodwin and Greenhall (1961) classified *M. megalotis* as a fruit-eating bat apparently fond of small ripe guavas, yet noted both insects and yellow fruit pulp in the stomachs of some specimens from Trinidad. The stomachs of specimens taken during the daytime in Veracruz, México, were empty; however, the stomachs of two collected at night were filled with the remains of insects (Hall and Dalquest, 1963). Howell and Burch (1974) reported that a Costa Rican specimen had consumed an “unknown green fruit.” The categorization of *M. megalotis* as a nectar-eating species by Valdivieso and Tamsitt (1962) appears to be unsupported.

*Micronycteris schmidtiorum*

Insects and probably fruit.

Howell and Burch (1974) reported two Costa Rican specimens of *M. schmidtiorum* that had consumed Lepidoptera.
**Micronycteris minuta**

Insects and fruit.

Goodwin and Greenhall (1961) believed *M. minuta* to consume fruit or insects or both. Fleming *et al.* (1972) examined 12 individuals from Costa Rica and Panamá and found 76 per cent insect and 24 per cent plant material, by volume, in the stomachs of four.

**Micronycteris hirsuta**

A variety of insects and fruits.

Goodwin and Greenhall (1961) considered this species to be fruit eating but said it may also consume some insects. Fleming *et al.* (1972), reporting on the stomach contents of three Panamanian specimens, found only the remains of insects. Wilson (1971) reported on the food remains he gathered at intervals between January and July from under roosting sites located on Orchid Island in the Panama Canal Zone. The major insect food items found represent the families Blattidae, Tettigoniidae, Scarabaeidae, Cerambicidae, Curculionidae, Cicadidae, Saturniidae, Sphingidae, Aeschnidae, and Formicidae. The insects recovered are winged forms capable of flight; however, they spend much of their time moving about on vegetation at night, suggesting that *M. hirsuta* may be gleaning them from vegetation as well as taking them in flight. The majority of the insect material, primarily whole wings, pieces of legs, and other hard parts, consisted of cockroaches (Blattidae), katydids (Tettigoniidae), and June beetles (Scarabaeidae). The remains of fruits recovered from the roosts represent *Caridovica palmata, Piper* sp., *Beilschmiedia* sp., *Anacardium excelsum, Vismia latifolia, Passiflora* sp., *Calycocarpus warrzezikianus*, and *Eugenia nesiota*. Wilson concluded that *M. hirsuta* is primarily insectivorous and that the small quantity of fruit eaten is consumed mainly in the dry season (February to March) when fruits are abundant. Howell and Burch (1974) reported the remains of Lepidoptera in a Costa Rican specimen.

**Micronycteris brachyotis**

Insects and fruit.

Goodwin and Greenhall (1961) reported finding fruit pulp, plant fibers, and insects in the stomachs of *M. brachyotis* from Trinidad. They also reported a "white milky substance" in the stomach of a juvenile. This individual probably was still nursing. Villa-R. (1967) noted that this bat feeds on pulpy fruits and insects as do other members of the genus. Howell and Burch (1974) mentioned insect remains (Hymenoptera and Coleoptera) recovered from a Costa Rican *M. brachyotis*.

**Micronycteris nicefori**

Fruit and insects.

A diet of fruit and possibly some insects was proposed by Goodwin and Greenhall (1961).
Micronycteris sylvestris

Fruit and insects.
A diet of fruit and possibly some insects was suggested by Goodwin and Greenhall (1961).

Summary.—Apparently there is no information available on the food habits of Micronycteris pusilla, M. behni, and M. daviesi.

According to Duke (1967) species of the genus Micronycteris are primarily insectivorous, although in Panamá they may be secondarily frugivorous. Walker et al. (1964) stated that the molar pattern is indicative of an insectivorous diet. The reports by Wilson (1971), Hall and Dalquest (1963), Fleming et al. (1972), and Howell and Burch (1974) support the contention that insects are the primary food source of these omnivorous bats. A variety of fruits are consumed by Micronycteris; however, their importance in the diet probably varies seasonally, as Wilsen (1971) found in Panamanian M. hirsuta.

Genus Macrotus Gray

Macrotus waterhousii

Large insects and fruit.
Osborn (1865:74) reported finding the wings and legs of large Orthoptera under a roost in a cave in Jamaica and mentioned that bats, presumed to be M. waterhousii, would drop the remains of the fruits of Morus tictoria, Brosimum alicastrum, and Eugenia jambos from their night roosts. He also described (p. 75) a female killing a nusffling bat (not hers, but one that was placed on her) and consuming its blood. This incident may have prompted Dobson (1878) to include small bats along with insects and fruit as food items of M. waterhousii. Dobson said the stomach of one specimen contained a yellowish mass with harder parts of insects, including the remains of orthopterans.

Macrotus californicus

A large variety of larger night-flying insects, some nonflying insects such as lepidopterous larvae, some fruits, and possibly green vegetative matter.

The remains of beetles of the species Ligyus gibbosus, Chlaenius sericeus, and Polyphylla decemlineata, plus parts of “various species of flies,” were reported by Grinnell (1918:256) as scattered over the floor of a cave inhabited by M. californicus in southern California. She also cited an incident (p. 257) where a Macrotus was caught in a mouse trap set in the open desert and suggested that this species seeks some of its food on the ground inasmuch as the bat likely was caught while attempting to capture ants or beetles attracted to the trap bait. This account probably was the basis for Sanborn’s (1954) mention of a specimen taken in a mousetrap. Additional reports on the food habits of M. californicus are also based on material gathered from under roosts in southern California. Howell (1920) found the wings of several diurnal butterflies, as well as parts of moths. Huey (1925) reported finding a willow leaf and the remains of grasshoppers.
(Trimerotropis sp. and Schistocerca sp.), cicadas, beetles (Meloidae), Sphinx moths (Celerio lineata and Smerinthus cerisyi), a noctuid moth (Peridroma marginata), and a cossid moth below the roosts. He assumed that some of these insects were diurnal and suggested that they had been taken from their resting places on vegetation (willows) by the bats and then carried to the roost to be eaten. Vaughn (1959) noted the remains of moths, butterflies, and dragonflies found under roosts. He also found fragments of orthopteran insects, noctuid moths, caterpillars, and beetles (Scarabacidae and Carabidae) in the stomachs of several *M. californicus* and concluded that this species was totally insectivorous, a supposition echoed by Novick (1963), Villa-R. (1967), Anderson (1969), and Barbour and Davis (1969). Supported by information in earlier reports and by finding the remains of caterpillars in stomachs, Vaughn (1959) also contended that *Macrotus* mainly takes insects that are on sparsely foliated vegetation or on the ground.

Burt (1938) reported on the stomach contents of five *Macrotus* taken in Sonora, México. Two had fruit and insects in their stomachs and three contained only fruit. Park and Hall (1951) treated *Macrotus* as a frugivore in their report on the tongue and stomach anatomy of several New World bats. Ross (1967: 214) cited observations which mentioned that *M. californicus* feeds on various cactus fruits. He also reported on the insect remains gathered beneath night roosts and on his analyses of 41 digestive tracts, mostly from bats collected in the vicinity of Tucson, Pima County, Arizona, but including a few from Sonora, México. The insect remains associated with roosts represented desert short-horned grasshoppers (Acrididae: Trimerotropis sp.), long-horned grasshoppers (Tettigoniidae: Microcentrum californicus, Schistocerca vaga, and other species), long-horned beetles (Cerambycidae: Derobrachus geminus), Sphinx moths (Sphingidae: Celerio lineata), and underwing moths (Phalaenidae: Catocala sp.). The stomach contents varied from purely insect remains to purely vegetable matter. Some stomachs from winter-taken *M. californicus* contained what appeared to be green vegetative parts of plants.

*Macrotus californicus* feeds primarily on the abdomens of larger night-flying insects within an average size range of 40 to 60 millimeters in length and, to a lesser extent, on lepidopterous larvae and other small insects approximately 20 millimeters in length, such as short-horned grasshoppers (Acrididae) and June beetles (Scarabaeeidae) (Ross, 1967: 211). Ross, disagreeing with the conclusions expressed in earlier reports, claimed that most, if not all, of the insects preyed upon by this bat are nocturnally active forms. He also asserted that no truly ground dwelling forms of insects were found in any of the digestive tracts he examined.

Vaughn's (1959: 34) observation that *Macrotus* regularly forages close to the ground, seems to hover easily, and is able to hover for several seconds at a time, suggests that these bats may glean insect prey from the ground and from vegetation, as well as capture flying insects. Therefore, *M. californicus* probably does include some flightless, ground-dwelling, or diurnal insects in its diet, as appears obvious from finding caterpillars in digestive tracts.
Genus Lonchorhina Tomes

Lonchorhina aurita

Insects and plant material.

Ruschi (1953c) stated that L. aurita eats insects exclusively. An examination of the stomach contents of two specimens from Trinidad only revealed the remains of insects (Goodwin and Greenhall, 1961). Duke (1967), citing unpublished information from Edwin Tyson, stated that this species probably eats nectar, some insects, and overripe fruit in Panamá. Fleming et al. (1972) examined two stomachs of Panamanian L. aurita. One contained about equal quantities of fruit pulp and insect remains. Nevertheless, Fleming et al. (1972: 560) considered L. aurita to be primarily insectivorous. Howell and Burch (1974) agreed after finding the remains of Lepidoptera in a Costa Rican specimen.

Lonchorhina orinocensis

The food habits are unknown, but the diet is probably similar to that of L. aurita.

Genus Macrophyllum Gray

Macrophyllum macrophyllum

A variety of insects.

Quelch (1892) believed M. macrophyllum to consume insects; however, on the basis of the large incisors, he also suggested that this species may supplement its diet with blood. Insects and fruit were mentioned by Ruschi (1953f) as foods eaten by Brazilian M. macrophyllum. Davis et al. (1964:378-379), commenting on the foraging behavior, body weight, and proportional size of the feet of this species in Nicaragua, suggested that aquatic insects or small fish were included in its diet. The stomachs of the specimens they collected were empty. Duke (1967) stated that Edwin Tyson thinks Macrophyllum eats swimming insects. Harrison and Pendleton (1974:691) reported finding the stomachs of four Salvadoran Macrophyllum “full of dark brownish, finely masticated material.” Wing fragments, which they suggested represented lepidopterans and dipterans, as well as many lepidopteran wing scales were found among the stomach contents. The stomach contents of two Macrophyllum that I examined from Panamá primarily consisted of the remains of waterstriders (Hemiptera, Gerridae: cf. Trepobates), which also appeared as brownish, finely chewed insect remains.

Genus Tonatia Gray

Tonatia bidens

Fruit and insects.

The diet probably includes fruit and insects as was reported by Ruschi (1953b) for this species in Brazil. Goodwin and Greenhall (1961) stated that it eats fruit.
**Tonatia brasiliensis**

Probably fruit and insects.

A diet of fruit and insects was proposed by Ruschi (1953c); however, the identification of his specimens is open to question because the "*Tonatia brasiliensis*" illustrated clearly is a *Carollia.*

**Tonatia sylvicola**

Fruit and insects.

Only 11 stomachs of the 22 Panamanian *T. sylvicola* reported on by Fleming et al. (1972) contained food, all of which was the remains of insects. Howell and Burch (1974) recovered legume pollen and the remains of fruit (*Stemmaderma*) from two Costa Rican representatives of this species.

Summary.—-The diets of *Tonatia carrikeri*, *T. nicaraguensis*, and *T. venezuelae* are not known. I suspect that species of *Tonatia* consume a large variety of arthropods, both flying insects and those gleaned from vegetation and other substrates. Tyson (quoted by Duke, 1967:8) believed *Tonatia* to be insectivorous, and thought that it probably gleans insects "off twigs about which they hover." *Tonatia* may consume a variety of fruits as well (see Howell and Burch, 1974) and probably has food habits similar to those of *Micronycteris.*

**Genus Mimon Gray**

**Mimon bennettii**

Fruit and insects.

The diet is reportedly insects and fruit (Ruschi, 1953c).

**Mimon cozumelae**

Plant material and various arthropods.

Dalquest (1957:46), commenting on several *M. cozumelae* he saw flying around half-spoiled fruit in an orange grove in southern Veracruz, México, suggested "they may have been eating the fruit, fermented juice, or insects stupefied by the juice." Hall and Dalquest (1963), perhaps reporting on the same incident, stated that *M. cozumelae* ate only very ripe, sometimes spoiled oranges, or possibly the insects that were feeding on the overripe fruit. They commented that the white droppings littering the floor in caves inhabited by *M. cozumelae* and *Trachops cirrhosus* resembled the droppings of hawks and owls, and concluded that both genera of bats are probably somewhat carnivorous. Villa-R. (1967) reported that *M. cozumelae* apparently eats fruit.

**Mimon crenulatum**

Insects.

Dobson (1878) reported finding portions of small coleopterous insects in the mouth and throat of a specimen. This information was apparently repeated without citation by Walker et al. (1964).
Summary.—There is no information on the food habits of Mimom koepckeae. Species of the genus Mimom probably consume a variety of arthropods and fruits.

Genus Phyllostomus Lacépède

Phyllostomus discolor

Insects, fruit, pollen, nectar, and vegetative parts of flowers.

Van der Pijl (1957:294, citing correspondence from Heinz Felten) noted that remnants of the fruit of Spondias purpurea were commonly found under the roosts of P. discolor in caves in El Salvador. Observations on bats visiting flowers in the Parque do Museu Goeldi, Belem, Brazil, reported by de Carvalho (1960, 1961), revealed that P. discolor consumes droplets of nectar secreted by the flowers of Parkia gigantocarpa and P. pendula as well as the pollen and vegetative flower parts of these species and of Ceiba pentandra. Digestive tracts examined by de Carvalho contained flower parts, pollen, fruit, nectar, and insects. Goodwin and Greenhall (1961:238) stated: "This is a fruit-eating bat; in captivity . . . will not eat flesh. It has a long extendible tongue, with a deep groove on the upper surface which is used to scoop out fruit pulp." Valdivieso and Tamsitt (1962), misinterpreting Goodwin and Greenhall (1961), included small vertebrates among the foods eaten by this species. Tamsitt and Valdivieso (1965) considered P. discolor to be frugivorous although they had once reported it to be a consumer of both flowers and fruit (Tamsitt and Valdivieso, 1961). Villa-R. (1967) remarked that this species was a frugivore in México and included Ficus sp., Diospyros ebenaster, and Achras sapota among those fruits consumed. The stomach of a Colombian specimen contained plant material and insects (Arata et al., 1967). The stomach contents of 128 Costa Rican and Panamanian P. discolor were reported on by Fleming et al. (1972). They found 73 containing approximately one per cent fruit and 99 per cent insect remains, by volume. Only one kind of seed was noted in the plant material suggesting that a single fruit type had been consumed. The stomachs of the remaining 55 bats were empty. Heithaus et al. (1974) found P. discolor carrying Bauhinia and Crescentia pollen on their fur and observed this species feeding at the flowers of Bauhinia pauletia in Costa Rica. Later, Heithaus et al. (1975) reported the recovery of Ceiba pentandra, Crescentia spp., Ochroma lagopus, Pseudobombax septinatum, Manilkara zapota, and Hymenaea courbaril pollen from the fur of Costa Rican P. discolor. They concluded that this species was primarily nectarivorous, at least during the dry season, and utilized a broad range of potential floral resources (79 per cent of the pollen loads were mixed). Fleming et al. (1972) were cited as the authority for including insects in the diet; nevertheless, Heithaus et al. (1975) found no remains of insects or fruit seeds and pulp in the feces. The diets of Costa Rican P. discolor reported on by Howell and Burch (1974) included vesicular plant material, fruit (Piper, Aenistis, and Musa), pollen (Hymenaea and Ceiba), and insects (Coleoptera, Hymenoptera, Diptera, and Lepidoptera). McNab (1969) stated that P. discolor is a fruiteater; but in captivity, requires a small, but regular intake of meat. Power and Tamsitt (1973) remarked that this species is known to feed on fruit, insects, pollen, and nectar.
**Phyllostomus hastatus**

A variety of insects, small vertebrates, and plant material including fruit, pollen, nectar, and flower parts.

Authors of early accounts on South American bats often confused this species with *Vampyrum spectrum* as well as attributing to it the “blood-sucking” habits of vampire bats. Bat species are difficult to recognize in some of these early narratives. Husson (1962:126) interpreted Waterton’s (1825) and Quelch’s (1892) observations on the habits of large Guianan bats they identified as *Vampyrum* as being correctly ascribed. Waterton (1825:175), while discussing *Vampyrum*, stated: “He does not always live on blood. When the moon shone bright, and the fruit of the Banana-tree was ripe, I could see him approach and eat it. He would also bring into the loft, from the forest, a green round fruit, something like the wild Guava, and about the size of a nutmeg. There was something also, in the blossom of the Sawarri nat-tree, which was grateful to him; for on coming up Waratilla Creek, in a moonlight night, I saw several Vampires fluttering round the top of a Sawarri tree, and every now and then the blossoms, which they had broken off, fell into the water, they certainly did not drop off naturally, for on examining several of them, they appeared quite fresh and blooming. So I concluded the Vampires pulled them from the tree, either to get at the incipient fruit, or to catch the insects which often take up their abode in flowers.” Quelch (1892:99), also relating observations on bats he believed to be *Vampyrum*, reported: “It had been tantalising the evening before to witness a continuous stream of these great winged creatures pouring out of one central hole high up in the trunk, and darting and wheeling, fluttering and hovering, about the fruit trees around the house, and helping themselves, no doubt, to the ripest fruits on the small branches, as they listed; but it was infinitely more tantalising to know that the same stream would issue undiminished next evening, after our departure.

“Though these bats are to a great extent insectivorous, yet from their size they must devour a large quantity of the mangoes, star-apples, sapodillas and other soft fruits where they occur, since their stomachs, when full, contain a considerable amount of pulpy matter. And indeed their great canine teeth, as in our bats generally, seem especially adapted for piercing and tearing open the skin, rind and fleshy parts of fruits, the power for the tear being derived from the force of their flight after they have seized the fruit with their teeth.” When these accounts by Waterton and Quelch are critically examined, however, they obviously apply to *Phyllostomus hastatus*, and perhaps to *Artibeus lituratus* as well, but not to *Vampyrum spectrum*.

Bates (1875:338) observed bats, which he called vampires, at Ega on the upper Amazon in Brazil. He discussed their habits and referred to their large numbers, frugivorous diet, and blackish and reddish color phases (he considered each color pattern to represent a distinct species)—characters identifying them as *P. hastatus*. Bates opened the stomachs of several and found a few remains of insects intermingled with masses of fruit pulp and seeds. Alston (1879-1882:39) and Goldman (1920:189), perhaps misled by Bates’ (1875:337) reference to their large size, assumed that these bats represented the species *Vampyrum spectrum*. 
Dobson (1878) noted that the stomach of a *P. hastatus* was filled with the remains of insects. However, he also assumed that they occasionally fed on bats and other small mammals. Ruschi (1953b) claimed that some of the feces of *P. hastatus* were like those of vampires and, therefore, presumed them to feed on blood. Nonetheless, Ruschi (1953d) gave the diet of this species in Brazil as insects, small birds and mammals (including bats), and the fruits of *Musa paradisiaca*, *Carica papaya*, *Psidium guajava*, *Eriobotrya japonica*, *Cecropia* sp., *Solanum paniculatum*, *Terminalia catappa*, *Livistona chinensis*, *Mangifera indica*, *Achras sapota*, *Lucuma cainiño*, *Eugenia uniflora*, *Myrcia jaboticaba*, *Vitis vinifera*, *Passiflora quadrangularis*, *Annona muricata*, *Pilocarpus pinatifolius*, *Artocarpus integrifolia*, *Rubbera glomerata*, *Diospyros kaki*, "etc." In Belem, Brazil, de Carvalho (1960, 1961) found *P. hastatus* feeding on the inflorescences of *Parkia gigantocarpa*, *P. pendula*, and *Ceiba pentandra*. He reported finding agglutinated masses of pollen, anthers, parts of the corolla, and a yellowish clear liquid, possibly nectar, in the stomach. De Carvalho described the diet of this species as insects, fruit, birds, other bats, blood, and flower parts. The inclusion of blood in the diet may have been prompted by Ruschi's (1953b) comments on the desmodontineline feces found in roosts.

Goodwin (1946) stated that the diet of Costa Rican *P. hastatus* included various kinds of fruit, birds, small bats, mice, and insects. This is essentially the same diet suggested by Williams *et al.* (1966) and Duke (1967). Goodwin and Greenhall (1961) noted the remains of fruit, fur, and feathers at the bases of roosts in Trinidad, and the inclusion of both fruit and flesh in the stomach contents. They mentioned that *P. hastatus* eats the fleshy funiculus of the Sapucaia nut (*Lecythis zabucajo*), a habit reported on in greater detail by Greenhall (1965). Greenhall (1966) reported *P. hastatus* feeding on ripe Valencia oranges in Trinidad. De la Torre (1963) remarked that several *P. hastatus*, captured as they attempted to enter a cave, were carrying large guava fruit. Bloedel (1955) reported on a group of about 30 *P. hastatus* that he observed several times at twilight following late afternoon rains as they fed on swarming termites at Juan Mina in the Panama Canal Zone. A Costa Rican specimen examined by Starrett and de la Torre (1964) contained fruit pulp, insect remains, a few bird feathers, and a partially digested tick in its stomach. The latter was probably consumed with its vertebrate host or was gleaned during grooming.

Arata *et al.* (1967) listed six stomachs of *P. hastatus* from Colombia as containing plant material and three with insect remains out of seven they examined. Fleming *et al.* (1972) gave the stomach contents of 19 of the 25 Costa Rican and Panamanian specimens they examined as 4 per cent plant material and 96 per cent insect remains, by volume; the remaining digestive tracts were empty. Tuttle (1970), reporting on Peruvian bats, mentioned that netted specimens were frequently dusted with pollen. I have noted this in *P. hastatus* netted in Costa Rica and eastern Perú. Howell and Burch (1974) did not report pollen from Costa Rican *P. hastatus*, but they did find the remains of fruit (*Cecropia* and *Piper*) and insects (Coleoptera, Hemiptera, Lepidoptera, and Diptera including Culicidae) in the feces and stomach contents.
Summary.—The food habits of *Phyllostomus elongatus* and *P. latifolius* are not known. Their diets, however, likely include flower parts, fruits, insects, and small vertebrates such as ancles and geckos gleaned from vegetation. As noted for *P. hastatus*, Tuttle (1970) frequently found the heads of netted *P. elongatus* covered with yellow pollen.

Bats of the genus *Phyllostomus* are omnivorous. Both *P. discolor* and *P. hastatus* feed on animal matter, but in the former this is probably restricted to insects, whereas *P. hastatus* preys on a variety of small vertebrates as well. Fruits, pollen, nectar, and insects caught in flowers probably are the major food items of *P. discolor*. The inclusion of blood in the diet of *P. hastatus* is without basis. The only blood consumed by this species is that of its vertebrate prey.

**Genus *Phylloperda* Peters**

**Phylloderma stenops**

Plant material and insects.

The only reference to the food habits of this species is that by Jeanne (1970) who captured a male in the act of eating the larvae and pupae from an active nest of a social wasp (*Polybia sericea*) near Santarem, Pará, Brazil. The stomach of this bat contained the well-masticated remains of both larvae and pupae, but no evidence of adults.

**Genus *Trachops* Gray**

**Trachops cirrhosus**

Insects, small vertebrates, and possibly some fruit.

Ruschi (1953c) recorded a diet of fruits, insects, and small reptiles for *T. cirrhosus* in Brazil. Burt and Stinton (1961) stated that the stomach of several specimens collected in El Salvador contained hair and flesh. Goodwin and Greenhall (1961) reported finding flesh and small sharp bones in the stomach of a *T. cirrhosus* from Trinidad and commented on finding the remains of a gecko (*Thecadactylus rapidicaudus*) in the stomach of a specimen from Panamá. Duke (1967) noted that Edwin Tyson had observed *Trachops* hovering up and down tree trunks in a manner suggestive of an insect gleaner. In Honduras, Valdez and La-Val (1971) found a freshly killed anole (*Anolis lemurinus*) in the same net pocket containing a *T. cirrhosus*. They suggested that *Trachops* feeds on a variety of lizards. Only two of the eight stomachs of Panamanian *T. cirrhosus* reported by Fleming et al. (1972) contained food. The contents of both consisted entirely of insect remains. Howell and Burch (1974) recovered a mixture of Lepidoptera and bat hair from each of four Costa Rican specimens.

I found *T. cirrhosus* commonly entering the houses of Cashinahua Indians at Balta, Departamento de Loreto, Perú, to feed on cockroaches during the evening. The bats were considered a nuisance because the sound of their flight as they moved along the walls and roof, the chewing noise as they consumed their prey, and the rain of urine, feces, and insect parts falling upon the mosquito nets below, disturbed the Cashinahua in their sleep.
Genus Chrotoperus Peters

Chrotoperus auritus

Small vertebrates, insects, and fruit.

Goodwin (1946) was among the first to comment that Chrotoperus is probably carnivorous. Ruschi (1953b) reported finding many bird vertebrae, solanaceous seeds (Solanum?), and blood in the feces as well as fragments of fruit, fruit seeds, and scattered vertebrae under a cave roost of C. auritus in Brazil. He also claimed to have witnessed a Chrotoperus land and commence feeding on the back of a calf. This observation was alluded to by Ruschi and Bauer (1957:41). Ruschi (1953f) listed the diet of Chrotoperus as small mammals, young birds, fruit, insects, and blood. The bat on the calf most likely was a Desmodus, and the only blood in the diet of C. auritus probably is that of the small birds and mammals preyed on by this bat. At least some of the seeds in the feces mentioned by Ruschi may have been in the stomachs and crops of birds eaten by Chrotoperus. Hall and Dalquest (1963) commented that the white stains beneath the roosts of these bats in Veracruz, Mexico, resembled those left by the excreta of hawks and owls. They also presumed C. auritus to be carnivorous, an opinion repeated by Villa-R. (1967) and McNab (1969). Villa-R. and Villa Cornejo (1969, 1971) reported finding the fragments of skeletons, skin, and hair below a roost of C. auritus in a mine in northern Argentina. Their suggestion that these fragments were the remains of Ctenomys is unlikely because of the fossorial habits of these rodents. Tuttle (1967) reported finding the remains of a gecko (Thecadactylus rapidiceps) in the stomach of a Venezuelan specimen. Olrog (1973) reported finding the remains of a mouse opossum (Marmosid) and a bird among the stomach contents of Argentinian Chrotoperus. Because the bird was being eaten in a mist net, Olrog concluded that Chrotoperus had been eating his mist-netted bats and birds.

Genus Vampyrum Rafinesque

Vampyrum spectrum

Birds, bats, rodents, and possibly some fruits and insects.

Vampyrum spectrum figured prominently in many of the early narratives on the South American fauna because of its awesome proportions and erroneously ascribed blood-feeding habits. Husson (1962:14, 122-126) discussed those accounts dealing with Guianan bats. Many of the early travelers, however, confused V. spectrum with Phyllostomus hastatus (see account of P. hastatus) and possibly with Arrius lituratus.

Dobson (1878:471) remarked on finding “some vegetable matter of rather firm consistence, apparently [a] portion of the rind of some large fruit” in the stomach of a V. spectrum. His remark (p. 471) that this species has been “shown by the observations of modern travellers to be mainly frugivorous” may have been influenced by Bates (1875, see account of Phyllostomus hastatus). Goodwin (1946) reported the diet of Costa Rican Vampyrum to be small birds, rodents, smaller bats, some fruit, and probably insects. Wehekind (1956:20) presented in-
formation on the food habits of *V. spectrum* in Trinidad. He found fur, feathers, and bone in the stomachs of three he collected and the remains of "blue birds," doves, and rodents at the base of a roost in a silk cotton tree (*Ceiba pentandra*). Two Costa Rican *V. spectrum* were reported on by Casebeer *et al.* (1963) who found the remains of a passerine bird in the digestive tract of one. Brosset (1966:54) and Goodwin and Greenhall (1961) noted that *Vampyrum* is largely, if not entirely, carnivorous, and the latter mentioned finding fur and feathers in the stomach of this bat and bat bones at the base of a roost. Greenhall (1968) also said these bats were carnivorous and mentioned that a variety of fruits offered to *V. spectrum* in captivity were never eaten. Duke (1967), however, listed *Anacardium* sp. and *Psidium* sp. as examples of fruits eaten by this species in Panamá in addition to bats, rodents, birds, and insects. Peterson and Kirmse (1969) reported on finding the remains of bats and an oryzyomyine rodent in the stomach of a Panamanian *Vampyrum*. They surmised that this bat had been eating other bats caught in mist nets without having become caught itself. However, their statement (p. 140) "that these bats were virtually eaten in situ in the net negated any evidence for birds of prey being responsible" is not necessarily correct. In Chiapas, México, I saw a barred forest-falcon (*Micrastur ruficollis*) in the act of eating small bats in a mist net at daybreak. The hawk hit a bat in the net, rebounded, and ate parts of it while hanging nearly upside down and free from the net. As I approached, the hawk released the bat (a *Sturnira lilium*) and flew off. The net contained other bats including some for which heads and upper parts of the body were missing. Later in the day, the hawk returned to the net and was captured while hanging and feeding on a small bird.

**Subfamily Glossophaginae**

**Genus Glossophaga E. Geoffroy St.-Hilaire**

**Glossophaga soricina**

Insects, fruits, pollen, nectar, and flower parts.

This species, which figured prominently in many early accounts of tropical American bats, was assumed to feed on blood. For example, Quelch (1892:101) stated: "It seems likely . . . that these bats supplement their ordinary insect diet, with the blood of the domestic animals." He noted, however, that the tongue seemed to be modified to lick out the pulpy matter of fruits. Gaumer (1917) stated that *G. soricina* feeds on insects and small or soft fruits in Yucatán, México, and mentioned the fruit of *Cordia dodecandra*. He remarked (p. 297) that they open holes in the fruit and lick the juice, and "aunque son vampiros nunca chupan sangre."

One of the earliest reports on the flower-feeding habits of *G. soricina* was by Porsch (1931), who observed this species at the flowers of *Crescentia cujete* and *Parmentiera alata* in Costa Rica. Vogel (1958) reported that they feed on flowers of *Kigelia aethiopica* and noted finding the pollen of *Maracurania* sp. on the heads of some specimens. Baker (1970) presented information on flowers visited by bats at the botanical gardens of the Tela Railroad Company, Lancetilla, Honduras,
and at Finca Lornessa, Santa Ana, Costa Rica. Even though the bats were not identified, examination of his photographs (figs. 1-4, 6-11) show G. soricina visiting the flowers of Durio zibethinus in Honduras. Those bats visiting the flowers of Mucuna andreana in Costa Rica are almost certainly this species as well, inasmuch as this is the only glossophagine I have ever netted at Finca Lornessa despite extensive collecting, and the species proved to be common there. Heithaus et al. (1974) reported capturing G. soricina dusted with Bauhinia and Crescentia pollen and mentioned observing this species at the flowers of Bauhinia pauletia near Cañas, Costa Rica. Heithaus et al. (1975) noted that 59.6 per cent of the 146 G. soricina they examined from the same region in Costa Rica carried pollen on the fur. The six most common plants represented by the pollen were Ochroma lagopus, Pseudobombax septinatum, Ceiba pentandra, Hymenaea courbaril, Manilkara zapota, and Crescentia sp. They also found that these bats had fed on the fruits of Piper tuberculatum, Muntingia calabura, Solanum sp., and Ficus sp. as well as on other fruits, the remains of which they could not identify. When contrasting frugivory and nectarivory in this species, Heithaus et al. (1975) remarked that G. soricina was primarily nectarivorous in both the wet and dry seasons in Costa Rica. The insect-eating habits of G. soricina were acknowledged, however; they cited Fleming et al. (1972) as the source for this information.

Test (1934) reported G. soricina feeding on ripening bananas in Honduras, and Tamsitt and Valdivieso (1965) considered this species to be frugivorous. Glossophaga soricina was thought to be nectarivorous by Park and Hall (1951), Wille (1954), Tamsitt and Valdivieso (1961, 1963), and McNab (1969). Goodwin (1946) also thought it was a nectar feeder and mentioned flowers of the calabash tree and night-blooming cacti as food sources. Piccinini (1971) noted that Brazilian G. soricina eat pollen and nectar. Dalquest (1953), reporting on mammals from San Luis Potosí, México, suggested that G. soricina feeds principally on nectar but consumes fruit juices and pulp as well. Hall and Dalquest (1963) stated that it was a nectar and fruit eater and mentioned catching a specimen in a banana-bated snap trap placed in a tree in Veracruz, México. A nectar and fruit diet was cited for G. soricina by Novick (1963) and Hall and Kelson (1959). Duke (1967), relating Edwin Tyson's information on Panamanian G. soricina, stated that they feed on overripe bananas and guavas and drink from the flowers of Musaceae, Bignoniaceae, and Bombacaceae. Pollen, nectar, and soft fruits were noted in the diet of this species in México by Villa-R. (1967), who also reported finding some specimens with their heads covered with Ipomoea arborea pollen.

Wied-Neuwied (1826) reported finding insects in the stomach of a G. soricina from Brazil. Alston (1879-1882:43) also stated that G. soricina preys on insects but mentioned that this species "feeds largely on fruits, lapping up the juices and soft pulp with their extensible tongues." Brosset (1965), on the basis of tongue structure, suggested that G. soricina may capture insects at flowers as well as drink the nectar. Felten (1956) reported this species feeding on flowers (especially Crescentia) in El Salvador; however, on the basis of observations on captive individuals, he said they prefer insects. Fruit juices and small insects were found in the stomachs of Trinidadian G. soricina (Goodwin and Greenhall,
1961). Ruschi (1953g) listed insects, fruits, nectar, and pollen in the diet of Brazilian *G. soricina*. He noted that this species consumes nectar from many kinds of flowers, including *Crescentia cujete* and *Vochysia* sp., as well as eating the fruits of *Musa paradisiaca*, *Carica papaya*, and *Solanum paniculatum*. De Carvalho (1960) reported on the stomach contents of *G. soricina* from Belem, Brazil. One stomach contained the remains of insects, a large quantity of reddish fragments, presumably flower parts, and yellowish and whitish masses, probably pollen. Another contained scales of lepidopterous insects and a gelatinous mass of proteinaceous material, presumably pollen. According to de Carvalho (1961) *G. soricina* eats fruit, flowers, nectar, and insects. Based on observations in the Parque do Museu Goeldi, Belem, he cited a variety of flowering plants of which the nectar, pollen, and sometimes the flower parts are eaten: *Crescentia cujete*, *Crescentia amazonica*, *Alexa grandiflora*, *Hymenaea courbaril*, *Bougainvillea spectabilis*, *Crataeva benthami*, and *Elizabetha paraense*. Also cited were the fruits of *Cecropia bureaniana*, *Cecropia* sp., *Piper* sp., and *Achras sapota* as foods consumed during periods of annual fruiting maxima (December to January). Starrett and de la Torre (1964) reported on *G. soricina* from El Salvador, Honduras, Nicaragua, and Costa Rica. They wrote (p. 57): “Fruit ‘pulp’ and seeds of a number of different kinds of plants were present to some extent in the digestive tracts of every *Glossophaga*. No pollen was found in any individual. Eight . . . had insect remains in their digestive tracts. In two cases the insect parts made up the bulk of the contents of the tract. The insects had been finely chewed but lepidopterous scales were readily recognizable, as well as portions of the wings of Diptera and Hymenoptera.” They also observed *G. soricina* feeding on ripe bananas at Los Diamantes, Costa Rica. Fleming *et al.* (1972) classified *G. soricina* as an omnivore after examining the stomachs of 217 specimens from Costa Rica and Panamá. Of these, only 38 stomachs contained food—34 per cent plant material (including 5 per cent pollen) and 66 per cent insect remains, by volume. Two collected in January and one in May contained insects exclusively. One taken in March only contained pollen, and two caught in September only held fruit. Two captured in February and six from December contained insects, fruit, and pollen, whereas the stomachs of bats in June, July, August, and October, contained fruit and insects. At least seven seed types were found in the plant matter recovered from these stomachs. Howell and Burch (1974) reported finding the pollen and nectar of *Crescentia*, *Inga*, *Hymenaea*, *Mucuna*, *Musa*, *Pitcairnia*, and an unidentified Bombacaceae in Costa Rican *G. soricina*. They also found the remains of fruit (*Acnistus*, *Muntingia*, *Musa*, and an unidentified Melastomataceae) and Lepidoptera in the feces or stomach contents. Lepidopterous insects were the only food items recovered from 24 of the 62 *G. soricina* they examined.

Alvarez and Gonzalez Q. (1970) presented information on their analyses of 174 *G. soricina* from the Mexican states of Veracruz, Oaxaca, Guerrero, and Morelos. Of these, 107 (61.6 per cent) did not contain pollen in their digestive tracts. Nevertheless, *G. soricina* contained the greatest diversity of pollen grains (at least 34 species recognized—see Table 2) of any of the other glossophagines studied (*Anoura geoffroyi*, *Choeronycteris mexicana*, *Leptonycteris sanborni*,
TABLE 2.—Plants identified by pollen grains in the stomachs of Glossophaga soricina, Anoura geoffroyi, Choeronycteris mexicana, Leptonycteris sanborni, L. Nivalis, and Hylonycteris underwoodii from México (modified from table 5 in Alvarez and Gonzalez Q., 1970:165).

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<th>C. mexicana</th>
<th>L. sanborni</th>
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Symbols: a. occurring in over 20 per cent of all stomachs containing pollen; b. exceeding 25 per cent of total volume of pollen; c. 99.8 per cent of stomach contents; d. includes Lemaireocereus.

L. nivalis, and Hylonycteris underwoodi). Alvarez and Gonzalez Q. (1970) considered G. soricina to be an opportunistic omnivore that utilizes pollen as a food source whenever nectar, fruits, or insects are not readily available. Their observations on this species extended from February to September, during which time the commonest pollen ingested varied seasonally from Cordia, Acacia, Conzattia, and Albizzia in the spring to Ceiba, Ipomoea, Myrtillocactus, and Agave in the summer, and Conzattia in September. The pollen grains in the diet were correlated with each habitat. For example, three samples of G. soricina collected in May from different localities on the Pacific versant of Michoacán demonstrated different pollen profiles. Specimens from the Tepalcatepec-Balsas Basin south of Nueva Italia principally contained the pollen of Lemaireocereus and Echinocactus. In the vicinity of Arteaga, the most abundant pollen found were Roupala, Agave, and Ceiba; however, in the Melchor Ocampo area on the coastal plain, the primary pollen grains consumed were Ceiba and Cordia.

Arata et al. (1967) presented data on the stomach contents of 16 Colombian G. soricina. They found that 15 contained plant material, and 6 contained the remains of insects. On the basis of a stomach containing matted hair, claws, and flesh, they ascribed carnivorous habits to this species. I suggest, however, that this observation not be interpreted as reflecting a normal aspect of the diet. As the authors noted (p. 653), the bats were collected at night and kept alive for processing the next day. According to Arata (personal communication), the bats were individually held in small cloth bags. Nevertheless, bats kept under these conditions sometimes will chew on themselves and, if pregnant, often abort and eat parts of the fetus. The finding of claws and flesh in the stomach of a G. soricina probably represents cannibalism induced by the treatment the bat received between the time it was caught and its death. Unfortunately, the sex and reproductive state of the bat was not presented. The information presented by Arata et al. (1967) may have prompted Phillips (1971) to include meat in the diet of G. soricina.

Goodwin (1934:9), commenting on G. soricina from Guatemala, said, "The single specimen taken at Barrillas was caught in a mouse trap hanging over a pile of raw sugar. Whether the bats were after insects drawn by the sugar or were there for the sweets, I cannot say, but I lean toward the former idea. The natives insist that bats eat the sugar." The owners of Finca Lornessa, Santa Ana, Costa Rica, often found dead bats hanging on the edge or floating in the large vats used to concentrate sap from sugar cane if these pots were left filled and uncovered during
the night. The Finca Lornessa sugar mill houses a large colony of *G. soricina*, and the owners believe the bats drink the concentrated sugar cane sap.

**Glossophaga commissarisi**

Insects, fruit, pollen, and nectar.

The remains of Lepidoptera, fruit (*Acnistus*), and the pollen and nectar of *Musa* and *Macuna* were recovered by Howell and Burch (1974) from Costa Rican *G. commissarisi*.

**Glossophaga longirostris**

Insects, fruit, pollen, nectar, and possibly other flower parts.

Wille (1954) and Valdivieso and Tamsitt (1962) considered *G. longirostris* to be nectarivorous. Goodwin and Greenhall (1961) said it feeds on fruit pulp and fruit juices, occasional insects, and some nectar. Pirlot (1964) said *G. longirostris* is nectarivorous and frugivorous. He also cited correspondence from Goodwin and Novick, who suggested that insects found among stomach contents have come from the fruit these bats have eaten.

**Summary.**—The diet of *Glossophaga alticola* is not known; however, its food habits likely are similar to those of *G. soricina* and *G. commissarisi*. Villa-R. (1967) reported the diet of *G. morenoi* as nectar, pollen, and pulpy fruits. I am uncertain to which of the three species of *Glossophaga* occurring in México he was referring. The diet of *Glossophaga* includes a variety of plants and insects. Many of the insects may be consumed in conjunction with the flower-feeding habits of these species; however, some insects likely are caught away from flowers.

**Genus Monophyllum Leach**

**Monophyllum redmani**

Nectar and fruit.

Osburn (1865) reported finding yellow pulp in the intestines of two *Monophyllum redmani* taken in Jamaica. Wille (1954) reported that this species was "nectar-eating" on the basis of tongue structure. Tamsitt and Valdivieso (1970) also considered *M. redmani* to be nectarivorous.

**Summary.**—Nothing has been reported on the diet of *Monophyllum plinthodon*. According to Walker *et al.* (1964), *Monophyllum* spp. are known to feed on the juices and pulp of fruits and presumably include insects in their diet.

**Genus Leptonycteris Lydekker**

**Leptonycteris nivalis**

Fruit, pollen, nectar, and insects.

Park and Hall (1951), on the basis of tongue and stomach anatomy, considered *L. nivalis* to be nectarivorous. Dalquest (1953:28) found *L. nivalis*, captured in
rooms of Hacienda Capulin, San Luis Potosí, México, with their stomachs filled “with thick, brilliant red fruit juice... almost certainly the juice of the fruit of the organ cactus.” Novick (1963) believed that this species feeds on flowers and fruits. Barbour and Davis (1969) remarked that *L. nivalis* feeds on nectar and pollen. Phillips *et al.* (1969) mentioned nectar, pollen, and soft fruit in the diet of *L. nivalis* in their report on the macroynysid mites inhabiting the oral mucosa of these bats. The mites were found in *L. nivalis* but not in *L. sanborni*, even when both species were found in the same cave. They implied that the presence of the mites in *L. nivalis* indicated a diet differing from that of *L. sanborni* and suggested that abrasive diets of insects or plant fibers might prevent the mites from inhabiting the oral cavity of *L. sanborni*.

Alvarez and Gonzalez Q. (1970) reported on pollen found in the stomach contents of 13 specimens from the Mexican states of Michoacán and Hidalgo. Pollen grains representing 22 kinds of plants were found in 12 stomachs (Table 2); one stomach did not contain pollen. *Leptonycteris nivalis* consumed the pollen of *Agave*, *Ipomoea*, *Ceiba*, and *Myrtilllocactus* in about the same proportions as did *L. sanborni*. Alvarez and Gonzalez Q. remarked on not finding any significant differences in the diets of the two species.

**Leptonycteris sanborni**

Fruit, nectar, pollen, and insects.

Wille (1954), on the basis of the throat musculature of specimens from Jalisco, México, considered *L. sanborni* to be nectarivorous. Hoffmeister and Goodpaster (1954) presumed *L. sanborni* to feed heavily on pollen and nectar after observing that nearly every specimen they collected in the vicinity of the Huachuca Mountains in southern Arizona had yellow pollen covering the head. An analysis of the stomach contents of six specimens revealed an average of 92 per cent pollen and 8 per cent insect remains. Hoffmeister and Goodpaster (1954) surmised that the pollen came from jimsonweeds (*Datura*), which have yellow pollen, are open at night, and are abundant in the area.

Alcorn *et al.* (1961) and McGregor *et al.* (1962) reported on experiments they conducted in southern Arizona with caged *L. sanborni* exposed to flowering saguaros (*Carnegiea gigantea*) and century plants (*Agave schottii*). They found 62 per cent of the saguaro flowers setting seed when pollinated by *L. sanborni* as opposed to 52 per cent for bees and 45 per cent for white-winged doves. Hayward and Cockrum (1971) presented information on analyses of digestive tracts collected from *L. sanborni* between 15 May and 2 September over a four-year period in southeastern Arizona. They found the tracts to contain 100 per cent saguaro pollen in mid-May. The pollen content shifted with increasing percentages of *Agave* pollen beginning in late May to early July and thereafter to early September, when the pollen content was 100 per cent *Agave*. The stomach of one bat taken on 7 November near Carbo, Sonora, México, contained a few grains of saguaro pollen. Hayward and Cockrum (1971) expressed the opinion that *L. sanborni* is a nectarivorous species in the United States and accidentally ingests pollen while feeding at flowers. They believed pollen to comprise the major proteinaceous portion of the diet and mentioned that, when nectar is not available,

Alvarez and Gonzalez Q. (1970) reported on the pollen found in the stomachs of L. sanborni over a six-month period in the Mexican states of Hidalgo and Guerrero. Fecal samples were collected in a cave in Xoxafi, Hidalgo, from February to September. Of the 279 stomachs examined, 249 contained identifiable pollen grains representing 28 kinds of plants (Table 2). The results from the fecal analyses duplicated the information obtained from the stomach contents. Leptonycteris sanborni first arrived at the cave in Xoxafi in February and, since their stomachs contained pollen grains of Bombax and Ipomoea, were presumed to have come from subtropical habitats. The pollens found in the stomachs of these bats reflected the plants that were flowering at the time as well as the changes in the flowering times of the flora from one season to another. For example, in the vicinity of Juxtlahuaca, a subtropical locality in Guerrero, bats contained large amounts of the pollen of Bombax, Ipomoea, Ceiba, and Agave on 3 February, as well as very small quantities of the pollen of Myrtillopectus. On 20 July, however, L. sanborni stomachs contained nearly 90 per cent Myrtillopectus pollen, no Bombax pollen, and greatly reduced amounts of Ceiba, Ipomoea, and Agave pollens. Comparisons of pollens found in the digestive tracts of L. sanborni taken in late July from Xoxafi and Juxtlahuaca demonstrated differences in the foods available in these two contrasting habitats. Agave pollen predominated (98.7 per cent) in the stomachs from Xoxafi, whereas the pollen of Lemaireocereus was commonest (87.7 per cent) in bats from Juxtlahuaca. No significant differences were noted in the pollens consumed by L. sanborni and L. nivalis.

Howell (1974) reported finding fragments of thrips (Carpophilus) and a bee (Halictus) in some stomachs of L. sanborni from southern Arizona. However, she suggested that, because these insects are associated with batflowers, they were consumed incidental to nectar feeding and are not actively pursued. Thirty stomachs contained an average of 4 grams of material each, of which about 25 per cent was pollen; the remainder, nectar. Howell's thesis is that L. sanborni is nectarivorous, prefers Agave and Carnegiea flowers as food sources while in Arizona, and that pollen supplies all of the dietary proteins. She supports her contention regarding the dietary role of pollen by pointing out the higher nitrogen content of pollen from chiropterophilous plants (when compared against anemophilous and entomophilous pollen) and demonstrating the array of "essential" amino acids present in Agave and Carnegiea pollen, two of which (proline and tyrosine) are recommended as being of special importance to bats.

Summary.—The food habits of Leptonycteris curasoae are unknown; however the diet likely is similar to those of L. nivalis and L. sanborni. There have been several reports concerning the food habits of Leptonycteris; however, it is nearly impossible at this time to determine to which North American species this information applies. Duges (1906) reported on finding an Ichmoglossa (= Leptonycteris) in Guanajuato, México, the fur of which was covered and stomach filled withMalvaviscus acerifolius.\)
Palmer (1954) stated that *Leptonycteris* probably feeds on flowers. Sanborn (1954) maintained that these bats feed on insects from night-blooming flowers because cactus pollen has been found in some of the stomachs examined. Hoffmeister (1957) gave the diet as nectar, pollen, and insects. According to Walker *et al.* (1964), *Leptonycteris* is known to visit the flowers of *Malaviscus* and perhaps jimsonweed (*Datura*) and to eat the fruits of cacti.

**Genus Lonchophylla Thomas**

*Lonchophylla mordax*

Insects, fruits, nectar, and pollen.

Ruschi (1953) recorded the diet as insects, succulent fruit, nectar, and pollen.

*Lonchophylla concava*

Pollen, nectar, and insects.

Howell and Burch (1974) reported the following food materials recovered from six Costa Rican specimens of *L. concava*: one with nectar and *Mucuna* pollen, two with nectar and *Musa* pollen, and three with the remains of Lepidoptera.

*Lonchophylla robusta*

Pollen, nectar, fruit, and insects.

Wille (1954) considered *L. robusta* to be a nectar-eating bat. Fleming *et al.* (1972) examined the stomachs of 17 specimens from Costa Rica and Panamá. Ten per cent plant material and 90 per cent insect remains were found in the only stomach containing food items. Howell and Burch (1974) did not find any plant material in their three *L. robusta* from Costa Rica; however, they did find the remains of Lepidoptera, Coleoptera, and Streblidae.

*Summary.*—Nothing has been published on the food habits of *Lonchophylla hesperia* and *L. thomasi*. Walker *et al.* (1964) remarked that *Lonchophylla* feeds on flowers and the diet may consist of nectar, pollen, insects, and fruit. Duke's (1967) mention of nectar and possibly overripe fruit, pollen, and insects in the diet of Panamanian species of *Lonchophylla* may apply to all species in the genus. Goodwin (1946:312) wrote that “*Lonchophylla* . . . is to some extent a nectar feeder, and uses its long tongue to lap up the honeyed liquid from the large night-blooming flowers.” I have seen *L. thomasi* feeding at banana flowers in eastern Perú and many of these bats had their heads and shoulders dusted with pollen.

**Genus Lionycteris Thomas**

*Lionycteris spurrelli*

The diet is unknown; however, the food habits of *Lionycteris* likely are similar to those of *Lonchophylla*. 
Genus *Anoura* Gray

*Anoura geoffroyi*

Fruit, pollen, nectar, and insects.

Perhaps the earliest account providing information on the food habits of *A. geoffroyi* is that of Tschudi (1844:73), who recorded the remains of Diptera in the stomach of a specimen from Perú. Ortiz de la Puente (1951) also found insects in the stomachs of Peruvian *A. geoffroyi*. According to him (p. 12), an examination of stomach contents revealed the remains of two species of small coleopterans, one of which is a member of the family Nitidulidae.

Knuth (1906:73) related J. H. Hart's observations (*in litt.*) on visits by *Glossonycteris geoffroyi* (= *A. geoffroyi*) to the flowers of *Eperua falcata* in Trinidad. This information was mentioned by Baker and Harris (1957:449) and given without citation by Walker *et al.* (1964). According to Goodwin (1946:312), "*Anoura* is in part a nectar feeder, and its long tongue is adapted for reaching into the corolla of various night-blooming tropical flowers. It is known also to visit blossoms where there is no secretion of nectar, and it may be supposed that there they are attracted by the insects drawn in by the perfume of the flowers." Ruschi (1953) mentioned visits to flowers of *Vochysia* sp. by *A. geoffroyi* in Brazil and listed insects, fruit, nectar, and pollen in the diet of this bat. Wille (1954) considered this species as nectarivorous. Vogel (1958) noted that *A. geoffroyi* visits the flowers of *Symbolanthus laefolius* and *Purpurella grossa*. Goodwin and Greenhall (1961) reported that *Anoura* feeds on nectar and the soft pulp of ripe fruit. Villa-R. (1967) gave nectar and pollen as the foods of *A. geoffroyi* in México. Duke (1967) stated that this species is a nectar feeder in Panamá that also eats overripe fruit. Goodwin (1934) remarked on catching an *A. geoffroyi* in Guatemala in a mousetrap hanging over a pile of raw sugar.

The high incidence of insect remains and the numerous stomachs without pollen prompted Alvarez and Gonzalez Q. (1970) to suggest that *A. geoffroyi* is a facultative pollen eater. Alvarez and Gonzalez Q. reported on 69 *A. geoffroyi* from the Mexican states of Michoacán, México, Guerrero, and Oaxaca. Of these bats, 34 contained identifiable pollen grains, representing 20 kinds of plants, in their stomachs (Table 2). The kinds of pollen present were similar to those found in other species and reflected the flora in the different habitats where the bats were found. The major differences noted between *A. geoffroyi* and the other species Alvarez and Gonzalez Q. (1970) studied were the increased representation of entomophilous plant pollen (for example, Compositae) and the high frequency of insects in the stomach contents. According to them, *A. geoffroyi* behaves like an insectivorous species with a partiality for pollen. This observation is supported by Howell and Burch (1974) who found only Lepidoptera in the specimen they examined from Costa Rica.

*Anoura caudifer*

Fruit, nectar, pollen, and insects.

Wied-Neuwied (1826:217) mentioned finding the remains of insects in the stomach of an *Anoura ecaudata* (= *A. caudifer*) from Brazil. Ruschi (1953)
claimed that Brazilian A. caudifer eat insects, soft juicy fruits, nectar, and pollen.

**Anoura cultrata**

Insects, pollen, and nectar.

The six A. cultrata examined by Howell and Burch (1974) contained only the remains of Lepidoptera. However, I collected several A. cultrata in Costa Rica, the heads and shoulders of which were dusted with pollen.

**Anoura werckleae**

Pollen and probably nectar, fruit, and insects.

Starrett (1969) reported A. werckleae visiting the flowers of Wercklea lutea, as he determined by finding *Wercklea* pollen on the fur of the head and shoulders.

**Summary.**—Very little is known of the food habits of *Anoura werckleae* and *A. cultrata*; the diet of *A. brevirostrum* is unknown. However, these species probably have diets similar to that of *A. geoffroyi*, which is a highly insectivorous glossophagine.

**Genus Scleronycteris** *Thomas*

**Scleronycteris ega**

Probably fruit, pollen, nectar, and insects.

Nothing has been reported on the diet of this species.

**Genus Lichonycteris** *Thomas*

**Lichonycteris obscura**

Pollen, nectar, and insects.

Goodwin (1946:315) wrote: “*Lichonycteris* is probably a nectar feeder as is indicated by its weak teeth and absence of lower incisors, to give the long tongue free play.” Tamsitt and Valdivieso (1961) included L. obscura among species that consume flowers and fruits. Carter et al. (1966) reported on two specimens netted near a plant bearing night-blooming flowers in Guatemala. They noted pollen on the rump and uropatagium of these bats.

**Summary.**—Nothing is known of the diet of *Lichonycteris degener* and little is known of the food habits of *L. obscura* other than the fact that these bats visit flowers.

**Genus Hylonycteris** *Thomas*

**Hylonycteris underwoodi**

Insects, pollen, and nectar.

Goodwin (1946) believed *Hylonycteris* to be a flower visitor and Hall and Kelson (1959) stated that it is a nectar feeder. Hall and Daiquest (1963:228) re-
porting on this species in Veracruz, México, wrote: “Beneath their resting place was a pile of guano about three inches high by six in diameter. There were several pits of jobo plums [Spondias lutea] on the pile, showing that some of this fruit is taken to the cave to be eaten.” Carter et al. (1966) reported a specimen with pollen grains on the rump and uropatagium netted near night-blooming flowers in Guatemala. Villa-R. (1967) stated that Hylomycteris feeds on nectar and pollen. He cited a specimen from Tabasco, México, with pollen that he suspected to be cacao (Theobroma cacao) on the vibrissae and hairs around the mouth. Walker et al. (1964) reported the diet as probably nectar, fruit, and some insects. Alvarez and Gonzalez Q. (1970) reported on the pollen found in the stomachs of two specimens from Chiapas, México. The stomach contents were composed almost entirely of the pollen of Lonchorhaphis (99.8 per cent). Pollen of Agave and Pinus were also present but in minute amounts (Table 2). Apparently, Howell and Burch (1974) were the first to demonstrate insectivory in H. underrwoodi. They recovered the remains of Lepidoptera from a specimen in Costa Rica.

Genus Platalina Thomas

Platalina genovensium

Probably pollen, nectar, and insects.
The food habits are unknown.

Genus Choeroniscus Thomas

Choeroniscus godmani

Probably pollen, nectar, and insects.

Goodwin (1946:313), commenting on Costa Rican C. godmani, wrote: “Tip of tongue has numerous thread-like papillae forming a brush, especially adapted for reaching the nectar at the base of the corolla in large blossoms.” Villa-R. (1967), while discussing C. godmani in México, cited the stomach contents given by Goodwin and Greenhall (1961) for C. intermedius from Trinidad.

Choeroniscus intermedius

Pollen, nectar, and insects.

Goodwin and Greenhall (1961:248) stated: “Microscopical examination of the stomach contents of one specimen [from Trinidad], however, revealed some minute particles that are possibly honey or fruit juice, many fragments of a coleopterous insect, and numerous brown and white, hair-like strands, probably either from insects or from fruit. This specimen, at least, had fed to a large extent on insects.”

Summary.—Nothing is known of the food habits of Choeroniscus minor, C. inca, and C. periosus. Their diets, however, probably include pollen, nectar, insects, and small juicy fruits.
Genus **Choeronycteris** Tschudi

**Choeronycteris mexicana**

Fruits, pollen, nectar, and probably insects.

Dalquest (1953) expressed the opinion that in San Luis Potosí, México, *C. mexicana* feeds principally on the nectar of desert flowers, probably of cacti. Park and Hall (1951), Wille (1954), and Hall and Kelson (1959) considered *C. mexicana* to be nectarivorous. Hoffmeister and Goodpaster (1954) noted several specimens from the Huachuca Mountains in southern Arizona that had yellow pollen on the fur around the face. Huey (1954) mentioned *C. mexicana* from San Diego, California, with yellow matter in their stomachs and pollen on their faces. Sanborn (1954) suggested that this species may have the same feeding habits as *Leptonycteris nivalis*. Villa-R. (1967:263) reported capturing four *C. mexicana* in Bahia de San Carlos, Sonora, México, the mouths of which contained remains of the fruit of pitahayas (*Lemaireocereus*) or garambulla (*Myrtilllocactus*). He also mentioned observing this species flying with *Leptonycteris* around fruiting cacti. In Guerrero, Villa-R. (1967) caught five specimens that had their heads and shoulders covered with *Ipomoea arborea* pollen. Walker et al. (1964) suggested a diet of nectar, pollen, fruit juices, and insects for this species. Barbour and Davis (1969) stated that *C. mexicana* probably feeds on nectar and mentioned individuals for which the heads and faces were covered with pollen when captured.

Alvarez and Gonzalez Q. (1970) reported on the pollen found in the stomachs of 16 *C. mexicana* from the Mexican states of Hidalgo, Guerrero, and Morelos. All stomachs contained pollen grains, and 17 pollen types were identified (Table 2). Noting that the major percentages of pollen were from *Lemaireocereus*, *Ceiba*, *Ipomoea*, *Agave*, and *Myrtilllocactus* (plants that are especially attractive to pollenophagus bats), Alvarez and Gonzalez Q. (1970:156) expressed the opinion that *C. mexicana* is an obligate pollen feeder.

Genus **Musonycteris** Schaldach and McLaughlin

**Musonycteris harrisoni**

Probably pollen, nectar, and insects.

Schaldach and McLaughlin (1960) remarked on *M. harrisoni* feeding on the nectar of banana flowers in Colima, México. I noted pollen on the heads and faces of several *M. harrisoni* caught in a small banana grove in Colima (some of these specimens were included in the report by Schaldach and McLaughlin, 1960). Villa-R. (1967) stated that this species feeds on pollen, nectar, and insects found in banana flowers.

**Subfamily Carollinae**

Genus **Carollia** Gray

**Carollia castanea**

A variety of fruits and insects.
Because *C. castanea* has been confused with *C. sub Rufa* and *C. breviceuda* by many investigators, it is difficult to ascribe correctly the information on food habits in many of the accounts on *Carollia* to this species even when the name *C. castanea* was cited. A notable exception is the report by Fleming *et al.* (1972) on bats from Costa Rica and Panamá. Sixty-nine of the 102 stomachs of *C. castanea* they examined were empty. The other 33 stomachs contained approximately 92 per cent plant material (fruit) and 8 per cent insect remains. Included among the plant matter were 10 kinds of seeds. The stomachs of 28 *C. castanea* from Costa Rica and Panamá collected during all months of the year, except July and September, contained plant material exclusively. The stomach of a bat collected in July contained only insect matter. No information was given on the stomach contents for September-caught *C. castanea*. The eight May-caught *C. castanea* from Costa Rica reported on by Howell and Burch (1974) had been feeding on *Piper*. They were able to identify *Piper auritum* in three of the bats.

**Carollia sub Rufa**

Probably fruit, flowers, and insects.

Many investigators have confused *C. perspicillata*, *C. breviceuda, and C. castanea* with this species. Information, however, in the accounts by Sanborn (1936) and Starrett and de la Torre (1964) probably apply to this species. Starrett and de la Torre (1964:58-59) stated: “Several types and colors of fruit pulp were taken from the digestive tracts of both specimens [from El Salvador], along with bat hairs. A small stalked inflorescence was also found in the small intestine of one, and a segment of an insect leg in the tract of the other.” Sanborn (1936) related catching a *C. sub Rufa* in a steel trap set on a bunch of bananas in Escobas, Guatemala.

**Carollia breviceuda**

A variety of fruits and probably insects as well.

According to Dalquest (1953:30), in San Luis Potosí, México, “*Carollia perspicillata* [= *C. breviceuda*—see Pine, 1972:35, 38] feeds entirely on fruit. It does some damage to stored bananas, but wild figs and other wild fruits constitute its principal food.” Hall and Dalquest (1963:231) reported that the stomachs of *C. perspicillata* (= *C. breviceuda*—see Pine, 1972:35, 38) taken in Veracruz, México, “held a semi-liquid mass of yellow pulp, probably of the wild sweet-lemon or wild orange.” They also referred to four occasions when *C. breviceuda* were caught in banana-baited snap traps. Three were taken in traps on the ground and the fourth was caught in a trap suspended above a stem of ripe bananas hanging in a tree. Villa-R. (1967-269) reported that he observed this species in San Luis Potosí, México, eating cakes of raw sugar that were hanging high up in the eaves of a house.

**Carollia perspicillata**

A variety of fruits, flowers, and insects.
Many reports on *C. perspicillata* simply call it a frugivore (Park and Hall, 1951; Goodwin, 1946; Valdivieso and Tamsitt, 1962; Tamsitt and Valdivieso, 1965; McNab, 1969). Davis (1945) recorded instances in Brazil where *C. perspicillata* were caught in banana-baited snap traps set on the ground. Tuttle (1970) also reported catching several of this species in rat traps (baited with bananas) set on the ground and mentioned that in Peru these bats entered Indian houses to eat bananas. Ruschi (1953) gave the diet of Brazilian *C. perspicillata* as fruit and insects. Goodwin and Greenhall (1961) and Greenhall (1956, 1957) cited the fruits of 23 species of plants consumed by this species in Trinidad (see Table 3). Goodwin and Greenhall (1961:250) also stated: "If the fruit is large, the bat eats it while hanging in the tree; if small, the fruit is plucked and carried by the bat to a temporary roost, called ‘digesting place’ to be eaten... Some fruit is carried to the regular daytime roost."

Starrett and de la Torre (1964:58) described the contents of the digestive tracts of four *C. perspicillata* from Honduras and Costa Rica as "several types of fruit pulp, seeds and vegetable fibers." Arata et al. (1967) reported on the stomach contents of 74 Colombian *C. perspicillata*. They found 71 with plant material, 16 containing insects, and 6 with matted hair, claws, and flesh. The remains of bats (claws and flesh) in the stomachs could be the result of holding the bats together for a period of time after they were caught and may not represent normal food items for this species (see account of *Glossophaga soricina* for the discussion of a similar situation). Howell and Burch (1974) reported recovering the following food items from Costa Rican *C. perspicillata*: the fruits of *Piper, Cecropia, Heisteria, Licania, Acmistus, Solanum, Mangifera*, an unidentified large-seeded Solanaceae, and the remains of unidentified insects as well as those of Coleoptera.

**Summary.**—Many of the reports on *Carollia* confused the species *C. castanea*, *C. subrufa*, *C. perspicillata*, and *C. brevicauda*. In some instances, species can be recognized because only one is known to occur in the region discussed; for example, *C. brevicauda* in San Luis Potosí, México (Pine, 1972:38). Villa-R. (1967:269) stated that *Carollia* eat *Musa* sp., *Diospyros ebenaster*, *Achras sapota*, *Casimiroa edulis*, *Ficus* spp., and pitahayas (*Lemaireocereus*) in México. Duke (1967) remarked that *Carollia* eat almost any fruit in Panamá, and he cited, as examples, *Cecropia, Ficus, Mangifera, Musa, Piper*, and *Psidium*. Fleming et al. (1972) acknowledged that their sample of *Carollia* from Costa Rica and Panamá included *C. brevicauda* and *C. perspicillata*. They examined 760 stomachs and found 272 with food items that consisted of about 87 per cent plant matter and 13 per cent insect remains, by volume. The plant material included a wide variety of fruits as determined from the 22 kinds of seeds present in the stomachs analyzed. Stomachs either contained all plant matter or a combination of plant and insect remains.

Heithaus et al. (1975) also pointed out that their *C. "perspicillata*" from Costa Rica probably included more than one species. Nevertheless, they concluded that these bats were primarily frugivorous but utilized nectar during the dry
Table 3.—Plants utilized in the diets of Carollia perspicillata, Artibeus jamaicensis, and Artibeus lituratus.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Part eaten*</th>
<th>C. perspicillata</th>
<th>A. jamaicensis</th>
<th>A. lituratus</th>
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</table>
season. The six most common pollens found on these bats were *Ochroma lagopus*, *Hymenaea courbaril*, *Pseudobombax septinatum*, *Crescentia sp.*, *Manilkara zapota*, and *Ceiba pentandra*. Identifiable fruit remains recovered in the feces of these bats included *Ficus* sp., *Muntingia calabura*, *Solanum* sp., and *Piper tuberculatum*. They reported 38.2 per cent of 186 bats with pollen, 32.4 per cent of which carried two or more species of pollen; 44.9 per cent of 316 bats with seeds in their feces; and 13.0 per cent of 272 bats had consumed insects (percentage by volume; data from Fleming et al., 1972).

Klute (1965) reported on the transit time through the digestive tract of dyed fruits in three Neotropical bat species from Panama including three individuals he identified as *C. perspicillata*. When India ink was used as a marker, two of the three *Carollia* passed stools containing the ink after a time lapse of 30 minutes. These results indicate that some frugivorous species are able to extract the nutritive components of their food in a very short time and may consume several times more fruit in a single night than the holding capacity of the stomach would suggest.

**Genus Rhinophylla Peters**

**Rhinophylla pumilio**

Presumedly fruit.

McNab (1969) considered *R. pumilio* to be frugivorous. Tuttle (1970) recorded capturing a male in a banana-baited trap set on the ground beneath ferns in dense mature forest in Peru.

**Summary.**—The food habits of *Rhinophylla alethina* and *R. fischeri* are not known. Bats of this genus are probably all frugivores, although they may consume insects as well.
**Biology of the Phyllostomidae**

**Subfamily Stenoderminae**

**Genus Surnira Gray**

*Surnira lilium*

A variety of fruits and possibly pollen and nectar as well.

Most accounts on *S. lilium* simply state that the species is frugivorous (Goodwin, 1946; Tamsitt and Valdivieso, 1961; Villa-R., 1967; McNab, 1969). Several investigators have mentioned finding the remains of fruit in the digestive tracts of these bats (Dalquest, 1953; Goodwin and Greenhall, 1961; Starrett and de la Torre, 1964; Arata et al., 1967; Fleming et al., 1972). Cockrum and Bradshaw (1963) reported on a *S. lilium* shot from among several bats observed feeding on wild figs (*Ficus*) growing along the Rio Cuchajaqui in southern Sonora, Mexico. Villa-R. and Villa Cornejo (1969, 1971) remarked that *S. lilium* take the fruit of the date palm and are attracted to ripe bananas in northern Argentina. Sanborn (1936) referred to a specimen caught in a steel trap placed on a bunch of bananas in Escobas, Guatemala. Gaumer (1917) reported that *S. lilium* in Yucatán, México, eat insects, although he said their principal food was fruit. Ruschi (1953k) also gave the diet of *S. lilium* in Brazil as fruit and insects. I have collected *S. lilium* at Balta on the Rio Curanja, Departamento de Loreto, in eastern Perú, the feces of which contained the seeds of Cecropia sp. and Piper sp. One entered a mist net while carrying a catkin of Cecropia sp. in its mouth.

Heithaus et al. (1974) reported recovering Bauhinia pauleia pollen from a specimen near Cañas, Costa Rica, and mentioned (p. 418) that “*S. lilium* visited other flowers in the study region.” The latter observation was substantiated by Heithaus et al. (1975) who reported finding pollen on 41.8 per cent of 110 Costa Rican *S. lilium* of which 47.8 per cent carried two or more species of pollen. The six most common pollens they recovered were Crescentia sp., Pseudobombax septinatum, Manilkara zapota, Hymenaea courbaril, Ochrosia lagopus, and Ceiba pentandra. Most of the fruit remains found in the feces were unknown; however, they were able to identify the seeds of Piper tuberculatum, Muntingia calabura, and Solanum sp. Howell and Burch (1974) reported the following food items recovered from *S. lilium* in Costa Rica: insects (Lepidoptera), pollen (Ceiba), and fruit (Piper, Lacantia, Muntingia, Acnistus, Solanum, melastomaceous fruit, and large-seeded solanaceous fruit).

*Surnira tilidae*

Fruit.

Goodwin and Greenhall (1961) reported finding purplish fruit juice in the stomach of a *S. tilidae* from Trinidad.

*Surnira mordax*

Fruit.
Howell and Burch (1974) reported recovering the identifiable remains of the fruits of *Centropogon*, *Anthurium*, *Musa*, and *Cecropia* from *S. mordax* in Costa Rica.

**Sturnira ludovici**

Fruit.

Dalquest (1953) wrote that he observed *S. ludovici* feeding on tree fruits in San Luis Potosí, México. Tschudi (1844) mentioned that *S. oporophium* (= *S. ludovici*) eats fruit, but he also believed that this species feeds on blood. Starrett and de la Torre (1964) remarked on *S. ludovici* from Costa Rica that had fruit pulp in their digestive tracts. Howell and Burch (1974) reported another specimen from Costa Rica that had consumed fruit.

**Sturnira erythromos**

Fruit.

The only account containing food habits information is that by Tschudi (1844), who stated that this species feeds on fruit. In addition, he (1844:67) related an incident where a bat he identified as this species bit a sleeping drunken Indian on the nose and became so engorged with blood that it could not fly. The bat was captured and taken back to Europe as a specimen. This bat was undoubtedly a desmodontine and not a *Sturnira*, and, inasmuch as Tschudi described the species *S. erythromos* in this publication (the holotype was not the same specimen mentioned above), he may not have witnessed the incident personally.

*Summary.*—No information has been published on the food habits of *Sturnira thomasi*, *S. magna*, *S. bidens*, *S. nana*, and *S. aratathomasi*; nevertheless, the diets of these species most likely include a wide variety of fruits. Duke (1967), relating information from Edwin Tyson, said the foods eaten by *Sturnira* in Panamá “consist mainly of fruits, e.g. *Piper*, *Psidium*.” Gaumer (1917) and Ruschi (1953a) mentioned insects in the diet of *S. lilium*; however, the actual role of insects as food items of *Sturnira* is unknown.

Genus **Uroderma** Peters

**Uroderma bilobatum**

Various kinds of fruit and insects.

Most references that allude to the food habits of *U. bilobatum* simply state that this bat eats fruit or is a frugivore (Goodwin, 1946; Tamsitt and Valdivieso, 1965; Villa-R., 1967; Duke, 1967; Walker et al., 1964; McNab, 1969). Bloedel (1955) reported *U. bilobatum* eating the pericarp of small unidentified palm fruits in Panamá. Fruits, particularly of three species of *Ficus*, were recorded by de Carvalho (1961) as food items for this species in Brazil. Goodwin and Greenhalgh (1961) mentioned finding the remains of *Psidium guajava* in the stomachs of two *U. bilobatum* in Trinidad. Fleming, et al. (1972) cited 405 stomachs of *U. bilobatum* they examined from Costa Rica and Panamá. Of these, 320 contained
food remains consisting of approximately 76 per cent plant matter, 13 per cent insects, and 11 per cent unclassified material, by volume. Howel and Burch (1974) reported finding *Brosimum* in one and an unidentifiable green fruit in the other of the two *U. bilobatum* they examined in Costa Rica.

Summary.—The diet of *Uroderma magnirostrum* has not been reported; however, it probably includes fruit, flower products, and insects. I collected several *U. magnirostrum* at Balta on the Río Curanja, Departamento de Loreto, Perú, the fur of which was stained yellow from flower pollen or the heads and shoulders of which were dusted with pollen.

Both species of *Uroderma* likely are frugivorous but many also consume quantities of pollen, nectar, and insects found in flowers and fruit as well.

Genus *Vampyrops* Peters

**Vampyrops vitatus**

Fruit.

Tuttle (1970) reported that he netted several *V. vitatus* in Perú that were carrying large figs (*Ficus*). Howell and Burch (1974) listed *Cecropia* and *Aenius* as food items eaten by this species in Costa Rica.

**Vampyrops dorsalis**

Fruit and insects.

Arata et al. (1967) reported on the stomach contents of four Colombian *Vampyrops* identified as *V. dorsalis*. Three of the stomachs contained plant material and one contained insect remains. Their paper does not indicate whether the stomach containing insects was one of the three with fruit or was the fourth they examined.

**Vampyrops helleri**

Fruit.

Goodwin (1946), reporting on Costa Rican *V. helleri*, stated that it is a frugivorous species. Villa-R. (1967) also reported that Mexican *V. helleri* are frugivorous.

The remains of fruit have been noted in most analyses of stomach contents (Goodwin and Greenhall, 1961; Starrett and de la Torre, 1964; Arata et al., 1967; Fleming et al., 1972); however, Howell and Burch (1974) reported two Costa Rican *V. helleri* that had eaten both fruit (*Cecropia*) and insects (Lepidoptera). The other eight they examined had been feeding on the fruit of *Aenius*.

**Vampyrops lineatus**

A variety of fruits and insects.

Ruschi (1953) recorded the foods of Brazilian *V. lineatus* as various fruits and insects (especially lepidopterans of the family Sphingidae). McNab (1969) reported the diet as fruit.
Summary.—Nothing has been reported on the food habits of *Vampyrops infuscus*, *V. aurarius*, *V. nigellus*, *V. brachycephalus*, and *V. recifinus*. The diets of these and other species of *Vampyrops* probably consist of a variety of fruits, some insects, and possibly some flower products. Walker *et al.* (1964) and Duke (1967) presumed *Vampyrops* to be frugivorous.

**Genus Vampyrodes Thomas**

**Vampyrodes caraccioloi**

Fruit.

*Vampyrodes caraccioloi* is considered to be a frugivore (Goodwin, 1946; Walker *et al.*, 1964; Duke, 1967). Goodwin and Greenhall (1961) and Fleming *et al.* (1972) reported the contents of the stomachs they examined as consisting entirely of the remains of fruit.

**Genus Vampyressa Thomas**

**Vampyressa pusilla**

Fruit.

Goodwin (1946) considered Costa Rican *V. minuta* (= *V. pusilla*) to be frugivorous. Starrett and de la Torre (1964) reported finding a small amount of fruit pulp in the digestive tract of a *V. thyone* (= *V. pusilla*) from Nicaragua. Fleming *et al.* (1972) reported the stomach contents of one *V. pusilla* out of the eight they examined from Panamá as 100 per cent plant material. The others apparently were empty. Howell and Burch (1974) listed five from Costa Rica that had fed on the fruit of *Acestus*.

**Summary.**—The diets of *Vampyressa meiissa*, *V. nymphaea*, *V. brocki*, and *V. bidens* are not known. These species probably subsist primarily on fruits as was suggested for the genus by Walker *et al.* (1964) and Duke (1967).

**Genus Chiroderma Peters**

**Chiroderma villosam**

Fruit.

This species is presumed to be frugivorous (Goodwin, 1946; Goodwin and Greenhall, 1961; Villa-R., 1967).

**Chiroderma salvini**

Fruit.

Fruit-eating habits were reported by Goodwin (1946). Jones *et al.* (1972) implied that *C. salvini* eats figs inasmuch as they mentioned catching one along with *Artheus* and *Sturnira* in a net under a fig tree replete with ripe fruit in Sinaloa, México.
Chirodema trinitatum

Fruit.
A diet of fruit was suggested by Goodwin and Greenhall (1961).

Summary.—Nothing has been reported on the diets of Chirodema doriae and C. improvisum. Although the fruit diets of C. villosum, C. salvini, and C. trinitatum are based only on conjecture, these species probably do subsist primarily on fruits as suggested by Walker et al. (1964) and Duke (1967).

Genus Ectophylla H. Allen

Ectophylla alba

Presumably fruit.
Casebeer et al. (1963) reported finding small amounts of unidentified green vegetable matter in the lower intestine of E. alba from Costa Rica. I also found similar material in the digestive tracts of five Costa Rican specimens.

Summary.—The food habits of Ectophylla macconnelli are not known; however, this species most likely is frugivorous. Duke (1967) mentioned that the food habits were not known for species of Ectophylla and attributed to Edwin Tyson the opinion that Panamanian species are insectivorous.

Genus Artibeus Leach

Artibeus cinereus

Fruit and insects.
Goodwin and Greenhall (1961) stated that A. cinereus eats a variety of fruits in Trinidad, and Piccinini (1971) mentioned that this species is frugivorous in Brazil. Arata et al. (1967) noted that the stomachs of five Colombian specimens contained plant material and one of these held insect remains as well.

Artibeus watsoni

Fruit.
Fleming et al. (1972) reported only finding plant matter in two of the 53 stomachs of A. watsoni they examined from Costa Rica and Panamá. The other 51 stomachs were empty. Howell and Burch (1974) were able to identify Cecropia as the fruit eaten by the two A. watsoni they examined in Costa Rica.

Artibeus phaeotis

Fruit.
Villa-R. (1966) reported that A. turpis (= A. phaeotis) is frugivorous in México. Fleming et al. (1972) examined the stomach contents of 90 A. phaeotis from Costa Rica and Panamá. Of these, only two contained food, which was 100 per cent fruit pulp in each case. Heithaus et al. (1975) determined that 40 per
cent of 15 A. phaeotis in Costa Rica were carrying pollen when captured. Of these, 33.3 per cent carried two or more species of pollen. They found seeds in the feces of 8 per cent of 25 of these bats but did not identify any of the fruits consumed. The five most common pollens recovered were Ceiba pentandra, Crescentia sp., Ochroma lagopus, Pseudobombax septinatum, and Hymenaea courbaril.

**Artibeus toltecus**

Fruit.

Villa-R. (1967) reported observing A. toltecus eating the fruits of “amate prieto” (*Ficus padifolia*) in México. *Cecropia* was listed by Howell and Burch (1974) as the food eaten by the six they examined in Costa Rica.

**Artibeus hirsutus**

Presumably fruit.

Jones *et al.* (1972:13) wrote: “A specimen from . . . [Sinaloa, México] was shot as it sought food in a strangler fig [*Ficus coomonolia*].” Villa-R. (1967) suggested that the food habits are similar to those of *A. jamaicensis*.

**Artibeus jamaicensis**

Insects and a variety of plant materials such as fruits, flower products, and leaves.

Osburn (1865) reported finding the kernels of *Brosumum* strewn on the floor of a cave in Jamaica inhabited by *Artibeus carpolegus* (*= Artibeus jamaicensis*): Some of the nuts (p. 64) had “germinated into young blanched trees on the thick deposit of dung.” In other Jamaican caves used by this species he found dried seeds, berries of *Cordia collococca*, and husks that included gnawed fragments of unripe mangoes and the fruit of the rose-apple (*Eugenia jambos*). He (1865:66) also mentioned finding yellow juice and small seeds that he suspected were those of the fustic (*Morus tinctoria*) in the digestive tract of a specimen. Ortiz de la Puente (1951) related finding the male inflorescences of maize and, occasionally, seeds of *Erabotrya japonica* under roosts of *A. jamaicensis* in caves in western Perú. Van der Pijl (1957:294) referred to Heinz Feilen’s observations (personal communication) on regularly finding remnants of *Spondias purpurea* under colonies in caves in El Salvador. Bond and Seaman (1958) remarked that seeds and partly eaten fruits of mango, East Indian almond, hogplum, and other easily recognized food items were abundant under *A. jamaicensis* roosts in the Virgin Islands. Goodwin (1970:575) stated that the presence of *A. jamaicensis* in caves in Jamaica is usually indicated by a “garden” of pale, spindly, seedling plants growing on the floor beneath the roosting site. He identified the plants from two caves as *Andira inermis* and observed that the fruits of this tree are a staple food of *Artibeus*. Allen (1939) mentioned the presence of sprouted nuts of *Acrocomia* in a cave in Puerto Rico and stated that *A. jamaicensis* was fond of the thin layer of pulp surrounding the small nutlike fruits of this palm. Tuttle
(1968) remarked on finding the remains of several kinds of fruit on a large pile of guano beneath an *A. jamaicensis* roost in Chiapas, México. The remains included many hard nuts, each of which had been chewed open at one end. Beneath the roost, Tuttle (1968) also found discarded leafy twigs of which many of the leaves were chewed and appeared to have been partly eaten. While conducting his reconnaissance on the roosting site, he recorded the following observations (p. 787): "While I sat quietly a few feet below them, the bats began to catch and eat large (about 6 mm long) blackflies. The bats would hang by one foot and rotate in nearly complete circles watching the flies. Whenever a fly flew within reach of one of the bats, the bat would capture it with a rapid thrust of one of its wings. Flies were caught in the wing-tips and were immediately eaten. This behavior was observed repeatedly."

Quelch (1892:102) described the foraging behavior of *A. jamaicensis* in British Guiana (Guyana): "During the fruiting season, when the sapodillas, star-apples, mangoes, and such like fruit are ready to be gathered, numbers of these large bats are to be observed at sunset, flitting in and out among the leaves and branches, picking out and feeding on the ripest fruit to be found. They dart up and down repeatedly at the same fruit, remaining momentarily almost stationary while their teeth are applied, and with the force of their flight they cause either the tearing away of part of the soft pulp, or of the whole fruit, according to its degree of ripeness." Jimbo and Schwassmann (1967) reported *A. jamaicensis* feeding on sapodilla plums (*Achras sapota*), guava (*Psidium guajava*), and figs (*Ficus* sp.) at Belem, Brazil. The fruits, some weighing as much as 50 grams, were carried off. If the fruit was dropped, the bat sometimes would drop to the ground and eat part of it before flying away. Tamsitt and Vukliveso (1961) mentioned two occasions in Costa Rica when *A. jamaicensis* entered mist nets while carrying pomarrosa fruit (*Syzigium jambos*) in their mouths. One of the fruits measured 34.8 millimeters in diameter. Tuttle (1970) related catching an *A. jamaicensis* in Perú that was carrying a large (about 30 millimeters in diameter) wild fig in its mouth. I recovered pomarrosa and guava fruit carried into a mist net by *A. jamaicensis* in Villavicencio, Colombia. One of the larger guavas measured 42 millimeters in its greatest diameter and weighed 35 grams. A second measured 48 by 42 millimeters and weighed 50 grams. The largest was not weighed but measured 64 by 50 millimeters. Jones *et al.* (1972:13) recorded observations on *A. jamaicensis* in Sinuáloa, México, and stated, "individuals of this species were seen emerging from a hollow limb of a fig tree. They foraged higher in the tree, sometimes returning in approximately 10 minutes with cut green figs to the hollow." Dalquest (1953) recorded this bat feeding on fruits such as jobo plums (*Spondias* sp.) and green wild figs (*Ficus* sp.) in San Luis Potosí, México. He noted that the mouths of caves used as day roosts were commonly heaped with cores and seeds of fruit and small pellets of fruit skin and rind, which the bats eject when they eat. Hall and Dalquest (1963) also mentioned jobo plums and wild figs as foods of *A. jamaicensis* in Veracruz, México. Vázquez-Yáñez *et al.* (1975) reported the kinds and percentages by weight for each month of occurrence of the fruits they recovered from a cave inhabited by *A. jamaicensis* in the Tuxtla region of Vera-
cruz, México. The fruits they identified are Cecropia obtusifolia, Spondias mombin, Ficus spp., F. glabrata, F. obtusifolia, Poulsenia armata, Cynometra retusa, Calophyllum brasiliense, Brosimum alicastrum, Piper auritum, P. hispidum, P. amalago, P. sanctum, Turpinia pinnata, Solanum spp., Dendropanax arboreus, Quarrarobe fanebris, Anthurium sp., Licania sp., Muntingia calabura, Pseudolmedia oxyphyllaria, and Rhedia edulis. Dalquest et al. (1952) reported on the mucous salivary glands opening in the lips at the ventral angle of the lower jaw in *A. jamaicensis*. They interpreted the function of these glands as supplying the mucous that binds together the pelletized ejected unpalatable portions of the fruit these bats eat.

Greenhall (1956, 1957) and Goodwin and Greenhall (1961) presented nearly identical lists of foods eaten by *A. jamaicensis* (Table 3). Their information was based primarily on debris found beneath roosting sites in Trinidad. De Carvalho (1961) described a number of fruits utilized as food by *A. jamaicensis* in Brazil (Table 3). Villa-R. (1967) noted a number of fruits in the diet of Mexican *A. jamaicensis* as well as pollen and nectar from the flowers of Ceiba pentandra (Table 3). He also related having observed *A. jamaicensis* entering a small house in San Luis Potosí, México, to eat cakes of sugar that were stored near the ceiling. Goldman (1920) commented on catching several of this species at Gatún, Panamá, in traps placed about a bunch of ripening bananas. Starrett and de la Torre (1964) gave the stomach contents of *A. jamaicensis* from Nicaragua and Costa Rica as fruit pulp, plant fibers, and bat hairs. They also noted (p. 61) that a specimen "from Costa Rica also had an ant (Formicidae: Ponerinae) embedded in a reddish amber-like substance in its intestine." Arata et al. (1967) related finding only plant material in the stomach of a specimen they examined from Colombia. Fleming et al. (1972) reported on the 23 stomachs containing food material among the 916 digestive tracts they examined from Costa Rica and Panamá. The stomach contents, by volume, consisted of about 66 per cent plant matter, 25 per cent insect remains, and 9 per cent unclassified material. They also expressed the opinion that figs (*Ficus insipida*) were a favorite food of *A. jamaicensis* in the Panama Canal Zone. Howell and Burch (1974) identified insects (Coleoptera), pollen (*Hyphania, Ceiba, and Bombax*), and fruit (*Licania, Genipa, Muntingia, Brosimum, Ficus, Cecropia*, and melastomaceous fruit) as the food items they recovered from *A. jamaicensis* in Costa Rica.

Palmer (in Miller, 1904:347), in reporting the habits of *A. jamaicensis* in Cuba, wrote that "they evidently capture much of their food among flowering trees, as their fur often contains pollen and parts of flowers. These are also found abundantly on the floors of caves where the bats roost." Silva Taboada and Pine (1969) implied that either Palmer's observations were unusual or were in error as they had never found flower parts in the fur of Cuban *Artibeus*. However, Piccinini (1971) noted that several *A. jamaicensis* collected in Brazil during October were stained yellow by the pollen of *Anacardium occidentale* and he assumed that these bats, although primarily frugivorous, eat pollen when fruits are not available. Heithaus et al. (1974) recovered *Bauhinia pauletii* pollen from the fur of two *A. jamaicensis* near Cañas, Costa Rica. Heithaus et al. (1975)
reported recovering pollen from the fur of 54.1 per cent of 477 individuals in Costa Rica of which 43 per cent were carrying two or more species of pollen. Only 8.6 per cent of 617 *A. jamaicensis* had seeds in their feces. The six most common pollens they recorded were *Crescentia* sp., *Manilkara zapota*, *Hymenaea courbaril*, *Pseudobombax septinatum*, *Ochroma lagopus*, and *Ceiba pentandra*. The identifiable fruit remains they recorded were *Piper tuberculatum*, *Solanum* sp., *Muntingia calabura*, and *Ficus* sp. Hall and Kelson (1959) described the food of *A. jamaicensis* as mainly ripe fruits, the small kinds of which are plucked and carried to the feeding sites. McNab (1969) and Tamsitt and Valdivieso (1970) merely stated that the species is a frugivore.

**Artibeus lituratus**

Insects and a variety of plant matter including fruit, flowers, and leaves.

Valdivieso and Tamsitt (1962), Tamsitt and Valdivieso (1965), and McNab (1969) considered *A. lituratus* to be frugivorous. Dalquest (1953) reported on finding the ground beneath the roosts of this species in San Luis Potosí, México, littered with the small, brown pellets of rind and skin of fruit ejected by the bats as they fed. Van der Pijl (1957:294) quoted Heinz Felten (personal communication) who told him of regularly finding remnants of *Ficus* sp. under colonies in caves in El Salvador. Bloedel (1955:235), writing about Panamanian bats, mentioned that *A. lituratus* “dropped many sparse beans below their habitual roosting place.” Villa-R. and Villa Cornejo (1969, 1971) reported that they observed numbers of *A. lituratus* taking either ripe palm fruit or pollen from flowers in northern Argentina. Tamsitt and Valdivieso (1963) commented on twice netting *A. lituratus* that were carrying ripe almond fruits in their mouths. Greenhall (1956, 1957) and Goodwin and Greenhall (1961) listed a number of plant species utilized in the diet of this species (Table 3). The plant foods listed by Goodwin and Greenhall (1961) were cited as foods for both *A. lituratus* and *A. jamaicensis*. Villa-R. (1967) also stated that these two species have similar food habits in México.

Ruschi (1953a) presented information on the stomach contents of *A. jamaicensis lituratus* (= *A. lituratus*) from Brazil. He claimed (p. 3) to have found coagulated blood in addition to fragments of fruit in the stomachs of these bats. Ruschi (1953b), in addition to listing a number of the principal fruits eaten by these bats (Table 3), elaborated on his earlier report on finding blood among the stomach contents. He referred to capturing several *A. lituratus* alive in a palm tree and later finding blood in their stomachs. I recommend, however, that blood not be considered a normal food for *Artibeus*; the blood in the stomachs may be explained as having come from the cleansing of wounds acquired during fighting among the bats as they were held together subsequent to their capture. Nevertheless, in support of his opinion on the alleged blood-feeding habits of this species, Ruschi mentioned (p. 7) having surprised an *A. lituratus* in the act of eating nestling robins (*Turdus rufiventris*) and noted that these bats accepted blood, in addition to fruit and insects, as food in captivity. Ruschi also observed *A. lituratus* pursue and capture sphingid moths.
Starrett and de la Torre (1964:61) remarked on finding “fruit pulp of several colors and types, plant fibers and bat hairs... [as well as] a few small scattered insect remains” in the digestive tracts of *A. lituratus* from El Salvador, Nicaragua, and Costa Rica. Arata *et al.* (1967) reported on four Colombian *A. lituratus* they examined; three stomachs contained plant material and one contained insect remains. Fleming *et al.* (1972) reported the contents of seven out of the 93 stomachs of *A. lituratus* they examined from Costa Rica and Panama as 75 per cent plant matter and 25 per cent insect remains, by volume. Howell and Burch (1974) listed a large-seeded *Piper* as having been consumed by a Costa Rican *A. lituratus*. Heithaus *et al.* (1975) identified the pollen of *Crescentia* sp., *Ochroma lagopus*, *Ceiba pentandra*, and *Manilkara zapota* taken from the fur of representatives of this species in Costa Rica.

Summary.—The diets of *Artibeus glaucus*, *A. aztecus*, *A. inopinatus*, and *A. concolor* are not known; however, these species probably have feeding habits similar to those of the other species of *Artibeus* previously mentioned. These bats are primarily frugivorous but consume pollen, nectar, flower parts, and insects as well. Duke (1967) cited *Acrocomia, Anacardium, Brosimum, Cecropia, Cordia, Eugenia, Ficus, Mangifera, Musa, and Persea* as plants of which fruit is utilized by Panamanian *Artibeus*. Howell and Burch (1974) reported six small *Artibeus* sp. that had fed on *Cecropia* fruit in Costa Rica. The finding of relatively large volumes of insect remains (25 per cent) in the stomachs of Costa Rican and Panamanian *A. jamaicensis* and *A. lituratus* (Fleming *et al.*, 1972) indicates that insects are an important food source for these bats. The utilization of blood and small vertebrates as foods by *A. lituratus* (Ruschi, 1953a; 1953b) is to be considered atypical.

**Genus Enchisthenes Anderson**

*Enchisthenes hartii*

Fruit.

Goodwin (1946) and Goodwin and Greenhall (1961) stated that *E. hartii* is frugivorous. From observations on this species in the vicinity of Ciudad Guzmán, Jalisco, México, de la Torre (1955:700) wrote: “The fruit [*Ficus* sp.] eaten in the area is small, about a centimeter in diameter. It is quickly snipped from the tree in flight, and carried to a convenient branch where it is eaten.” Villa-R. (1967:319), reporting on two specimens from the same area in Jalisco, claimed also to have observed *E. hartii* plucking ripe figs.

**Genus Ardops Miller**

*Ardops nichollsi*

Presumably fruit.

Walker *et al.* (1964) commented that *A. nichollsi* was presumed to damage cacao (*Theobroma cacao*) by eating the fruits. Additional information on its food habits is lacking.
Genus Phyllops Peters

Phyllops falcatus and Phyllops haitiensis

Presumably wild figs.

Hall and Kelson (1959) employed the common names “Cuban Fig-eating Bat” (P. falcatus) and “Dominican Fig-eating Bat” (P. haitiensis) for these species. Allen (1942) also considered them to be frugivorous; however, detailed information on their food habits is lacking.

Genus Ariteus Gray

Ariteus flavescens

Fruits and insects.

Gosse and Hill (1851) reported A. achradophilus (= A. flavescens) eating the fruit of the naseberry tree (Achras sapota) in Jamaica. The bats either fed on the fruit in the tree or carried large pieces away to be eaten elsewhere. They also mentioned that this species feeds on the rose-apple (Eugenia jambos). Walker et al. (1964) repeated this information, and remarked that A. flavescens eats insects as well. Hall and Kelson (1959) referred to A. flavescens as the “Jamaican Fig-eating Bat.”

Genus Stenoderma É. Geoffroy St.-Hilaire

Stenoderma rufum

Fruit.

Although considered to be a frugivore (Allen, 1942; Tamsitt and Valdivieso, 1970; Genoways and Baker, 1972) the diet is unknown. According to Thomas (1894:132), S. rufum is “said to do much damage to the cacao plantations” on the island of Montserrat. Hall and Kelson (1959) applied the name “Red Fig-eating Bat” to this species.

Genus Pygoderma É. Geoffroy St.-Hilaire

Pygoderma bilabiatum

Probably fruit.

The species is alleged to feed on fruits (Goodwin, 1946; Walker et al., 1964).

Genus Ametrida Gray

Ametrida centurio

Probably fruit.

The diet is unknown.

Genus Sphaeronycteris Peters

Sphaeronycteris toxophyllum

Probably fruit.

The diet is not known.
Genus Centurio Gray

Centurio senex

Fruit.

Goodwin and Greenhall (1961) mentioned finding yellow fruit pulp in stomachs of C. senex from Trinidad. Walker et al. (1964) gave the diet as “soft mushy fruits.” Felten (1956) may have meant to imply that C. senex feeds on figs (Ficus sp.) in El Salvador when he mentioned collecting a specimen when it was flying around a fig tree.

Subfamily Phyllonycterinae

Genus Brachyphylla Gray

Brachyphylla cavernarum

Fruits and insects.

Bond and Seaman (1958:151), reporting on a roost of B. cavernarum in the Virgin Islands, noted, “an examination with a hand lens of the washed guano shows it to contain a high proportion of insect fragments, and some amorphous material which may or may not be fruit pulp. Seeds and partly eaten fruits are [present] in Arthaeus guano. No such material was found in the guano of Brachyphylla, although a few small seeds of what appears to be a species of Eugenia were seen. These seeds could have passed through the bats or been brought in by mice. These observations could mean either that Brachyphylla is entirely insectivorous, or that it eats fruit but avoids small seeds, and cannot carry larger-seeded fruits back to the roost as does Arthaeus.” Nellis (1971) found B. cavernarum on St. Croix, Virgin Islands, feeding on the fruits of Manilkara zapota. Hall and Kelson (1959) and Tamsitt and Valdivieso (1970) referred to this species as the “St. Vincent Fruit-eating Bat.”

Brachyphylla nana

Fruit, pollen, nectar, and insects.

Silva Taboada and Pine (1969) presented information on the contents of 43 stomachs of B. nana from Cuba. All stomachs contained masses of what appeared to be partially digested pollen grains. One stomach contained lepidopteran scales and another held fragments of a fly (Diptera). In Cuba, Silva Taboada frequently encountered individuals the head, chest, and shoulders of which were dusted with pollen. Silva Taboada and Pine (1969:15) considered B. nana, as well as Cuban Phyllonycteris and Erophylla, primarily to be “pollen eaters which probably also feed on soft fruit pulp and nectar.”

Genus Erophylla Miller

Erophylla bombifrons

Fruit, pollen, nectar, and insects.

Hall and Kelson (1959) referred to E. bombifrons as the “Brown Flower Bat”; however, Tamsitt and Valdivieso (1970) said it is frugivorous.
Erophylla sezekorni

A variety of fruits, pollen, nectar, and insects. Osburn (1865) reported on finding breadnut kernels and munched berries of the clammy cherry (Cordia collococca) associated with cave roosts of bats he referred to as Monophyllus (= Erophylla sezekorni) in Jamaica. The stomach of one specimen he examined (p. 82) "was filled with a yellowish frothy pulp." Osburn described the feeding behavior of a captive: "The tongue was rapidly protruded and drawn in again, and the juice and softer pulp cleared away with great rapidity. I noticed he was very particular in cleaning out the bit of loose skin of the berry [Cordia collococca]." Osburn also noted (p. 84) the similarity of the berries eaten by this bat and those found beneath the cave roosts. Silva Taboada and Pine (1969) presented information on the stomach contents of 30 E. sezekorni from Cuba. They found masses of partially digested pollen grains in all stomachs. In addition, three contained seeds of broneliaceous fruits (Hohenbergia) and four held insect remains identifiable as parts of an elaterid beetle (Conoderus), a roach (Orthoptera, Blattidae), Diptera, Lepidoptera, and Microlepidoptera. Silva Taboada and Pine (1969:15) expressed the opinion that E. sezekorni (along with Cuban Brachyphylla and Phyllonycteris) "are primarily pollen eaters which probably also feed on soft fruit pulp and nectar." Hall and Kelson (1959) referred to E. sezekorni as the "Buffy Fruit Bat."

Genus Phyllonycteris Gundlach

Phyllonycteris poeyi

Probably a variety of fruits, pollen, nectar, and insects. Allen (1942:26-27) commented that P. poeyi have "long protrusive tongues, which are useful in licking up fruit pulp and juices on which they largely feed. Probably pollen and nectar are also eaten." Silva Taboada and Pine (1969) reported the stomachs of 42 P. poeyi they examined from Cuba as containing masses of what appeared to be partially digested pollen grains. One stomach also contained lepidopteran scales. They commented (p. 15) "that the Cuban representatives of Brachyphylla, Phyllonycteris, and Erophylla are primarily pollen eaters which probably also feed on soft fruit pulp and nectar."

Summary.—The diets of Phyllonycteris major and P. aphylia are not known; however, these "Flower Bats" (Hall and Kelson, 1959) likely have food habits similar to those of P. poeyi and include fruit, pollen, nectar, and insects in their diets.

Subfamily Desmodontinae

Genus Desmodus Wied-Neuwied

Desmodus rotundus

Blood of warm-blooded animals.

The folklore surrounding the sanguivorous habits of D. rotundus, enhanced by the imaginations of the early explorers and naturalists who visited the New World
tropics, produced fascinating narratives on the bloodsucking vampires. A few of these accounts have been related by Husson (1962:12-18, 192-197). Most of the early naturalists ascribed awesome proportions and properties to vampires and mistakenly attributed the feeding habits of the desmodontines to Vampyrus spectrunc, Phyllostomus hastatus, and Chrototperus auritus, among other bats.

The majority of the reports concerning the prey of D. rotundus has been limited to man and his domestic animals. Darwin (Waterhouse, 1838:2) was apparently one of the first to witness D. rotundus on its prey and, on this subject, Waterhouse observed, "Before the introduction of the domesticated quadrupeds, this Vampire Bat probably preyed on the guanaco, or vicugna, for these, together with the puma, and man, were the only terrestrial mammalia of large size, which formerly inhabited the northern part of Chile." Dalquest (1955) did not find scars from vampire bites on any of the white-tailed deer, brockets, collared and white-lipped peccary, and tapir he examined from eastern Mexico. Apparently the selection of prey varies from one region to another because Dalquest (1955) observed that Desmodus seems to prefer the blood of burros and calves over that of horses and adult cattle, and does not appear to feed on domestic fowl in Veracruz, Mexico. In eastern San Luis Potosí, Mexico, however, Desmodus extensively preys on domestic turkeys and chickens as well as on adult cattle. On the Mexican Plateau in western San Luis Potosí, horses, cattle, and burros again are favored, but chickens are rarely molested. Despite clear evidence that children had been bitten by vampire bats in both Veracruz and San Luis Potosí, their parents denied that bats were responsible. Instead, they attributed those bites to brujas (witches). Dalquest (1955) also stated that children seemed to be bitten more often than adults, and, of the latter, women more often than men.

Many authors (see Linhart, 1971, for a partial bibliography of the literature pertaining to vampire bats), have mentioned D. rotundus feeding on domestic livestock, poultry, and humans. Two of the more informative accounts are those of Goodwin and Greenhall (1961:268-269) and Villa-R. (1967:30-37, 334-336). Detailed information, particularly relating to observations on the mode of attack, biting, bite sites, and feeding behavior, has been reported by Mann (1951), Greenhall (1972), Greenhall et al. (1969, 1971), and Turner (1975).

Wimsatt and Guerreire (1962) and Wimsatt (1969) suggested a conservative daily consumption of 20 milliliters of blood per day or about 7.3 liters per year per individual. They projected a minimum annual consumption of 730 liters of blood for a moderate-sized colony (approximately 100 adults). This is about one-third the estimated consumption per individual postulated by Goodwin and Greenhall (1961:269). Miller (Allen, 1916:603) remarked, "It is said [in Brazil] that blood-sucking bats vary their diet with insects." Arata et al. (1967) reported on the stomach contents of 23 D. rotundus from Colombia. Although all stomachs contained blood, four contained insect remains and four contained flesh. They stated (p. 654) that "the insect remains found in Desmodus stomachs consisted of a whole ingested ectoparasite... and well-broken remains of larger insects." Rouk and Glass (1970:456) stated that "a few insect remains [found] in one specimen... supports the observation of Arata (et al., 1967) [sic]."
Greenhall (1972:485), commenting on these observations, remarked, “I have examined thousands of *Desmodus* stomach contents and have also found the remains of some insects as well as flesh ‘divots.’ Presumably the insects became trapped in the viscous blood and were thus swallowed.” The insects also could have become caught in the congealing exudate from the wound and ingested with the scab at a later bout of feeding. The ectoparasite was probably consumed either during grooming activities by the bat or when preparing the bite site on a prey animal.

Villa-R. *et al.* (1969) related the results from analyzing the stomach contents of 79 *D. rotundus* from Brazil. They found 58 (73.4 per cent) contained mammal blood, 8 (10.1 per cent) with mixed bird and mammal blood, and 13 (16.5 per cent) held milk. The 13 *Desmodus* containing milk were judged to be juveniles although they were the size of adults. These investigators concluded that *D. rotundus* tends to prefer the blood of mammals and augmented their observations by noting (p. 296) that Guillermo Mann had communicated to Amelio Malaga Alba information on the predation by *Desmodus* on seals (Otaridae) along the Pacific coast of Chile.

**Genus Diaemus Miller**

**Diaemus youngii**

Avian and mammalian blood.

Very little is known of the food habits of *D. youngii* except that it seems to prefer avian blood. Goodwin and Greenhall (1961) stated that this species preys upon poultry, pigeons, and goats in Trinidad. They commented (p. 272), “Usually, when poultry and goats are attacked in an area, to the obvious exclusion of cattle and equines, *Diaemus* have been collected.” Villa-R. (1967:341), relating a personal communication from Reaznet Darnell, reported that a *D. youngii*, captured near El Encino, Tamaulipas, México, was feeding on the blood of a chicken.

**Genus Diphylla Spix**

**Diphylla ecaudata**

Avian and mammalian blood.

Moojen (1939:7) reported *D. ecaudata* preying on chickens in Brazil. Ruschi (1951) reported *D. ecaudata*, also in Brazil, feeding on the blood of mammals and birds. He mentioned (p. 2) domestic chickens, turkeys, Guinea fowl, ducks, and geese as preferred prey, but stated that *Diphylla* feeds on pigs, cattle, and equines as well. Later, Ruschi (1953a:7) described a *D. ecaudata* feeding on a sleeping man in the state of Bahia, Brazil. Dalquest (1953:40-41) wrote, “Vampire bats, probably of this species, attack chickens near Xilitla [San Luis Potosí, México], biting them on the lower part of the leg where the feathers are scant. *Diphylla ecaudata* probably preys on horses, burrows, and cattle.” This is essentially the same information given by Walker *et al.* (1964) and Duke (1967). Koopman (1956:548) cited a specimen from San Luis Potosí, that “according to the field
tag, was killed while feeding on chickens.” Villa-R. (1967) stated that *D. ecaudata* appears to prefer the blood of birds. The stomachs of 18 Brazilian *D. ecaudata* examined by Villa-R. *et al.* (1969) contained bird blood exclusively.

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BIOLOGY OF THE PHYLLOSTOMATIDAE


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MOVEMENTS AND BEHAVIOR

M. BROCK FENTON AND THOMAS H. KUNZ

The published information on movements and behavior of phyllostomatids is limited and mainly anecdotal. However, owing to several technological developments, notably the availability of image intensifiers and microcircuits, new advances are anticipated in these areas. Both these tools have already been used to good advantage (see Schmidt and Greenhall, 1972; Williams and Williams, 1970) by providing means of studying, with minimal disturbance, the behavior and movements of bats under natural conditions. Concurrently, the successes of several workers (for example, Racey and Kleiman, 1970; Rasweiler and Ishiyama, 1973; Wimsatt et al., 1973) at maintaining various bats in captivity will encourage comparative studies of specific behavior patterns and responses under controlled conditions.

We expect that together these developments will produce a series of important studies of the movements and behavior of phyllostomatids in particular and bats in general. The results of such studies, when considered in the context of other work (such as the evolutionary and energetic implications of fruit and nectar feeding—Morton (1973) and Heinrich and Raven (1972), respectively—will permit observations on bats to be placed in a general biological context.

The availability of the aforementioned instruments and successes at maintaining bats in captivity would not be as significant as they are if it were not for the work that has been done on the systematics, distribution, and natural history of phyllostomatids. Only when such technological developments can be applied in areas where a good basic knowledge of the bats exists do they assume great importance. Specific areas that come to mind in this context include Trinidad (Goodwin and Greenhall, 1961; Williams and Williams, 1970), Costa Rica and Panamá (Brown, 1968; LaVal, 1970; Fleming et al., 1972), and various islands in the West Indies (Goodwin, 1970; Jones and Phillips, 1970).

MOVEMENTS

Circadian

The roosting and feeding habits of bats govern the frequency and magnitude of daily movements between roosts and feeding grounds. Presently, little detailed information is available concerning foraging movements and territories of bats, but phyllostomatids provide one partial exception to this general situation.

Using radio tracking, Williams and Williams (1970) documented the feeding flights of *Phyllostomus hastatus* from three caves in Trinidad. Upon leaving the caves (the day roosts), bats flew directly to areas where they alternately roosted and made short flights in the feeding area. Feeding areas ranged from one to five kilometers in straight-line distances from the caves, and some individuals travelled four kilometers to reach a feeding area only three kilometers distant.
This study appears to be the only instance in which the movements of phyllostomatids between day roosts and feeding grounds have been documented.

Data obtained by banding (LaVal, 1970; Fleming et al., 1972) indicate that some phyllostomatids have regular feeding grounds. Further evidence of this is provided by the observations of Baker (1973) concerning the visits of some glossophagines and one stenodermine to flowers. *Leptonycteris sanborni*, *Glossophaga sp.*, *Glossophaga soricina*, and *Artibeus jamaicensis* have been observed to make fleeting visits to flowers (Baker, 1973). Baker (1973) and others (Vogel, 1968-69; Baker et al., 1971) have remarked on the “trap lining” nature of these visits, which appears to indicate regular patterns of movements.

Phyllostomatids, including *Macrotrus waterhousii* (Vaughan, 1959), *Lonchorina aurita* (Nelson, 1965), and *Leptonycteris sanborni* (Hayward and Cockrum, 1971), but especially the Phyllonycterinae and the Desmodontinae, are active later in the evening than are many other bats (see Silva Taboada and Pine, 1969; Leen and Novick, 1969; Wimsatt, 1969; Crespo et al., 1972). In lowland rainforest in Guyana, one of us (Fenton) made similar observations. Using mist nets and ultrasonic detectors (Fenton et al., 1973), it was established that emballonurids, mormoopids, vespertilionids, and molossids were most active around dusk and dawn, whereas phyllostomatids (including *Phyllostomus elongatus*, *Glossophaga soricina*, *Carollia perspicillata*, *Rhinophylla pumilio*, *Stenira lilotum*, *Uroderma bilobatum*, *Vampyrops helleri*, *Vampyressa bidens*, *Chiroderma villosum*, *C. trinitatum*, *Ectophylla macconnelli*, *Artibeus cinereus*, *A. concolor*, *A. lituratus*, *Amotrita centuria*, and *Desmodus rotundus*), based on captures in mist nets, were active later in the evening and throughout the night until about one hour before dawn. Further observations on phyllostomatid activity have recently appeared (Heithaus et al., 1974; Tuttle, 1974; Davis and Dixon, 1976).

In part, these temporal differences can be accounted for by the sequence of departures from the day roosts. At Mount Plenty Cave in Jamaica, Leen and Novick (1969) observed that *Monophyllus redmani* was the first species to depart in the evening, followed by *Pteronotus psilotis*, *P. parnellii*, *Artibeus jamaicensis*, and *Phyllonycteris sp.* Whether or not these departures represent differential sensitivity to light, roost locations, or differences in circadian periodicity remains to be determined.

Captures of bats at different locations during the night have been used to indicate activity patterns (Brown, 1968; LaVal, 1970). However, comparison of activity patterns from different areas or seasons is difficult because the basic patterns of activity reflect, among other things, the proximity of the study site to day and night roosts.

For example, when the activity patterns of *Artibeus jamaicensis* in Costa Rica (Fig. 1a and 1b) are compared with those we obtained in Puerto Rico for this species (Fig. 1c), marked differences are evident. Given that the values provided by Brown (1968) are absolute numbers and the other values are proportions, different levels of bat activity occur. Brown (1968) and LaVal (1970) obtained similar patterns of activity of *A. jamaicensis* in forests and banana groves, and we studied its activity at the entrance to a large cave system, parts of which were used
as day roosts by this species. The three patterns indicate that some individuals of this species are active throughout the night. Adult male *Artibeus jamaicensis* in Puerto Rico were more active one hour after dark and one hour before dawn, but did show sporadic activity throughout the night (Fig. 1c).

Williams and Williams (1970) found that much of the activity of *Phyllostomus hastatus* in Trinidad occurred in the first few hours after sunset, considering the times when most individuals returned to their daytime refuges. They also noted an additional period of activity just before sunrise, although LaVal (1969) failed to observe comparable predawn activity for other phyllostomatids in Costa Rica. The disparity of these two reports may reflect differences in behavior of bats as a function of proximity to the day roost, since predawn feeding may be restricted to the immediate vicinity of the day roost.

The effect of roost proximity and, of course, season and weather on activity patterns of bats makes detailed comparisons from different areas tenuous. Inasmuch as we lack detailed analyses of activity patterns of bats from any area.
(with the possible exception of Nyholm's, 1965, data from some species of *Myotis*), a comprehensive understanding of the situation is presently unrealistic.

Similarly, other than anecdotal observations, there are few data on the effects of weather on the activity of Phylllostomatidae. Tamsitt and Valdivieso (1961) reported a strong inhibiting effect of moonlight on bat activity in Costa Rica, but this was not observed by LaVal (1970), who noted that his mist nets had been set in closed forest, whereas Tamsitt and Valdivieso (1961) had been working in more open situations. Crespo *et al.* (1972) found a strong inhibiting effect of moonlight on the activity of *Desmodus rotundus*. Other studies have documented the effects of moonlight on bat activity (Erkert, 1974; Turner, 1975), which may be related in some areas to the threat of predation (Fenton and Fleming, 1976; Fenton *et al.*, n.d.). However, responses to possible predators is not a uniformly terable explanation of the effects of moonlight on the activity of bats. Wimsatt (1969) suggested that heavy precipitation had a suppressing effect on foraging activity of *D. rotundus*, and pointed out the need for detailed work on the effects of local environmental conditions on the activity of bats.

Interpretation of nightly activity patterns and comparisons of activity between sympatric taxa also must consider competitive strategies of resource use. Horizontal and vertical patchiness of habitat (including food and roost sites) probably are important parameters selecting for a reduction in interspecific competition. Vertical stratification of Neotropical bat faunas has been noted by Handley (1967), McNab (1971), and Fenton (1972). For example, among phylllostomatids, *Vampyressa bidens* and *Artibeus lituratus* were more commonly taken in canopy sampling than at ground level, whereas the reverse was true of *Carollia subrufa* and *C. perspicillata* (Handley, 1967). Before reliable temporal comparisons of different species can be made, vertical sampling must be undertaken in a variety of habitats.

The sensitivity of bats to disturbance is the main drawback to studies of bat activity that involve capture and marking of animals (either by banding or punch marking—Bonaccorso and Smythe, 1972). This is clearly reflected in the band recoveries reported by LaVal (1970) and Fleming *et al.* (1972), and further accentuated by our own experiences in Puerto Rico. Over four nights in May 1973, a total of 314 phylllostomatids was banded at Aguas Buenas Cave in Puerto Rico (168 *Artibeus jamaicensis*, 40 *Monophyllus redmani*, 80 *Brachyphylla cavernarum*, and 26 *Erophylla bombifrons*) and during this same period a total of 55 band recoveries was made (14.3 per cent of the total banded).

Remote sensing systems have been used to monitor the activity of some bats that use high intensity echolocating cries (Fenton *et al.*, 1973). This approach avoids disturbance to the bats, but is not particularly useful for most phylllostomatids, which are low-intensity echolocators. Photocells, photographic apparatus, and thermister sensors may provide means of remote monitoring of phylllostomatid activity and thus permit analysis of the effects of various environmental parameters on the activity of these bats without introducing biases resulting from disturbance.

The tendency of some bats to use alternate roosts—as reported for *Desmodus rotundus* by Wimsatt (1969) and *Erophylla sezekorni* by Goodwin (1970)
—further complicates the problem of the impact of disturbance on roost-oriented
studies (Turner, 1975). Knowledge of the location of alternate roosts has definite
survival value for bats, because it permits them to vacate roosts that are tem-
porarily or permanently rendered unsuitable in favor of roosts that have not
been jeopardized.

Seasonal

The seasonal movements (or migrations) of bats long have been of interest to
biologists (see Allen, 1939), but most knowledge about them has been obtained
in the temperate regions of the northern hemisphere and concerns rhinolophids,
vespertilionids, and a few molossids. (Allen, 1939; Brosset, 1966; Leen and
Novick, 1969; Griffin, 1970). Some Pteropodidae in various parts of their ranges,
but particularly in eastern Africa and in Australia, have been shown to migrate,
but the Phyllostomidae are conspicuous by their absence from the roster of
migratory bats.

Anderson (1969) suspected migration by *Macrotrach pilosus*, (= *M.*
californicus*, part), and their seasonal absence from the American Southwest
led Barbour and Davis (1969) to suggest migration for *Leptonycteris nivalis*, *L.*
sanborni, and *Choeronycteris mexicana*. There is now evidence that some nectar-
vorous species (for example, *L. sanborni*) return year after year to the same sum-
mer colony (Hayward and Cockrum, 1971) and that seasonal movements in these
species are probably in response to the flowering seasons (Leen and Novick,
1969). Davis (1945) reported declines in numbers of *Carollia perspicillata*, *Anoura
goffroyi*, and *Desmodus rotundus* from October through December in Brazil.
Greenhall (1956) suggested that similar declines reflect shifts of populations in
response to exhaustion of local food supplies. Local migration in response to
reduced flower availability is characteristic of nectar-feeding birds throughout
the world (Wolf, 1970; Keast, 1968) and similar movements can be expected
to occur in nectar-feeding phyllostomatids. Why such movements may be more
characteristic of flower feeders than frugivorous kinds is in the ephemeral nature
of flowers as compared to fruits (Leck, 1972).

The use of multiple roosts also may account for local shifts in the distribution
of bats. Wimsatt (1969) pointed out that use of alternate roosts presented an
adaptive advantage to *Desmodus rotundus* because of the restricted water budget
of vampires. Local population shifts by this species to areas near food resources
would concurrently lower evaporative water loss related to movements to and
from the roosts, and, for the same reason, reduce levels of food consumption.
We suspect that strategies employed by other phyllostomatids throughout their
ranges will involve local, latitudinal, and altitudinal displacements.

The absence of marked migrations by phyllostomatids stands in sharp contrast
to the situation as it is known for some pteropodids, which is obviously a function
of at least size and habitats. The pteropodids for which migration is known are
large and tend to form conspicuous “camps,” which makes them easy to observe.
The generally smaller and more secretive phyllostomatids are considerably less
conspicuous.
Perhaps more significant, however, than size and roosting habits, are the differences in climate between South and Central America and Africa and Australia. Keast (1969) provided a convenient comparison of these three areas, whereas 32 percent of South and Central America is rainforest, this habitat accounts for 10 per cent and 5 per cent, respectively, of the area of Africa and Australia. Habitats in which marked seasonal fluctuations occur (with resultant seasonally available food sources) are more conducive to the evolution of migratory patterns than are habitats with less drastic fluctuations.

Climatic fluctuations also may account for the higher diversity of fruit and nectar-feeding bats in the Neotropics (relative to the Old World tropics). The larger size of the Pteropodidae (relative to the Phyllostomatidae) may reflect migratory habits because movement over long distances is proportionally less costly (energetically) for larger as opposed to smaller organisms (Schmidt-Nielson, 1972; Thomas and Southers, 1972; Thomas, 1975).

**Homing**

Griffin's (1970) review of studies of homing by bats included one phyllostomatid, Williams et al. (1966) and Williams and Williams (1967, 1970) used radio tracking to examine homing by *Phyllostomus hastatus* and showed that bats displaced more than 30 kilometers from their homes were less effective at returning there than those displaced shorter distances. These studies also demonstrated the importance of visual cues to homing in *P. hastatus*. Banding studies have indicated homing by *Macrotrus californicus* (Bradshaw, 1961; Davis, 1966) and *Leptonycteris sanborni* (Hayward and Cockrum, 1971).

The whole question of homing in bats was succinctly addressed by Wilson and Findley (1972) who, after examining the available evidence, including the aforementioned studies of Williams and colleagues, concluded that no one had demonstrated other than random movements by displaced bats. We concur with this opinion and with the importance of having information concerning the familiarity of bats with the area involved (for *P. hastatus*, up to 20 kilometers from home—Williams and Williams, 1970).

The size of the familiar area is greatly influenced by the roosting habits of the bats involved and, as indicated by Fleming et al. (1972), by the size of the bat. Future studies involving displacements of bats from their home roosts probably will demonstrate that larger bats and bats that form large colonies will have proportionally larger spatial areas of familiarity than small or solitary bats. Migratory species such as *Leptonycteris nivalis*, *L. sanborni*, *Choeronycteris mexicana*, and *Macrotrus californicus* will have a greater degree of spatial familiarity than sedentary species of the same size.

Using rates of recovery of marked individuals, LaVal (1970) suggested that *Phyllostomus discolor*, *Carollia brevicauda*, and *C. castanea* (for which he obtained high recovery rates) may have smaller home ranges than species for which he had low recovery rates, such as *Artibius jamaicensis*, *Glossophaga commissarisii*, and *Uroderma bilobatum*. Because body size or colony size (or both) generally reflect resource requirements and distribution of resources, it is clear that
the local and geographic differences in areas of familiarity will in part be a function of resource distribution and density. Present agricultural practices and high cattle densities in some areas of the Neotropics may select against a large familiar area for bats using such artificial concentrations of food resources (for example, *Desmodus rotundus*).

**Behavior**

**Sensory**

The eyes of phyllostomatids probably serve regular complex visual functions (Chase and Suthers, 1969), such as surveillance for predators (Suthers, 1970), distance orientation (Williams *et al.*, 1966), and the location of feeding areas (Williams and Williams, 1970). Suthers (1970) postulated that passive visual surveillance by a resting bat may function to permit it to select visually important events before making a more detailed acoustical investigation. The relative importance of visual as opposed to acoustical information in the responses of phyllostomatids is not well understood, but probably depends upon light conditions (as it does for *Rousettus* sp.) and the general circumstances (Manske and Schmidt, 1976). The importance of vision in surveillance for predators also is suggested by some anatomical features such as the transparent dactylopatagium minus of some phyllostomatids (Vaughan, 1970).

The hypothesis that vision is important in orientation and feeding is supported from experiments conducted by Williams and colleagues (Williams *et al.*, 1966; Williams and Williams, 1967, 1970) and from theoretical constraints relating to the relatively short effective range of echolocation (Griffin, 1958, 1971; Suthers, 1970; Fenton, 1974).

Well-developed vomeronasal organs and associated olfactory bulbs as reported by Schneider (1957), Mann (1961), and Suthers (1970) and anecdotal observations indicate well-developed olfactory senses in the Phyllostomatidae. *Phyllostomus hastatus* can locate fruit hidden from view (Mann, 1961) and the sniffing behavior of *Desmodus rotundus* before licking and biting prey (Greenhall, 1972; Schmidt, 1973) points to the importance of olfaction. The acute odor discrimination shown by *D. rotundus* probably permits it to detect differences between breeds of cattle (Schmidt, 1973). Olfaction may be equally important for nectar and pollen-feeding bats; Baker (1973) noted that one of the characteristics of flowers visited by bats is a sour smell. Recent comparisons of the olfactory systems of some phyllostomatids with those of other bats (Bhatnagar, 1975; Bhatnagar and Kallen, 1974, 1975) further emphasizes the importance of odor in the lives of bats.

**Intraspecific**

Phyllostomatids show a variety of roosting habits with respect to numbers of individuals occupying a roost. Estimates of colony size vary considerably and have usually been based on visual counts during emergence or directly in roosts under low light levels (usually after the bats have been disturbed). Some phyllostato-
matids appear to roost alone or in small groups (for example, *Micronycteris megalotis*, *M. minuta*, *M. hirsuta*, *M. brachyotis*, *Lonchorina aurita*, *Tornata sylvicola*, *Tornata bidens*, *Phyllostomus elongatus*, and *Artibeus pheoitis*—Goodwin and Greenhall, 1961; Leen and Novick, 1969; Tuttle, 1970; Goodwin, 1970). Others are sometimes found in small aggregations or on other occasions in large colonies (for example, *Carollia perspicillata*—Pine, 1972; *Phyllostomus hastatus*—Williams and Williams, 1970; *Artibeus jamaicensis*—Leen and Novick, 1969), whereas still others appear to occur only in large aggregations (such as *Brachyphylla cavernarum* in Puerto Rico). The size of the roost may exert an important limiting factor on the size of the colony, as is indicated by the occurrence of larger aggregations of individuals of some species in artificial structures than are known from natural roosts (*Desmodus rotundus*, for example). Species that regularly roost in large rooms in caves probably are more commonly encountered in large aggregations than are those that roost in cavities of trees.

Aside from observations on colony or cluster size, little has been published on intraspecific behavior of bats in colonies. Some evidence is available indicating that there are social units of groups within colonies and that these may play important roles in reproduction, food gathering, and orientation. It seems logical to expect more elaborate social interactions in gregarious than in solitary species (as in some Canidae—Kleiman, 1972).

Williams and Williams (1970) reported “coherent social groups” for *Phyllostomus hastatus* ranging from five to 20 individuals and consisting of groups of both sexes with one or more dominant males. Bradbury (n.d.) has provided more information on the social groups of *Phyllostomus hastatus* and *P. discolor*.

*Phyllostomus hastatus* forms large colonies in caves and the population in any roost site consists of harems (25 to 30 females per male) and nonharem juveniles and males. Harem males protect their females and perform elaborate displays when another male approaches. To feed, females leave the harem singly and in twos, whereas the male departs when the number of remaining females is at its lowest, and remains away for only a short time. Removal of a harem male results in his replacement by another male with little or no turnover among the harem females.

*Phyllostomus discolor* establishes colonies in hollow trees and again the populations include harem (one to 12 females per male) and nonharem bats. However, harem composition in this species is more variable than in *P. hastatus*, with some females being regularly present in the harem and others somewhat nomadic. Female *P. discolor* are more aggressive than female *P. hastatus* and are actively involved in maintaining the integrity of the harem. A bat returning to a harem group performs elaborate displays, which include tactile, olfactory, and vocal cues, to gain admission to the group. Allogrooming by members of harems is common.

In both species, the nonharem groups may be quite stable in their composition and tend to be more nomadic than the harems. F. Potter (personal communication) has observed harem structures in *Carollia perspicillata* and it seems likely that this situation may be common in phyllostomatids that aggregate in large numbers.
Departures of groups of bats from roosts (for example, *Leptonycteris sanborni*—Hayward and Cockrum, 1971; *Desmodus rotundus*—Wimsatt, 1969, and Greenhall et al., 1971) also suggest the presence of social groupings. Similar observations have been reported for other bats (Rhinolophidae—Möhres, 1967; Vespertilionidae—Hall and Brenner, 1968, and Dwyer, 1970) and indicate that this behavior may be widespread in the Chiroptera.

Segregation of females into discrete groups prior to parturition and until the young are weaned has been reported for *Artibeus jamaicensis* (Leen and Novick, 1969) and implied by the observations of Jones et al. (1973) for *Desmodus rotundus*. The observations of Leen and Novick (1969) for *A. jamaicensis* and those of Schmidt (1973) for *D. rotundus* indicate that olfactory cues may be important in social organization and mother-young relationships. However, other information, some of it from phyllostomatids, suggests that vocalizations are important in interactions between females and their young (Brown, 1976; Gould, 1975a, 1975b; Gould et al., 1973; Schmidt and Manske, 1973) and in a variety of other intraspecific contexts (for example, Bradbury and Emmons, 1974; Wickler and Sieb, 1976).

Evidence from other mammals strongly suggests that bats will be shown to exhibit various patterns of social dominance within groups. Places where these interactions may be expected are roosts and common feeding sites. Laboratory observations of Schmidt and Greenhall (1972) on the interactions of feeding vampires support this suggestion; they suggested that certain "dominant" animals in a group feed first and that, while they are feeding, they chase off other individuals as in some carnivores (Ewer, 1973). Similar interactions will certainly be reported from situations where food resources are localized (for example, concentrations of ripe fruit). However, species that are nectarivorous or carnivorous (including insectivorous) where food resources are diffuse are more apt to demonstrate territorial interactions than dominance hierarchies at feeding sites (see, for example, Baker’s, 1973, observations of trap-lining in some nectar-feeding bats).

The whole subject of sexual behavior and the details of mother-young interactions are poorly known, and we were unable to find any published information on this subject for phyllostomatids.

**Interspecific**

Various species of bats are known to share the same roosts, but in some cases, use of a roost by one species will result in its being abandoned by another species (for example, *Artibeus jamaicensis* and *Molossus* sp.—Leen and Novick, 1969). Often several species of bats may roost in one structure (tree, cave, building, and so forth) and not come into physical contact with one another except possibly at times of arrival or departure. There is little information on interspecific behavior of bats, although biting is presumed to occur and possibly be involved with the epidemiology of rabies virus (Constantine, 1970). As with intraspecific interactions, it is likely that interspecific altercations will occur where food resources or roosts are localized or limited. The work of Colwell (1973) on the interactions of some hummingbirds suggests that similar interspecific behavior patterns may
be described for nectar-feeding bats, especially in the light of the trap-lining nature of the visits of some of these bats to flowers.

Miscellaneous

Several species of bats are known to carry their young with them away from their roosts. Tamsitt and Valdivieco (1965) observed this for *Artibeus lituratus* in Colombia, but Fenton (1969) found no evidence of it for *A. jamaicensis* in Puerto Rico. In a review of the literature on this subject, Davis (1970) reported that some phyllostomatids had been found to transport their young after disturbances in their roosts (*Macrozyga californica, Choeronycteris mexicana, Lepionycteris sanborni*), whereas others would do this even in the absence of disturbance (*Glossophaga soricina* and *Leptonycteris sanborni*). It is likely that species that use alternate roosts will be found to transport their young more regularly than those that do not, but certainly the presence of disturbance is an important consideration in this regard.

Tuttle (1970) reported that the vocalizations of a captured *Mimom crindatum* attracted other individuals of the same species to the site of capture, and similar effects were elicited by the “distress calls” of several species of bats. At present we have no definite information as to which frequencies of bat cries are important in “distress” or other calls that evoke responses from other individuals. Recent work has indicated that some bats respond preferentially to “distress” calls of conspecifics (Fenton et al., 1976).

Further Research

From the preceding discussion, it should be obvious that almost any aspect of the movements and behavior of phyllostomatids will provide productive topics for research. Documentation of the daily and seasonal patterns of the activity of these bats with respect to various environmental parameters such as meteorological conditions, lunar cycles, and seasonal changes in the abundances of food (from insects to fruit) should be a primary goal. At the same time, the whole spectrum of intra and interspecific behavior patterns (territoriality, partitioning of food and roost resources, reproductive, and mother-young behavior) requires close attention.

As we have pointed out, many of these subjects may now be addressed with the aid of electronic equipment (notably for telemetry and observation at low light levels) and a reasonable knowledge of the phyllostomatids that occur in different areas. This situation is reflected by a variety of recent studies ranging from roosting behavior (Timm and Mortimer, 1976), through feeding and orientation behavior (Howell 1974a, 1974b; Fleming et al., n.d.), to detailed studies of specific bats (Turner, 1975).

The programs of recent North American Symposia on Bat Research indicate that work on some of these subjects is in progress for some species. We expect that the next few years will see the publication of results that will greatly advance our knowledge of the movements and behavior of bats in general and the Phyllostomatidae in particular.
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