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Frank J. Bonaccorso[1]

SYNOPSIS: Resource partitioning, reproduction, and community structure in a tropical moist forest community of 35 bat species were studied on Barro Colorado Island, Panama Canal Zone. Over a three-year span 2884 bats were captured, banded, and released; data were collected on food habits, activity cycles, habitat selection, and reproductive timing. Information on seasonality and abundance of fruit, flower, and insect resources used by bats also was collected.

Fluctuating levels of food resources require that many bat species utilize different habitats and foraging strategies through a year. Competitive interactions, predator avoidance, and climatic fluctuations further influence foraging strategies. The bat community is divided into nine feeding guilds on the basis of diet and method of food procurement. Within the most complex guilds food resources are partitioned temporarily, spacially, and by size and quality. Within the simplest guilds food resources are partitioned primarily by particle size.

Reproduction coincides with high levels of food availability. Species utilizing food sources abundant over most of the year have two litters per year.

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INTRODUCTION

The words "tropical forest" typically engender visions of species-rich communities, complex competitive interactions, and relatively stable environments. Indeed, faunal lists in the tropics are large, and food webs are intricately complex. It is also true that organisms inhabiting tropical lowlands usually are subjected to less extreme environmental fluctuations than are their counterparts in temperate or polar regions. However, it is too infrequently emphasized that even species in tropical forests must possess behavioral flexibility to counter and survive climatic and biotic environmental change. There are two major reasons for this oversight. First, few detailed studies of tropical organisms have spanned periods of several years or even seasons, and second, behavioral responses of tropical species to environmental fluctuations are often quite subtle. Whereas temperate animals commonly exhibit obvious and dramatic responses to seasonal change such as hibernation or long distance migration, tropical species may need only to switch food types or microhabitats, or briefly halt reproduction (Kaufmann 1962, Wolf 1970, Mares and Wilson 1971a, Snow and Snow 1972, Orians 1973, Montgomery and Sunquist 1973). Nevertheless, genetic and behavioral flexibility are requisites of survival for most tropical as well as temperate species.

Tropical bats are particularly good subjects for studies of diversity, competitive interaction, and response to environmental fluctuation because of their individual abundance and the complex taxonomic and ecological communities they form. About 100 species of bats occur in each of the small countries of Central America (Hall and Kelson 1959). It is common to find 30 to 50 species in one macrohabitat measuring a few square kilometers in area.

Among tropical bat species, few are known or suspected to reproduce year round or to specialize on constantly abundant food resources; the common vampire bat, *Desmodus rotundus,* being a notable exception on both counts (Wimsatt and Trapido 1952, Turner 1975). Most bats in equatorial regions are seasonally polyestrous or monestrous in reproduction (Baker and Baker 1936, Mutere 1970, Fleming 1973) and make seasonal shifts in diet (Wilson 1971b, Fleming *et al.* 1972, Heithaus *et al.* 1974).

The objective of this paper is to delineate adaptive strategies used by tropical bats that enable them to survive and reproduce under fluctuating environmental conditions and coexist with numerous similar species in complex communities. The field work represented herein documents seasonal changes in food resources, mechanisms of resource partitioning, and reproductive timing through one complete year and portions of two other years.

STUDY AREA

The primary research site was Barro Colorado Island (BCI), which lies within freshwater Lake Gatun, Panama Canal Zone, at 9° 10′ N Lat, 79° 51′ W Long. This site was selected because it has a rich bat fauna, relatively undisturbed mature moist forest, modern living and laboratory facilities, and reference collections of animals and plants. A second site was located on the mainland opposite BCI at the base of Buena Vista Peninsula (Fig. 1).

The climate of this lowland area of Panama is warm and humid, with a 7-month (May through November) wet season and a 3-month (January through March) dry season. Dry season months each receive less than 60 mm of rain, whereas wet season months typically receive in excess of 250 mm of rain. April and December are transition months between the dry and wet seasons and receive amounts of rain that vary considerably from year to year. Thus in years when April and December are very dry, the dry season may last for five months. Average annual rainfall since 1926 has been 2820 mm (Smythe 1974). Monthly sums of rainfall for 1973 are shown in Figure 3.

During night-time sampling of bats, relative humidity under the forest canopy never fell below 80 percent. Measurements were made at 2 m above ground with sling pyschrometer. Daily temperatures on the forest floor fluctate from a mean minimum of 22.1°C to a mean maximum of 28.0°C, with no significant seasonal variation (Smythe 1974).

Barro Colorado is in the Tropical Moist Forest life zone (Holdridge 1967). This 15 km² island is covered with forest that is over 60 years in age. The only physical disturbance results from recutting forest trails, maintaining a small laboratory clearing, and an undetermined amount of poaching. Further details on the geology, climate, biology, and history of the island are given by Kaufmann (1962) and Foster (1973).

MATERIALS AND METHODS

There were 17 sampling stations in an approximately 2 km² central strip of BCI and one station on Buena Vista Peninsula (Fig. 1). Habitats sampled during the study were classified as mature forest (14 stations on BCI), creeks (3 stations on BCI), and second

growth (1 station on Buena Vista). The mature forest, a minimum of 60 years old in all places, had a completely closed canopy. Creeks were lined with rich shrub growth and the creek beds received direct sunlight. Second-growth habitat at Buena Vista was approximately 20 years old and consisted of thick shrub growth and scattered small trees that formed a discontinuous canopy.

Each sampling station consisted of four or six 6 x 2 m mist nets and one or two Tuttle harp traps (Tuttle 1974) set across permanent trails. Nets were set in pairs at 100 m intervals, with one of each pair at ground level (0-3 m) and the other at subcanopy and lower canopy level (3-12 m). Early in the study nets were rigged in the canopy as high as 25 m above ground, but use of these nets was soon discontinued because few bats were captured in them, which seemed to reflect little flight activity in the canopy. Harp traps were usually set at ground level in low, narrow tunnel-like passages created by vegetation and trails. At a few stations where the vegetation permitted, harp traps were rigged in subcanopy level "tunnels."

Nets and traps were open from sunset to sunrise 67 times between 11 January and 31 December 1973. On 28 other nights during that period, sampling was conducted for less than a full night. Total sampling during 1973 involved 4376 net-hours, 1213 trap-hours, and 2324 captured bats.

In 1971, a pilot study of 347 net-hours yielded 282 bats between 20 June and 18 August. In 1974 between 10 June and 17 July, 454 net-hours of additional sampling yielded 278 bats. No harp traps were available during these times.
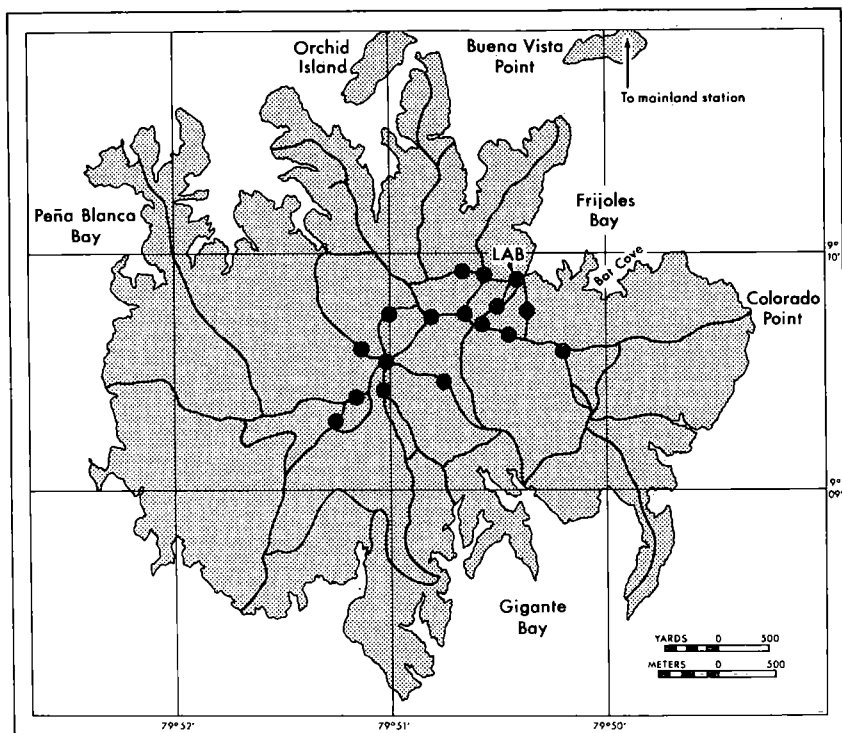

FIGURE 1.—Barro Colorado Island study area showing the 17 sampling stations.

Crespo *et al.* (1972) and Morrison (in press) have demonstrated that vampires and fruit bats avoid flying during intense moonlight. Whole-night samples were taken only between the last and first quarter of the moon. Thus activity cycles were measured during phases of the lunar cycle that did not produce enough light to influence bat flight activity.

Nets and traps were checked at least twice every hour. When possible net checks were made more frequently to prevent bats from chewing out of nets. Upon removal from a net or trap each bat was placed in an individual cloth bag. Usually within an hour after capture the bats were banded, as described in Bonaccorso *et al.* (1976), and released at the sampling station. The following data were recorded for each individual: species, hour and location of capture, sex, age class, reproductive condition of females, food in feces or mouth, weight, and forearm length.

Age classes were distinguished as follows: infants were unable to fly and were encountered only when carried by the mother; juveniles were able to fly but still had the infant pelage; subadults had the adult pelage but were smaller in weight than adults and were reproductively immature; adults possessed both adult pelage and weight.

Pregnancy, lactation, and reproductive inactivity of adult females were determined by palpation. Additionally, females could be distinguished as nulliparous or post-lactating by examining the condition of the teats.

Fecal pellets obtained from individual animals were placed in separate glassine envelopes for laboratory identification of food species. Fruits and pollens in fecal pellets were identified to species by comparing unknowns with seeds, pulp fibers, and pollen grains in a reference collection I assembled. Pellets collected from insectivorous bats are in the process of analysis, and this information will be published elsewhere. Pollen on the fur was collected by swabbing with a gelatin as described by Beattie (1971). The pollen-containing gelatin was then melted on slides for microscopic identification. In calculating feeding niche breadths and overlaps the fecal pellets in a single glassine envelope were scored as a sample of one for the given food species it contained (pollen or fruit). For the stenodermine fruit bats the fecal pellets from a single defecation seemed to represent part of a single fruit that was eaten. Food passage along the digestive tract is very rapid (Klite 1965), and a given defecation probably represents the last fruit eaten by the bat. For carolline bats a single fecal pellet sometimes contained two types of seeds. This probably resulted from eating very small fruits and switching food species within very short intervals.

Occasionally animals were captured with whole fruits held in the mouth. Additional information on food habits was gathered by placing plastic sheets under two roost trees of *Carollia perspicillata* to gather discarded fruits and fecal matter.

Niche breadth is calculated as $\log_e B = -\Sigma p_i \log_e p_i$, where p_i is the number of the ith food species divided by sample size (Levins 1968). Values approaching zero indicate narrow niche breadths and specialists. Values approaching one indicate niche breadths of generalists. Niche overlap is calculated as $\hat{C}\lambda = 2\Sigma X_i / \Sigma X_i^2 + Y_i^2$, where X_i is the proportion of the ith food species in the diet of bat species X, and Y_i is the proportion of the ith food species in the diet of bat species Y (Morista 1959). I follow Zaret and Rand (1971) in considering species with overlap values greater than 0.6 to be critically similar in terms of food overlap.

PHENOLOGY OF FOOD RESOURCES

Most of the bat species on BCI depend largely on fruit, flowers, or insects as food resources. Only a few species eat flesh or blood of vertebrates or non-insect invertebrates. The abundance and diversity

of fruits, flowers, and insects in Central America, even in Moist and Wet Forests, show marked seasonal fluctuations (Foster 1973, Smythe 1974, Frankie *et al.* 1974, Morrison 1978).

Pollen and nectar on BCI are available to bats as reliable food sources only in the dry season, and only four species of flowering plants are known to be used by bats (Fig. 2). Two common species, *Ochroma lagopus* and *Pseudobombax septenatum,* flower from mid-December to mid-March. While these two species are in bloom, nectar and pollen are very abundant. The other two pollen types used by bats remain unidentified. One of these is known only from February to March and the other from August to September.

Fruits from 45 plant species were eaten by bats on BCI (Fig. 2). These included 19 trees, 11 shrubs, 4 vines, 4 epiphytes, and 7 undetermined. Mature fruits were available to bats all year, but most species bearing fruits eaten by bats produced ripe fruits for periods of only one to four months. Only *Ficus insipida, F. obtusifolia,* and *F. yoponensis,* have ripe fruits available nine or more months per year. Individuals in the populations of these fig species fruit asynchronously one to four times per year. *F. insipida* and *F. yoponensis* populations show two major fruiting peaks and troughs each year (Morrison 1978). Ripe figs are scarce in March and again from late August until late November.

The plant genera *Cecropia, Spondias, Vismia,* and *Piper* have two or more bat-dispersed species that set fruit in sequential time periods (Fig. 2). Ten species of pipers are eaten by bats on BCI. Though none of these species is available for more than a few months, two or more species have ripe fruit at any one time through the year. Pipers also are important bat fruits in Costa Rica where several species fruit in sequential series (Heithaus *et al.* 1974).

During 1973 a maximum of 19 fruiting species was available from mid-March to mid-April, and a minimum of 6 species was available in November-December (Fig. 2). Two of the fruits available in November-December, *Ficus insipida* and *F. yoponensis,* were relatively scarce, but *Spondias radlkoferi* and *S. mombin* were very abundant.

Biomass and numbers of nocturnal insects caught in light traps in Barro Colorado forest over a 3-year period were reported by Smythe (1974). Though these samples represent all nocturnal flying insects, they provide a useful index of abundance and fluctuations of the potential food resources for insectivorous bats. Smythe's light trap collections showed that nocturnal insect biomass in the early wet season is as much as eight times that at the end of the wet season and during the dry season (Fig. 3). Large insects (> 5 mm length) were responsible for this seasonal change in biomass, with Isoptera, Diptera, and Lepidoptera among the orders eaten by bats that have particularly

dramatic population increases in the wet season. By contrast, small insects (< 5 mm length) were abundant throughout the year.

RESOURCE PARTITIONING

Of 35 species of bats captured or sighted on BCI in 1973, 31 species were captured in nets or traps and 4 other species were seen in flight or at roosts. *Noctilio leporinus, N. labialis,* and *Molossus molossus* appeared to be abundant but restricted their flight activities to habitats not sampled—the shallow inlets of the lake *(Noctilio)* and above the forest canopy *(Molossus).* The fourth species not captured, *Vampyrum spectrum,* is a top carnivore and may be represented by very few individuals on the island. A pair of *V. spectrum* was netted by A. L. Gardner and D. E. Wilson on 5 January 1973. In June 1973 I saw a single animal flying at dawn.

A first step at understanding how 35 species of bats partition food resources on this small island can be made by dividing the fauna into feeding guilds distinguished on the basis of two parameters—diet and method or place of food procurement. This permits examination of small complexes of species with similar foraging behaviors and diets. I have divided the bats on BCI into nine feeding guilds with one to nine species per guild. Justification for the placement of species into specific feeding guilds will be provided in succeeding sections. For the moment, the guilds are defined as follows:

(1) "Canopy frugivores"—forage mostly on fruits that grow in the trees of the canopy and subcanopy level of the forest, above 3 m from the ground.

(2) "Groundstory frugivores"—forage mostly on fruits of shrubby groundstory plants, 0 to 3 m above ground level.

(3) "Scavenging frugivores (or juicers)"—feed mostly on very soft ripe fruit, and/or over-ripe fruit.

(4) "Nectar-pollen-fruit-insect omnivores"—forage for pollen and nectar when available during the dry season and for fruits and insects at other times.

(5) "Sanguivores"—feed only on the blood of mammals and birds.

(6) "Gleaning carnivores"—forage for small animals (arthropods or vertebrates) that are perching or moving on vegetation or on the ground.

(7) "Slow-flying hawking insectivores"—forage for flying insects in small openings beneath or in the forest canopy or over streams.

(8) "Fast-flying hawking insectivores"—forage for flying insects above the forest canopy or in very large open spaces (e.g. pastures).

Phenology chart — flowering and fruiting periods by month (JAN–DEC).

PLANT SPECIES	PLANT TYPE
FLOWERS	
Ochroma lagopus	T
Pseudobombax septenatum	T
Unknown 201	U
Unknown 202	U
FRUITS	
Ficus insipida	T
F. obtusifolia	T
F. popenoaei	T
F. yoponensis	T
F. 102	T
Spondias mombin	T
S. radlkoferi	T
Dipteryx panamensis	T
Calophyllum longifolia	T
Quararibea asterolepsis	T
Cecropia eximia	T
C. obtusifolia	T
Anacardium excelsum	T
Solanum hayesii	T
Vismia species 1	T
Vismia species 2	T
Astrocaryum standleyanum	T
Tetrathylacium johanseni	T
Poulsenia armata	V
Cassia undulatum	V
Markea panamensis	V
Clusia odorata	V
Unknown 126 (Passifloraceae)	E
Unknown 101 (Araceae)	E
Unknown 103 (Araceae)	E
Aechmea tillandsiodes	E

FIGURE 2.—Monthly availability of fruits and flowers used by bats on Barro Colorado Island. Solid bars indicate food present in fecal samples. Striped bars indicate food known to be available, but not present in fecal samples. Empty bars indicate probable availability of food. Lunar months begin about the 12th day of each calendar month. Plant types: T = tree, S = shrub, V = vine, E = epiphyte, U = unknown.
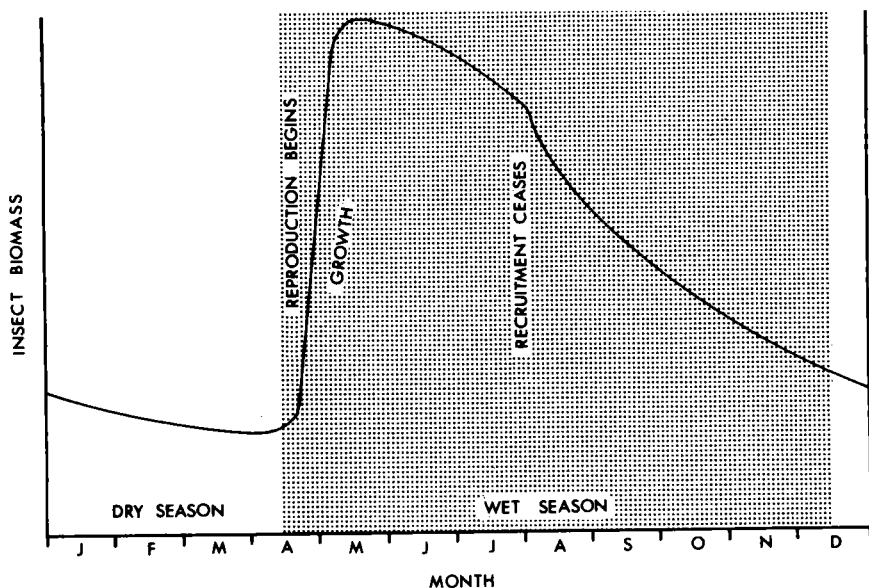
FIGURE 3.—Schematic representation of fluctuation in biomass of nocturnal flying insects through the year (Based on samples from three years, after Smythe 1974). Bars represent rainfall in millimeters.

(9) "Piscivores"—forage for fish or aquatic invertebrates at or just above the surface of lakes and large streams.

CANOPY FRUGIVORE GUILD

BODY SIZE.—Eight species, all in the subfamily Stenoderminae of the family Phyllostomatidae, constitute the canopy frugivore guild on BCI. These eight species range from 8.1 to 69.3 g in mean body weight (Table 1.). There is a mean increment of 1.44 between the body weights of adjacently sized animals designated as fig specialists. *Artibeus*

TABLE 1.—WEIGHTS OF CANOPY FRUGIVORE BATS ON BCI.*

Species	$\overline{X}$	S.D.	n	Wgt/wgt$_{sm}$	Remarks
V. pusilla	8.1	0.6	22	—	common, fig specialist
C trinitatum	12.3	1.2	7	1.53	very rare, fig specialist
A. phaeotis	13.0	1.2	30	—	common, fruit generalist
V. helleri	16.2	2.2	8	1.31	very rare, fig specialist
C. villosum	22.4	2.1	13	1.38	rare, fig specialist
V. caraccioloi	36.0	2.3	27	1.61	common, fig specialist
A. jamaicensis	47.2	3.4	30	1.31	superabundant, fig specialist
A. lituratus	69.3	5.6	30	1.47	common, fig specialist
	mean ratio of weight increment = 1.44				

*$\overline{X}$ = mean weight in grams; S.D. = standard deviation; n = sample size; Wgt/Wgt$_{sm}$ = weight of species divided by weight of next smallest species.

phaeotis, a feeding generalist, and *Chiroderma trinitatum* are nearly equal in size.

FOOD SELECTION.—All eight canopy frugivore species feed primarily on fruits of large canopy and subcanopy trees, in particular figs of the genus *Ficus.* Over 60 percent of the annual diet (by frequency of occurrence of fecal pellets containing a given species of plant seeds) of the seven fig specialists consists of fig fruits (Table 2). *A. phaeotis* depends on figs for only 30 percent of its diet. Five species of *Ficus,* all of which are green-colored at maturity, are eaten and dispersed by these stenodermines on BCI. Fig trees that produce small fruits like *F. yoponensis* and *F. popenoaei* are preferred by small bat species, and trees that produce larger fruits like *F. insipida* and *F. obtusifolia* are preferred by the larger bats.

Figs form the bulk of the diet of *Artibeus jamaicensis* throughout most of the year. However, during the latter part of the wet season and the beginning of the dry season mature fig fruits are very scarce (Morrison 1978). At this time *A. jamaicensis* turns more heavily to other fruits and pollen (Table 3). The relative importance of pollen in the diet of *A. jamaicensis* may be underestimated in Table 3, because my sampling schedule did not coincide precisely with the period in late December and early January when figs were very scarce and flowers were very abundant. Similar seasonal switches in diet also probably occur for *A. lituratus* and *V. caraccioloi,* but the data are weak. No conclusions are made from the scant data on the smaller canopy frugivores about seasonal changes in diet.

Unlike fig specialists, *A. phaeotis* eats a more even distribution of many types of fruits (Table 2 and 3) with no one species dominating the diet. Throughout the year figs are a minor component of the diet, while other fruits are very important in certain months. *Cecropia eximia* is an important food item from July to September, as is *Spondias radlkoferi* in November to January.

TABLE 2.—PERCENT OF DIET FROM MOST IMPORTANT FOOD PLANT GENERAL AND SPECIES TAKEN FROM FECAL SAMPLES OF BATS IN THE CANOPY FRUGIVORE GUILD.

Bat species	Percent most important genera*	Most Important species	Number of fecal samples
V. pusilla	92 *Ficus*	*F. yoponensis*	13
C. trinitatum	60 *Ficus*	*F. popenoaei*	5
A. phaeotis	30 *Ficus*	*Spondais radlkoferi*	33
V. helleri	67 *Ficus*	*F. insipida*	6
C. villosum	100 *Ficus*	*F. popenoaei*	6
V. caraccioloi	76 *Ficus*	*F. insipida*	17
A. jamaicensis	78 *Ficus*	*F. insipida*	185
A. lituratus	65 *Ficus*	*F. insipida*	20

*By frequency of occurrence as explained in Materials And Methods.

TABLE 3.—BIMONTHLY SAMPLES OF IMPORTANT FOOD GENERA IN DIETS OF *Artibeus* AND *Vampyrodes*. NUMBERS INDICATE FECAL SAMPLES WITH A GIVEN FOOD PRESENT. SAMPLING PERIODS BEGIN AT MID-MONTH.

Food species	Jan-Mar	Mar-May	May-Jul	Jul-Sep	Sep-Nov	Nov-Jan
Artibeus jamaicensis						
Ficus spp.	18	25	25	35	21	17
Cecropia spp.		3		3		
Spondias spp.				1	8	6
Quararibea					9	
Pollen	1					
Total fecal samples*	20	30	32	39	35	37
Artibeus lituratus						
Ficus spp.	2		4	2	1	4
Spondias spp.				1	1	1
Pollen	1					
Total fecal samples*	3		4	5	2	7
Artibeus phaeotis						
Ficus spp.		2	1	2	1	3
Cecropia spp.			1	5		
Spondias spp.						8
Total fecal samples*		5	6	9	1	11
Vampyrodes caraccioloi						
Ficus spp.	1	2		4	3	1
Pollen	2					
Total fecal samples*	3	3		4	3	2

*Includes genera of lesser importance not shown here.

Feeding niche breadths based on frequency of occurrence of food species in the diet are presented in Table 4. Large niche breadth values represent food generalists and small values food specialists. *A. phaeotis* stands alone at the generalist extreme of this index. Among the other species, *A. jamaicensis* has an intermediate position;

TABLE 4.—FEEDING NICHE BREADTHS OF CANOPY FRUGIVORES. SAMPLE SIZES FOR CALCULATING NICHE BREADTHS ARE FROM TABLE 2.

Bat species	Genera of known food plants	Species of known food plants	Niche breadth (log. B)
V. pusilla	2	4	0.94
C. trinitatum	3	4	1.33
A. phaeotis	10	12	2.10
V. helleri	2	3	1.01
C. villosum	1	3	1.01
V. caraccioloi	4	5	1.04
A. jamaicensis	9	16	1.61
A. lituratus	5	7	1.33

however, the very narrow niche breadths of the other specialists seem to be the result of small samples in calculating niche breadths. There is a significant positive correlation between sample size and the number of plant species in Table 4 (r = 0.865).

Niche overlap in food species is compared in Table 5. The highest values of overlap occur between species most similar in size. *A. phaeotis* overlaps little with all the fig specialists, except for *V. helleri*, which is similar in size to *A. phaeotis*. The high values of overlap between many of the fig specialist species indicate that some mechanism other than selection of food species must reduce behavioral interference and/or interspecific competition for food in this guild if food is a limiting factor.

Several types of evidence suggest that, at least during some parts of the year, food is a limiting factor for fruit bats on BCI. The biomass of fruit and the number of species of fruiting trees fluctuate quite drastically on a seasonal basis (see Phenology section). During the late wet season fruit availability is low, and an increased proportion of captured fruit bats have empty stomachs (83% in Oct-Nov) as compared to times of fruit abundance (71% in Mar-Apr). Also in the late wet season various other frugivorous mammals come to the laboratory clearing with increased frequency to seek food (Foster 1973). By the late wet season several species of fruit bats have temporarily moved out of the study area in response to low food levels (Bonaccorso and Humphrey, in prep.). Even when fruit is very abundant in terms of total biomass, many types are concentrated in a limited amount of space, the few trees fruiting at any moment, and may still be a limiting factor for population size.

VERTICAL STRATIFICATION..—Handley (1967) and Harrison (1962)

TABLE 5.—FEEDING NICHE OVERLAPS (C) AMONG SPECIES OF CANOPY FRUGIVORES. LOWER DIAGONAL INDICATES OVERLAP BETWEEN FIG SPECIALISTS MOST SIMILAR IN SIZE.

	A. lituratus	A. jamaicensis	V. caraccioloi	C. villosum	V. helleri	C. trinitatum	V. pusilla
A. phaeotis	.215	.345	.615	.241	.465	.485	.518
V. pusilla		.968	.452	.796	.679	.272	.152
C. trinitatum			.893	.743	.644	.209	.412
V. helleri				.798	.886	.852	.452
C. villosum					.727	.200	.310
V. caraccioloi						.994	.962
A. jamaicensis							.983

demonstrated a vertical stratification of flight activity in tropical bat species, with most canopy frugivores preferring upper levels of the forest. On BCI *V. pusilla, A. phaeotis, C. villosum, V. caraccioloi,* and *A. lituratus* were captured with significantly greater frequency in the nets and traps set above 3 m (Table 6). *V. helleri* and *C. trinitatum* also were captured most frequently in subcanopy and canopy levels, but samples sizes for these species are small, and frequency differences are not statistically significant. *A. jamaicensis* is the only species of the guild to show a significant preference for activity at the groundstory level, yet 42 percent of the captures of this species too were in the upper levels of the forest. Though most of its food items grow in the upper levels of the forest, *A. jamaicensis* may fly close to the ground to avoid predators, or because it is more efficient for a large bat to fly along cleared trails than to echolocate and avoid the dense vegetation above. At any rate this behavior seems an artifact of human management of the forest.

HABITAT SELECTION.—Comparison of netting samples from the young open forest of Buena Vista and the mature closed canopy forest and creek habitats is presented in Fig. 4. As a group fig specialists are much more common in closed forest and creeks lined by closed forest than in shrubby open forest where few mature trees of their preferred food species are found. *A. phaeotis* and *A. jamaicensis* are common to very abundant in all three habitats, as would be expected from their generalized food requirements. Except for *A. jamaicensis,* none of the fig specialists are common on Buena Vista Peninsula.

FEEDING BEHAVIOR.—Canopy frugivores usually carry fruits by mouth from fruiting trees to night roosts (Goodwin and Greenhall 1961, Morrison 1978). On BCI Morrison found that the night roosts of

TABLE 6.—VERTICAL STRATIFICATION OF CANOPY FRUGIVORES. STATISTICAL SIGNIFICANCE INDICATES PREFERENCE FOR ONE OF THE TWO VERTICAL STRATA. YATES CORRECTION FOR CONTINUITY IS USED FOR ALL TESTS OF SAMPLES WITH N < 200 (Sokal and Rohlf 1969).

Bat species	No. of bats captured at ground level, 0 to 3 m	No. of bats captured at subcanopy levels, 3 to 12 m
V. pusilla	5	25**
C. trinitatum	2	4
A. phaeotis	36	56*
V. helleri	3	6
C. villosum	4	24**
V. caraccioloi	4	30**
A. jamaicensis	467**	326
A. lituratus	23	66**

*Significant by Chi Square Test (P < .05)
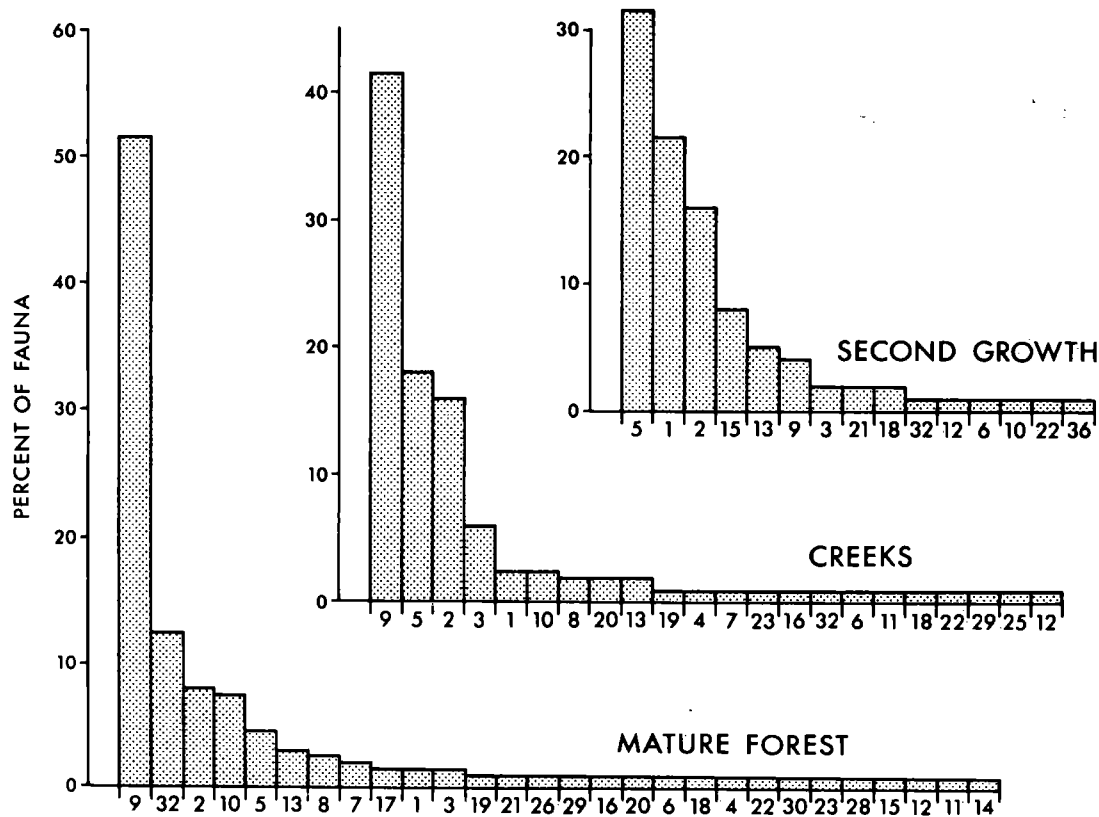**Highly significant by Chi Square Test (P < .01)

FIGURE 4.—Relative abundance of bat species in three habitats. Numbers along horizontal axes refer to species as assigned in Fig. 16.

A. jamaicensis are frequently several hundred meters from the trees where fruits are picked. Only when feeding on fruits of *Dipteryx panamensis* did *A. jamaicensis* feed in fruiting trees, apparently because *Dipteryx* fruits are too large for this species to carry efficiently (pers. obs.). *Vampyrodes caraccioloi, A. jamaicensis, A. lituratus,* and *A. phaeotis* were observed carrying whole or partially eaten fruits in flight. These animals were transporting food items to a night roost for consumption. It was not determined whether the less common guild members use night roosts as eating sites.

Fruits carried in flight by fruit bats vary in weight from less than 1 g to about 20 g. Most bats carry fruits that weigh 20 to 40 percent of their own body weight. Table 7 lists the range in weight of some fruits eaten by stenodermine bats. There is considerable variation in the weights among and within species for these fruits (even in fruits from an individual tree).

There is a highly significant correlation ($P < .01$) of fruit weight with bat weight for fruits carried into nets by the three largest species of bats in the canopy frugivore guild (Fig. 5). Most of the points in this figure represent *Ficus insipida* fruits, the most important food species in the diet of all three bat species. Thus, even though these three bats have high overlap in food species (Table 5), individuals specialize on food particles proportional to their body weights. Smaller canopy frugivore species probably do the same with *F. yoponensis* which is quite variable in fruit weight.

Each fig specialist has a distinct temporal cycle of flight activity. The three largest species, *V. caraccioloi, A. jamaicensis,* and *A. lituratus,* have activity peaks at different times of the night (Fig. 6). Since these three species frequently feed in the same individual trees in the course of the night, offsetting activity patterns probably function

TABLE 7.—WET WEIGHTS IN GRAMS OF SOME BAT FRUITS COLLECTED BENEATH FRUITING TREES ON BCI.

| Plant species	Fruit weights			
	Range	Mean	S.D.	N
Ficus insipida	7.1-11.4	9.1	1.5	10
Ficus obtusifolia	14.2-19.0	17.1	2.5	3
Ficus yoponensis	1.5- 5.6	3.1	1.1	12
Anacardium excelsum	4.2- 6.2	5.1	0.7	7
Calophyllum longifolium	9.3-17.7	14.7	3.3	7
Dipteryx panamensis	18.0-26.3	22.3	3.6	5
Spondias radlkoferi	8.6-13.0	10.6	1.4	9
Quararibea asterolepis	4.9- 6.3	5.4	0.6	4
Astrocaryum standleyanum	17.0-20.5	18.8	1.8	4
Piper cordulatum	0.5- 2.0	1.2	0.5	15
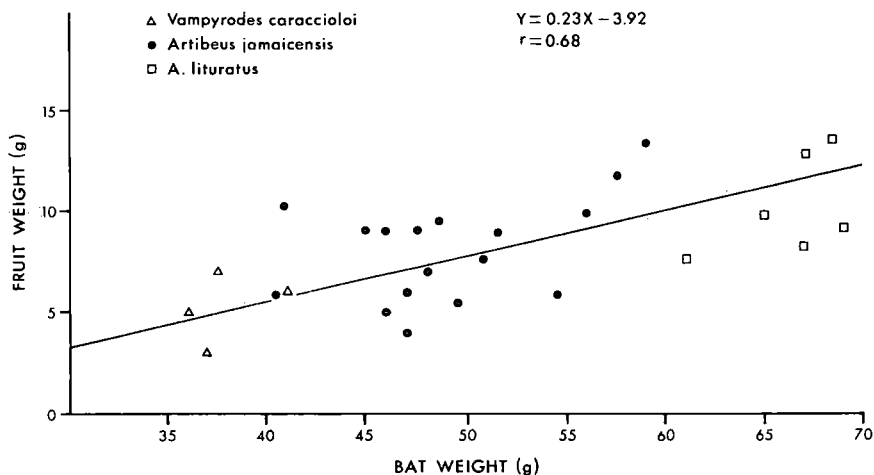
FIGURE 5.—Linear regression of fruit weight on bat body weight for fruits carried into nets by *V. caraccioloi, A. jamaicensis,* and *A. lituratus.*

FIGURE 6.—Frequency of capture through the night as a measure of flight activity for three large canopy frugivorous species.

to minimize interspecific interference from crowding at resource trees. This is evident especially when single trees are in fruit near capture sites where two or more species are found with feces from the same fruits. Indeed, there were instances when only a few trees of a given species were in fruit on BCI and all fig specialists were known to be eating such fruits. Reduced crowding at resource trees presumably is important in permitting efficient feeding and in making these bats less obvious to arboreal and aerial predators (Humphrey and Bonaccorso 1978, Morrison in press).

A similar pattern of offsetting major activity peaks should be expected in the small canopy frugivores, which feed heavily on *Ficus yoponensis* and *F. popenoaei*. Figure 7 shows that *V. pusilla* is more active in the first two hours after sunset, and *C. villosum* is most active later in the night. Small sample sizes prevent a similar comparison of other small fig specialists.

Artibeus phaeotis, the feeding generalist, has a more even distribution of activity through the night than any other canopy frugivore (Fig. 7). Many of the fruits eaten by *A. phaeotis* are not eaten by other stenodermine bats, and it need not compromise its feeding times to avoid resource trees crowded with other bat species.
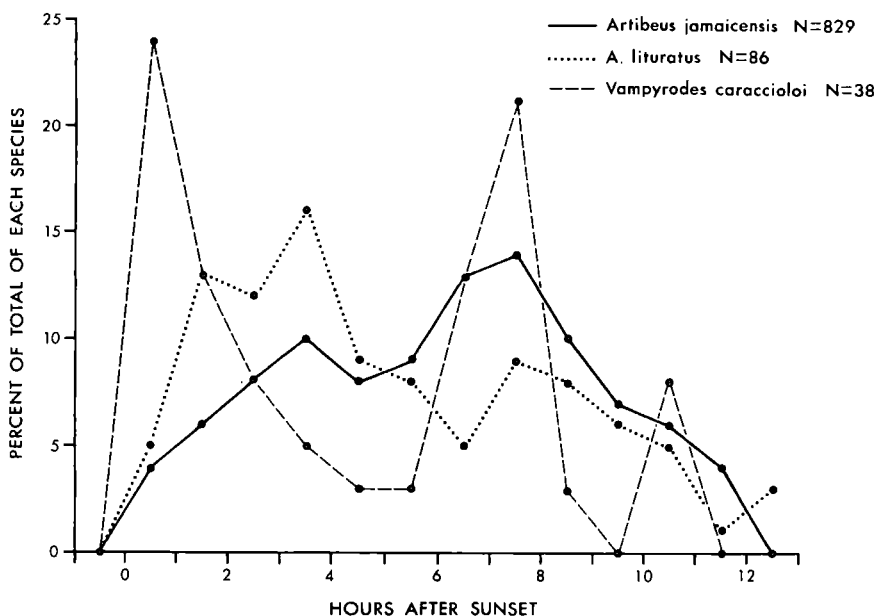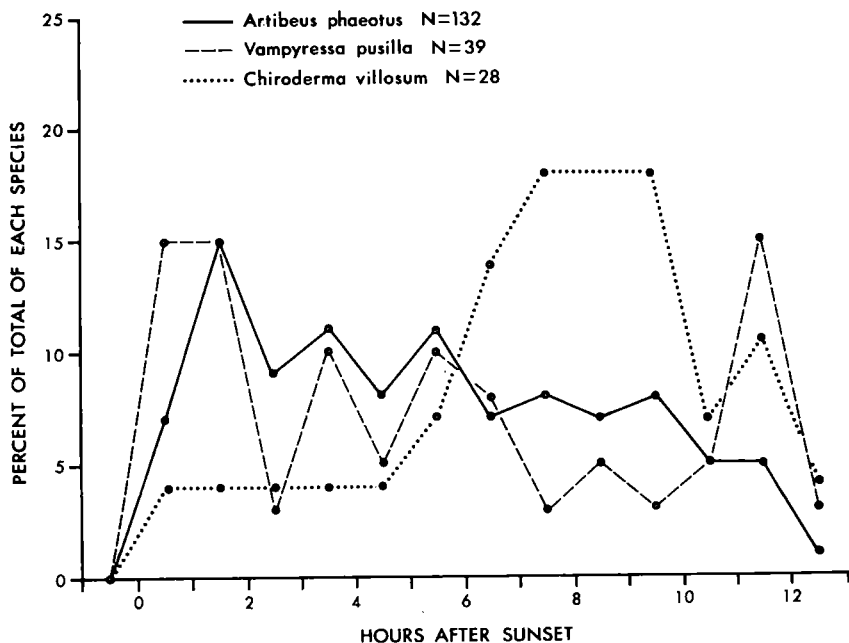

FIGURE 7.—Frequency of capture through the night as a measure of flight activity for three small canopy frugivorous species.

GROUNDSTORY FRUGIVORE GUILD

BODY SIZE.—Two species, *Carollia castanea* and *C. perspicillata*, in the subfamily Carollinae of the Phyllostomatidae constitute the groundstory frugivore guild on BCI. These have mean body weights of 12.4 and 17.9 g, thus differing in body weight by a factor of 1.44.

A few *Carollia subrufa* were captured and banded by R. K. LaVal in 1972 on BCI (pers. comm.). In 1973 and 1974 I recaptured some of LaVal's banded *C. castanea* and *C. perspicillata*, but I have not encountered any of the *C. subrufa* he marked. It is difficult to distinguish *C. perspicillata* and *C. subrufa* by field characters, and it is possible that I lumped a few individuals of *C. subrufa* with *C. perspicillata* because I was not aware that *C. subrufa* was present on BCI. I believe *C. subrufa* is very rare on BCI, and that lumping a few of them with *C. perspicillata* would influence my data negligibly.

FOOD SELECTION.—*C. castanea* and *C. perspicillata* are food generalists eating a fairly even distribution of a large number of kinds of fruits and have large niche breadth values (Tables 8 and 9). Though no one food species dominates their diet in any one season, 11 species of the woody shrub genus *Piper* (Piperaceae) constitute the bulk of the diet of *C. castanea* and nearly one-third of the diet of *C. perspicillata*. I identified 10 species of pipers in *C. castanea* fecal samples and 9 species from those of *C. perspicillata*. At least one species of piper has mature fruits in any month on BCI (see Fig. 2). *C. castanea* and *C. perspicillata* eat pipers all year long, but pipers were less important in the diet of *C. perspicillata* from mid-September through mid-November. *C. perspicillata* appears to feed almost exclusively on subcanopy and canopy fruits in the late wet season; particularly important is *Quararibea asterolepis*. Other fruiting trees are important food species along with pipers at other seasons. Though fruiting shrubs dominate the diet of *C. castanea*, fruiting trees are somewhat more important than shrubs for *C. perspicillata*.

In addition to fecal samples from captured animals, food habits data for *C. perspicillata* were obtained by monitoring droppings below two day roosts of this species. Both roosts were in hollow *Anacardium excelsum* trees. With the exception of fruit from *A. excelsum*, all common food items identified from the day roost droppings appeared as important food items in fecal samples from captured bats during the same bimonthly periods (Table 10).

Why did the fruit of *A. excelsum* never show in the fecal material from captured bats? Probably because *Anacardium* is the only tree species that commonly serves as both day roost and food source for *C. perspicillata*. These bats need only fly to the canopy of the roost tree, pick a fruit, and carry it inside the roost to eat it. The bats would

TABLE 8.—FOOD SPECIES OF *C. castanea* AND *C. perspicillata*. NUMBERS INDICATE FECAL SAMPLES WITH A GIVEN FOOD PRESENT. SAMPLING BEGINS AT MID-MONTH.

Plant species	C. castanea				C. perspicillata			
	Nov-Mar	Mar-Jul	Jul-Nov	Tot.	Nov-Mar	Mar-Jul	Jul-Nov	Tot.
Shrubs								
P. aequale	9		6	15		1	.	1
P. carrilloanum		1	1	2				
P. cordulatum		8	1	9	.	10	1	11
P. marginatum	4	1	1	6	1	2		3
P. reticulatum	2		3	5			7	7
Piper 109	3	1		4	1	4	1	6
Piper 114	1			1	1	1		2
Piper 116					1			1
Piper 120	1	1		2	1	2		3
Piper 122		3		3				
Piper 150		2		2		2		2
Trees								
Carludovica palmata		1		1		1		1
Solanum hayseii		2		2	1	7	1	9
Markea panamensis		9	2	11	1	4		5
Vismia 1		2	1	3		4	5	9
Vismia 2						2		2
Brosimum bernadettae			1	1		3		3
Cecropia exima						1	2	3
Quararibea asterolepsis							6	6
Dipteryx panamensis	1			1	7	1		8
Cassia undulata						3		3
Epiphytes								
Aechmeia tillandsoides	1			1				
Unknowns								
Unknown 104		1		1				
Unknown 123			1	1				
Unknown 125			.				4	4
Unknown 127					2			2
Insects						6		6

TABLE 9.—FEEDING NICHE BREADTHS OF GROUNDSTORY FRUGIVORES. SAMPLE SIZES FOR CALCULATING NICHE BREADTHS ARE AS IN TABLE 8.

	C. castanea	C. perspicillata
Genera of known food plants	8	10
Species of known food plants	18	24
Percent of diet composed of pipers	78 (N = 60)	27 (N = 103)
Niche breadth (log, B)	2.47	2.63

digest and excrete the fruit, usually before flying away from the roost to forage for other fruits; thus little chance would exist for this pulp to show up in netted animals. The *Carollia* colonies in the *Anacardium* trees observed consist of 6 to 8 individuals, and each colony probably had access to more *A. excelsum* fruits than they could eat.

Anacardium excelsum is the only fruit eaten by bats on BCI that is not effectively dispersed by them (*Dipteryx panamensis* though not dispersed by *Artibeus jamicensis* is dispersed by *A. lituratus.*). In the colonies I observed that *Anacardium* fruits are carried within the hollow tree roosts, but even if they are eaten elsewhere, it is the single large seed, and not the fruit pulp, that is eaten.

There are significant seasonal changes in diet and niche breadths of both species of *Carollia* (Table 9). These bats are extreme fruit generalists in the first half of the wet season. In the dry season and latter half of the wet season, niche breadths are narrower. *C. castanea* feeds almost entirely on pipers during the dry season, but in much of the wet season *Markea panamensis,* a tree, is an important dietary item. Throughout the year pipers constitute 30 to 40 percent of the food items eaten by *C. perspicillata* with various trees sequentially becoming important food sources. Most important are *Dipteryx, Anacardium,* and *Quararibea* in the dry, early wet, and late wet seasons respectively. Also in the early wet season insects are important in the diet of *C. perspicillata.*

Overlap between the diets of the two *Carollia* is moderate in terms of food species. A $\hat{C}\lambda$ value of 0.585 is obtained from lumping the dietary data from the year's fecal samples. Food overlap was highest in the May-July sampling, $\hat{C}\lambda$ is 0.798. This latter value and the annual value of overlap would be somewhat smaller if it were possible to correct for *Anacardium* eaten in roost trees by *C. perspicillata.* Even though roosts were not monitored, it is unlikely that *C. castanea* eats much of this fruit, as it is larger than all other important fruits in the diet of *C. castanea* and probably too large for efficient handling.

HABITAT SELECTION.—Of the three habitats sampled, the Carollinae were most common in the second growth forest and least common in the mature forest, as are their most important food plants. *C. castanea* accounted for 21.7% of all bats captured in second growth young forest, 2.7% of the bats in creeks, and 1.4% of the bats in mature forest (Fig. 4). *C. perspicillata* constituted 15.8%, 16.0%, and 5.4% of the individuals captured in those habitats. Whereas many species of pipers grew abundantly in the sunlight of the open canopy second growth and along the creeks (though less so along creeks), only one species, *P. cordulatum,* was abundant in the shade of the mature forest.

VERTICAL STRATIFICATION.—*C. castanea* and *C. perspicillata* were both captured more frequently at ground level than at upper levels of the forest (*C. castanea* = 20 ground level, 14 upper levels; *C. perspicillata* = 50 ground level, 34 upper levels), but the difference was not statistically significant. Both species feed on plants of ground and canopy levels. Known groundstory fruits make up 78.4% of the diet of *C. castanea* and 38.0% of the diet of *C. perspicillata*. During seasons when these bats feed mostly on canopy fruits, they are captured more frequently in high nets and traps.

FEEDING BEHAVIOR.—*Carollia castanea* and *C. perspicillata* both have been captured carrying fruits and presumably use night roosts as do canopy frugivores. Some fruits are carried back to the day roost for consumption (Table 10).

Both species of *Carollia* show major peaks of flight activity in the first hour of darkness (Fig. 8). This is earlier than the start of most canopy frugivores' activity and is probably due to the groundstory becoming dark about an hour before the canopy level of the forest. Patterns of flight activity in groundstory frugivores are bimodal or trimodal as are those of canopy frugivores.

SCAVENGING (OR JUICER) FRUGIVORE GUILD

BODY SIZE.—*Centurio senex* (Stenoderminae, Phyllostomatidae), the wrinkle-faced bat, is the sole member of the scavenging frugivore guild. A lactating female weighed 22 g, and a pregnant female weighed 27 g. No other weights are available from BCI for this species, nor are there data on vertical stratification or habitat use.

FEEDING BEHAVIOR.—Goodwin and Greenhall (1961) mentioned finding fruit pulp in stomachs of *C. senex* from Trinidad. Of the individuals that I captured on BCI, one defecated an unidentifiable fruit

TABLE 10.—FREQUENCY OF OCCURRENCE OF FOOD SPECIES OF A COLONY OF *Carollia perspicillata* AS DETERMINED FROM FRUIT DROPPINGS AND SEEDS BELOW THE DAY ROOST. SAMPLING PERIODS BEGIN AT MID-MONTH.

Plant species	Jan-Mar	Mar-May	May-Jul	Jul-Sep	Sep-Nov	Total
Anacardium excelsum	5	83	39			127
Piper cordulatum		39	35	9		83
P. reticulatum				6		6
Piper 109					6	6
Solanum hayseii		1			1	2
Vismia 1				2	2	4
Quararibea asterolepsis				5	15	20
Cassia undulata		5	1			6
Unknown 155					12	12
Unknown R-1		3				3

pulp and the other carried a fresh *Spondias radlkoferi* fruit in its mouth. From several morphological features, particularly the small teeth and narrow esophagus, Paradiso (1967) concluded that *C. senex* probably feeds on a "soft fruit or fluid" diet. Its small teeth and lack of facial hair suggest that it possibly feeds on very juicy, over-ripe fruit or decaying fruit. The amount of rotting fruit on the forest floor was incredibly large on BCI and potentially could have provided an abundant food resource for such a bat. I have tentatively designated it a "scavenging frugivore".

An alternative suggestion is that *Centurio* may feed on very juicy fruits still clinging to trees. S. R. Humphrey (pers. comm.) believes from analysis of jaw structure that *Centurio* is best adapted for feeding on large, ripe, soft fruits that have very thick pericarps, such as papayas and mangos.

Nectar-Pollen-Fruit-Insect Omnivore Guild

Body Size.—The nectar-pollen-fruit-insect omnivore guild (hereafter called the omnivore guild) contains three species, all of the
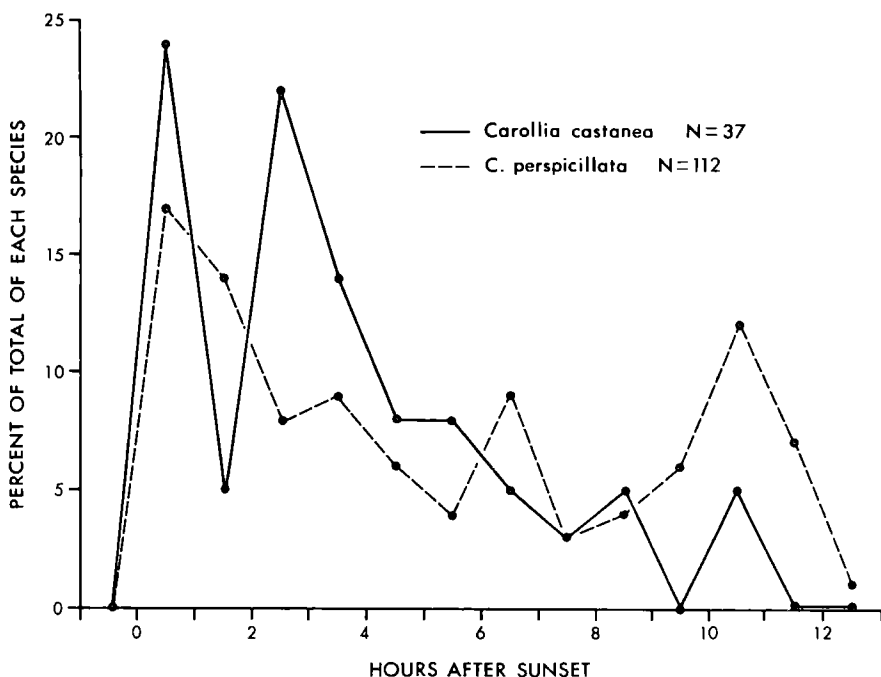

Figure 8.—Frequency of capture through the night as a measure of flight activity for two groundstory frugivorous species.

family Phyllostomatidae: *Glossophaga soricina* (Glossophaginae), *Phyllostomus discolor* (Phyllostominae), and *Phylloderma stenops* (Phyllostominae). Mean body weights for these species are given in Table 11. The dimorphism in body weights between male and female *P. discolor* is significant (P < .05, Student's t-test).

FOOD SELECTION.—Nectar and pollen are consumed by guild members almost exclusively in the dry season, as large flowers suitable for bats are in bloom only then (see Phenology). The few data available suggest that during the wet season fruit and insects become dietary staples (Table 12). Insects were not present in the food samples of *G. soricina* on BCI, probably because of poor sample size and the fact that this species moved out of the study area during the wet

TABLE 11.—WEIGHTS OF OMNIVOROUS BATS ON BCI. COLUMN HEADINGS ARE DEFINED IN TABLE 1.

Bat species	$\overline{X}$	S.D.	N	Wgt/wgt$_{sm}$
G. soricina	9.8	1.0	9	—
P. discolor	42.2	3.9	27	4.36
males	44.6	3.6	17	—
females	39.7	2.1	10	—
P. stenops	61.8	—	1	1.42

TABLE 12.—SEASONAL USE OF POLLEN AND FRUIT BY THE OMNIVORE GUILD. NUMBERS INDICATE POLLEN SWABS AND FECAL SAMPLES COMBINED.

Food species	Dry season samples	Wet season samples
P. discolor (N = 23)		
Pollen:		
Ochroma lagopus	6	
Pseudobombax septenatum	6	
Unknown 202		1
Fruit:		
Cecropia exima		2
Unknown 124		3
Insects:		3
G. soricina (N = 6)		
Pollen:		
Ochroma lagopus	3	
Unknown 201	1	
Fruit:		
Cecropia exima		1
Piper 109		1
P. stenops (N = 2)		
Fruit:		
Unknown 110		1
Unknown 151		1

season. Howell and Burch (1974) reported that it ate insects. Nothing beyond Jeanne's (1970) observations of *P. stenops* eating social wasp larvae and my two observations of fruit eating is known about the diet of this bat.

Phyllostomus discolor is neither an extreme specialist nor a generalist in food species (niche breadth = 1.65). Several types of flowers are visited for pollen and nectar in the dry season and, in addition to insects, several types of fruit are eaten in the wet season. The available data are too limited to consider niche breadth values for *P. stenops* and *G. soricina.*

VERTICAL STRATIFICATION.—All flowers and fruits eaten by *P. discolor* and 83 percent of those eaten by *G. soricina* in this study grow in the subcanopy and canopy of the forest. Both species were captured most frequently in upper levels of the forest, 3 of 4 for *Glossophaga* and 40 of 54 for *Phyllostomus.* For *P. discolor* preference for flying above groundstory shrubs is highly significant (P < .01, Chi Square Test).

HABITAT SELECTION.—*Phyllostomus discolor* was common in the mature forest and second growth but uncommon over creeks. Some of the important tree species producing flowers and fruits eaten by *Phyllostomus* are common only in second growth (e.g. *Ochroma*), others are common only in mature forest (e.g. *Pseudobombax*), and still others are common in both habitats (e.g. *Cecropia*).

FEEDING BEHAVIOR.—During the dry season bats are frequently captured with pollen heavily dusted over the anterior body. It is likely that these animals visit numerous flowers in succession, consuming nectar and performing pollination services at each flower, and later while roosting ingest pollen by grooming it from the fur and skin. None of the bats in this guild were captured carrying fruit.

Of the *P. discolor* captured in all-night samples, 69 percent were taken within two hours of sunset. Such a strong unimodal pattern of flight activity (Fig. 9) also is reported by LaVal (1970) and suggested by Heithaus *et al.* (1974) for this species in Costa Rica. My data are insufficient for discussing flight activity cycles of *Glossophaga,* but LaVal (1970) reported a strong activity peak at dusk and in the first hour of darkness, just before peak *P. discolor* activity.

SANGUIVORE GUILD

BODY SIZE.—Of the three extant vampire species, only *Desmodus rotundus,* the common vampire, inhabits BCI and surrounding areas. The mean prefeeding body weight of *D. rotundus* is 33.5 g.

FOOD SELECTION.—Wild vampires feed only on the blood of homoiothermic vertebrates (McNab 1973). While vampire feeding

behavior and prey selection are well documented in agricultural areas where domestic livestock is the food source (Turner 1975), nothing is known about prey selection of vampires in areas where only wild animals are potential hosts.

VERTICAL STRATIFICATION.—Where domestic animals are the source of food, vampires usually fly within 3 m of ground level (Bonaccorso, unpubl. data). It is possible that vampires more commonly fly at the canopy level in forest where no livestock is available, but where arboreal species (e.g. monkeys and birds) may provide sources of blood. On BCI two vampires were captured in subcanopy nets and one in a ground net.

HABITAT SELECTION.—Vampires were clearly more abundant on Buena Vista Peninsula than on BCI. *Desmodus* was the fourth most abundant species in the Buena Vista second growth (7.9% of total captures), whereas on BCI *Desmodus* was one of the least common species (0.2% total captures; see Fig. 4). Horses, cattle, pigs, and fowl on scattered farms in the Buena Vista-Frijoles area provide a dependable and abundant food source that "los vampiros" constantly parasitize (Fulo Sanchez, pers. comm.).
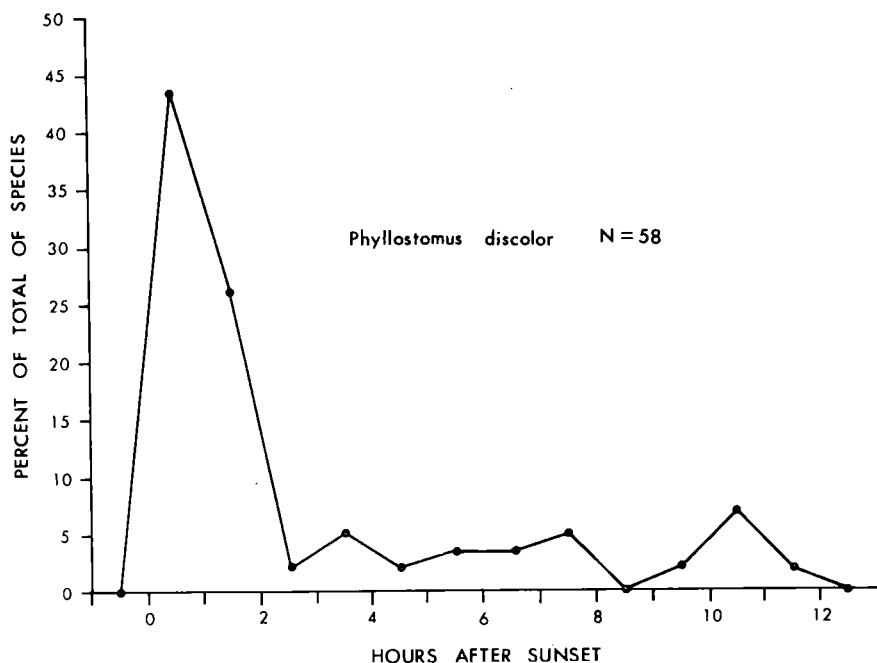

FIGURE 9.—Frequency of capture through the night as a measure of flight activity for *Phyllostomus discolor.*

GLEANING CARNIVORE GUILD

BODY SIZE.—The largest feeding guild within the bat fauna of BCI, the gleaning carnivore guild, consists of nine phyllostomine species which exhibit the largest range in body size in any of the feeding guilds (Table 13). *Micronycteris megalotis,* one of the smallest bats on the island, has a mean body weight of 6.3 g, while *Vampyrum spectrum,* the largest species, weighs about 120 g.

FOOD SPECIES SELECTION.—Except for the vertebrate diet of *V. spectrum,* guild members feed predominantly on insects; however, fruits, pollen, arachnids, or lizards supplement the diet of various species. The collected fecal samples from these species are now being analyzed and will be published elsewhere.

Novick (1971) hypothesized that large-eared insect- and vertebrate-eating bats, such as the species in this gleaning carnivore guild, are adapted to distinguish and capture prey items resting on foliage by echolocation. Recent information cited below demonstrate that olfaction and sound produced by prey are used by some of these bats to find prey.

Ross (1967), Wilson (1971b), and Vehrencamp *et al.* (1977) have shown that many large-eared bats do feed primarily by gleaning large insects and birds that nocturnally perch on vegetation or on the ground. Gardner's (1977) review of the food habits of bats in this guild further confirms that food items such as lizards and large insects are gleaned from foliage.

MICRONYCTERIS. Wilson (1971b) reported that large roaches, orthopterans, and scarabeid beetles are the most important items in the diet of *M. hirsuta* on Orchid Island, a small island adjacent to BCI. During the dry season fruit became an important component of the diet of this species as indicated by droppings below the study roost. My data show that *M. megalotis* and *M. brachyotis* also switch in part

TABLE 13.—WEIGHTS IN GRAMS OF GLEANING CARNIVORES. COLUMN HEADINGS ARE DEFINED IN TABLE 1.

Bat species	$\overline{X}$	S.D.	N	Wgt/Wgt$_{sm}$
M. megalotis	6.3	0.6	6	O
M. brachyotis	9.7	1.1	3	1.53
M. crenulatum	14.7	0.7	12	1.52
M. hirsuta	15.2	1.2	7	1.03 (1.57*)
T. cirrhosus	31.0	3.8	13	2.09
T. sylvicola	32.6	3.6	10	1.04
T. bidens	35.6	2.3	7	1.09
P. hastatus	91.2	4.0	7	2.56
V. spectrum	120.0	—	1	1.31

*Ratio between weights of *M. hirsuta* and *M. brachyotis.*

to fruit diets in the dry season. *M. brachyotis* also eats nectar and pollen. An individual captured in mid-December was thoroughly dusted with the pollen of a balsa tree (*Ochoroma lagopus*).

TONATIA. Insect, arachnid (spiders), and lizard fragments were found in the fecal samples of *T. bidens.* Insects, arachnids (whipscorpions), and plant materials were found in the feces of *T. sylvicola* on BCI. A very large male cicada (*Fidicina mannifera*) that weighed 2.5 g was carried into a net by a *T. bidens* in July of 1974. The prothorax of the dead cicada had been crushed by the bat's teeth. Because this event occurred in the mating season of the cicadas, during the loud nocturnal chorusing, it posed the question of how *Tonatia* locates such insect prey. Do these bats find such prey via echolocation or by sounds produced by the insects?

Two *T. bidens,* one male and one female, were released on separate occasions into a large outdoor flight cage on BCI. Both individuals were immediately attracted to calling male cicadas that I held by forceps inside the cage. The cicadas were plucked from the forceps by the flying bats and eaten after the bats had roosted. Female cicadas (which are not capable of singing) held so that their wings could not move in the forceps were ignored by these bats; however, when the wings were allowed to flap noisily, the bats again were attracted to the cicadas and ate them. During later experiments large nocturnal grasshoppers, katydids, beetles, and moths placed on the inside cage screening were "gleaned" from the screening and eaten by these bats. It is obvious that *T. bidens* was able to locate cicadas from sounds produced by the cicadas, but whether other large foliage-clinging insects were echolocated or detected from insect-produced sounds or detected by some other sensory system remains an interesting question.

PHYLLOSTOMUS. Insects and fruits were found in the fecal samples of *P. hastatus* on BCI. It also has been reported by several authors to eat birds and rodents (Gardner 1977).

VAMPYRUM. V. spectum (the false vampire bat), the largest New World bat, feeds primarily on birds, rodents, and bats (Vehrencamp *et al.* 1977). A hollow roost monitored by Vehrencamp *et al.* in Costa Rica had remains of doves, parrots, trogons, cuckoos, anis, and many other birds weighing between 20 and 150 g. These authors suggested that *Vampyrum* locates prey primarily by olfaction, striking animals at communal roosts with strong odors. D. J. Howell and I kept a *Vampyrum* alive in captivity for three weeks on a diet of small bats and birds (10-120 g). When released in a large room with small fruit bats (10-20 g), the false vampire would fly up behind its flying victim and slap it into its jaws with a wingtip. One morning at sunrise on BCI, a false vampire circled about an *Artibeus jamaicensis* I was untangling

from a net. The *Vampyrum* was apparently attracted by the alarm calls of the fruit bat and circled for over a minute before leaving.

MIMON. Fecal samples of *Mimon crenulatum* from BCI contained insect, arachnid, and lizard remains.

TRACHOPS. Fecal samples of *Trachops cirrhosus* from BCI contained insect, whipscorpion, and lizard remains and fruit pulp. Elsewhere this species is reported to eat lizards, such as anoles and geckos, that are gleaned from vegetation, as well as fruit and insects (Gardner 1977, Howell and Burch 1974).

VERTICAL STRATIFICATION.—*Mimon crenulatum, Trachops cirrhosus,* and *Tonatia sylvicola* show a significant preference for flight in the groundstory level of the forest, and the small samples for *Micronycteris brachyotis* and *Tonatia bidens* are just below significance levels for showing a subcanopy-canopy preference (Table 14). Thus the two similarly sized *Tonatia* species appear to forage in different vertical strata.

Phyllostomus hastatus and *Vampyrum spectrum* were captured or seen flying only in the subcanopy-canopy levels of the forest. The groundstory (0 to 3 m) on BCI has the densest foliage of the vertical strata of the forest (E. Leigh, pers. comm.). *P. hastatus* and *V. spectrum* may be too large to maneuver well through the thick groundstory vegetation.

HABITAT SELECTION.—Several of the gleaning carnivores prefer either creek or forest habitats on BCI to the exclusion or near exclusion of the other. *Micronycteris brachyotis* and *Tonatia sylvicola* are both common in the forest but are totally absent from the creek samples (Fig. 4). *Trachops cirrhosus* represents 4 percent of all individuals sampled at creek stations (8th most abundant species in

TABLE 14.—VERTICAL STRATIFICATION OF GLEANING CARNIVORES. YATES CORRECTION FOR CONTINUITY IS USED ON ALL CHI SQUARE TESTS (SOKAL AND ROHLF 1969).

Bat species	No. of bats captured at ground level, 1 to 3 m	No. of bats captured at subcanopy level, 3 to 12 m
M. megalotis	1	3
M. brachyotis	6	12
M. hirsuta	6	3
M. crenulatum	9*	1
T. cirrhosus	14**	0
T. sylvicola	18**	3
T. bidens	2	8
P. hastatus	0	4
V. spectrum +	0	3

*Significant by Chi Square Test (P < .05).
**Highly significant by Chi Square Test (p < .01).
+ Based on two net captures in Costa Rica and one visual sighting on BCI.

creek samples) but only 0.5 percent of the individuals sampled at forest stations (17th most abundant species in forest stations). All other species in the guild are approximately equally abundant in creek and forest samples. Comparisons with Buena Vista second growth samples are not made, because most species in this guild were under-represented at Buena Vista from lack of harp-trapping.

It appears that a spatial mechanism, specialization in foraging microhabitat, permits *Trachops cirrhosus, Tonatia sylvicola,* and *Tonatia bidens,* all similar-sized gleaning carnivores, to partition food resources within the same macrohabitat. *T. cirrhosus* seems to specialize on prey in low foliage along creeks, *T. sylvicola* on prey from groundstory forest foliage, and *T. bidens* on prey from trees in the forest and along creeks.

FEEDING BEHAVIOR.—The gleaning carnivores eat rather large prey items relative to their body weight. It probably is common for them to carry prey to a night or day roost for consumption (Wilson 1971b, Vehrencamp *et al.* 1977, pers. observation).

Data on activity cycles are too scant for meaningful analysis. *M. brachyotis, M. crenulatum, T. sylvicola,* and *T. cirrhosus* appear to have a major peak of flight activity in the first two hours after sunset.

SLOW-FLYING HAWKING INSECTIVORE GUILD

Eight species belonging to three families constitute the slow-flying hawking insectivore guild. Four species belong to the Emballonuridae, two to the Vespertilionidae, and two to the Mormoopidae. An additional species, *Thyroptera tricolor* (Thyropteridae), is known only from a single 1973 sighting in recent years on BCI. *T. tricolor* perhaps should be included in this guild if a population still exists on BCI; however, the species is probably near extirpation on the island because of plant succession that has resulted in the disappearance of most large-leaved groundstory plants (e.g. *Musa* and *Callithea*) used as roosts (Findley and Wilson 1974).

BODY SIZE.—Mean body weights of species in this guild range from 4.2 to 22.6 g (Table 15). Wing morphology and flight behavior (Bonaccorso, unpubl. data) suggest that species within the same family are most similar in foraging behavior. Thus, species are grouped in subguilds by families.

FOOD SELECTION.—All species of this guild feed largely on small flying insects. Prey items are eaten on the wing rather than carried to roosts. Some emballonurids hover around tree foliage and feed to some extent on insects attracted to host trees (Bradbury and Vehrencamp 1976). One BCI fecal sample from *Pteronotus parnellii* examined by Terry Erwin contained leg parts of a small alleculid beetle. All other samples await species identification.

TABLE 15.—WEIGHTS OF SLOW-FLYING HAWKING INSECTIVORES. COLUMN HEADINGS ARE DEFINED IN TABLE 1.

Bat species	$\overline{X}$	S.D.	N	Wgt/wgt$_{cm}$
Emballonuridae				
S. leptura*	4.2	—	1	—
C. maximiliani*	5.2	—	1	—
S. bilineata males	7.7	0.56	11	1.47
S. bilineata females	8.7	0.70	3	—
P. kappleri*	11.2	—	2	1.46
Vespertilionidae				
R. tumida	4.2	—	2	—
M. nigricans	4.4	0.67	11	1.05
Mormoopidae				
P. saupurensis	16.5	—	1	—
P. parnellii	22.6	1.48	30	1.37

*Males and females are probably dimorphic in body weight.

VERTICAL STRATIFICATION.—*Pteronotus parnellii* usually fly within 3 m of the ground (Table 16). *Myotis nigricans* and *S. bilineata* commonly fly in groundstory and subcanopy levels of the forest. *Peropteryx kappleri* is a specialist on insects of the subcanopy (Bradbury and Vehrencamp 1976). This also is indicated by the capture of all four BCI individuals in high nets, and numerous visual observations I made in Belize.

HABITAT SELECTION.—*P. parnellii* is the second most abundant species in the forest but is very rare over creeks (Fig. 4). The single specimen of *P. suapurensis* was captured in forest.

Myotis nigricans was captured only at forest stations, whereas *Rhogeessa tumida* was captured only at or near creeks. These two-similar-sized species thus may differ in habitat requirements.

Visual observations of *Saccopteryx bilineata* during its crepuscular foraging indicate that individuals repeatedly fly in circles around feeding territories in small clearings of the forest (e.g. treefalls) or over creeks. Frequently I have watched *Saccopteryx* chase intruding con-

TABLE 16.—VERTICAL STRATIFICATION OF SLOW-FLYING HAWKING INSECTIVORE SPECIES.

Bat species	No. of bats captured at ground level, 1 to 3 m	No. of bats captured at subcanopy levels, 3 to 12 m
S. bilineata	7	4
C. maximiliani	2	0
P. kappleri	0	4
R. tumida	1	0
M. nigricans	3	3
P. parnellii	74*	1

*Highly significant by Chi Square Test (P < .01) with Yates Correction for Continuity (Sokal and Rohlf 1969).

specifics out of their territories, emitting high pitched audible sounds as they fly. Bradbury and Vehrencamp (1977) reported that individual males defend noctural feeding territories admitting only females that roost and mate with them.

FLIGHT BEHAVIOR.—*Pteronotus parnellii* is one of the most commonly seen species on BCI as it flies low along forest trails. Ultrasonic pulses picked up by a bat detector indicate that *P. parnellii* feeds as it flies back and forth in long loops along forest trails and groundstory vegetation.

Flight activity of *P. parnellii* through the night is bimodal, with a major activity peak occurring 1 to 4 hours after sunset (Fig. 10). Data on activity cycles of the other guild members are limited, but *P. parnellii* may be the only species that has no peak of activity the first hour after sunset. Based on netting, visual observations, and ultrasonic detection, the emballonurids are active from an hour before sunset to an hour after sunset and again at a similar period around sunrise.

REPRODUCTION

Three patterns of reproduction occur in Neotropical bats: seasonal monestry, seasonal polyestry, and year-round polyestry (Fleming
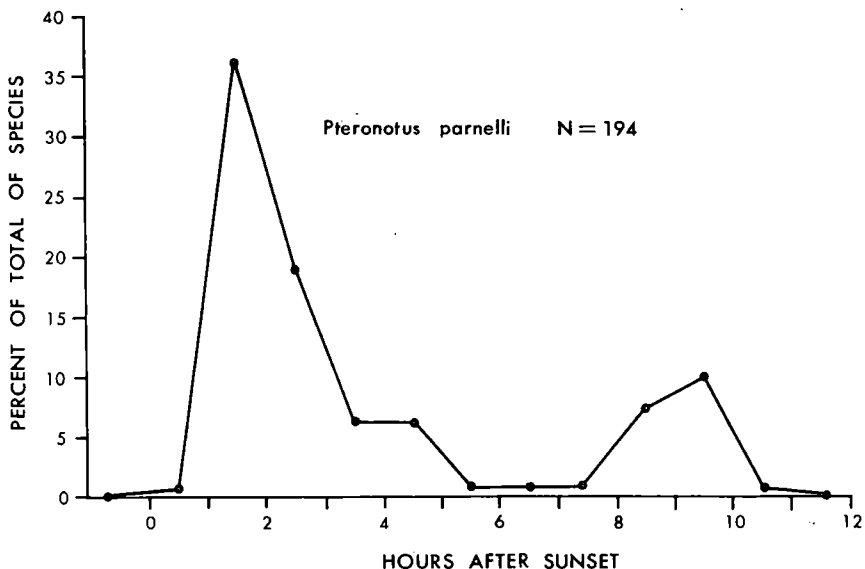

FIGURE 10.—Frequency of capture through the night as a measure of flight activity for *Pteronotus parnellii*.

1973). Present information indicates that a single young is born per litter, except in the genus *Rhogeessa* in which the usual litter size is two (Humphrey and Bonaccorso 1978). Reproductive patterns within bat species vary with geography and ecological conditions, all data below refer to BCI except where otherwise stated.

CANOPY FRUGIVORE GUILD

Canopy frugivores are seasonally polestrous, with one birth peak at the end of the dry-to-wet transition and a second about the middle of the wet season (Figs. 11-13, Table 17; Wilson 1979). The first birth peak for all species coincides with the beginning of the first predictably steady rains of the year in late April and May, a time of fruit abundance. Large species, such as *A. jamaicensis* and *A. lituratus,* are pregnant (as detectable by palpation) by the first week of January. Small species like *A. phaeotus* are not in a similar stage of pregnancy until late January. Lactation then proceeds for 1 or 2 months (during continued food abundance). There is a postpartum estrus, and females are well advanced in the second pregnancy of the year while lactation is still underway (Fleming 1971, this study).

The second birth and lactation peaks are less synchronized among species because of differences in gestation and lactation periods; the same is true to a lesser degree within species because of individual
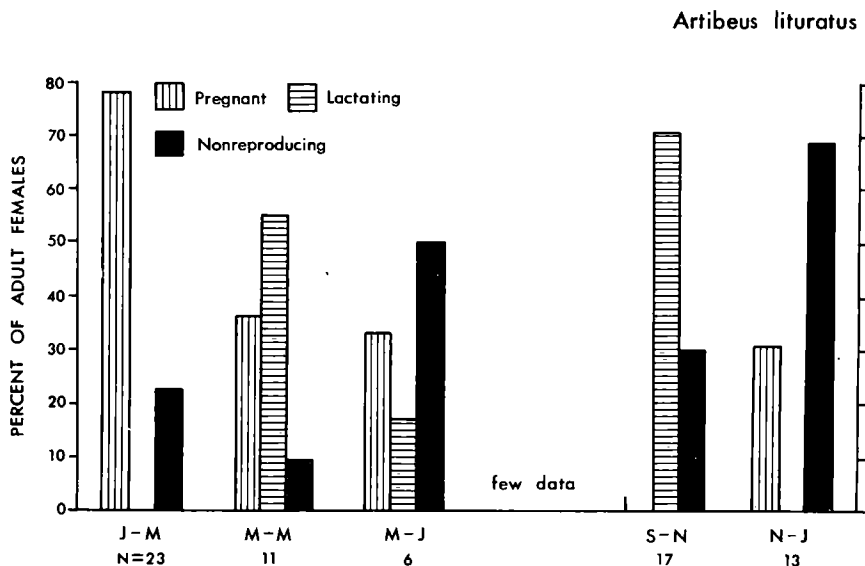

FIGURE 11.—Reproductive timing in female *Artibeus lituratus.*

variation. For example, the second peak of lactation occurs in July-September for *A. jamaicensis* and *A. phaeotis,* but not until September-November for the larger *A. lituratus.*

All canopy frugivores are reproductively quiescent in the late wet season. Females of small species appear inactive from October through December. The two largest species of the guild appear reproductively inactive from mid-October through December, at least by external signs, but histological preparations (Fleming 1971) indicate that *A. jamaicensis* females are in early stages of pregnancy with drastically slowed embryonic growth occurring in these months. Whether other species also pass through a period of delayed development at the end of the wet season is not known. Nevertheless, the energy channeled into reproduction by canopy frugivores is markedly reduced during the late wet season, a time of fruit scarcity.
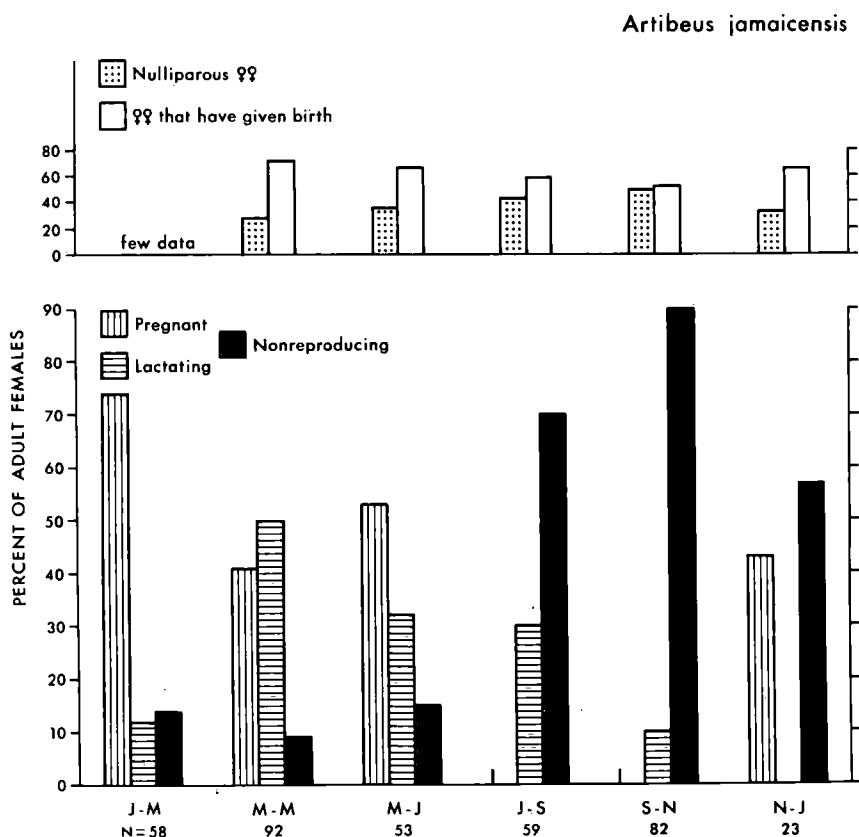

FIGURE 12.—Reproductive timing in female *Artibeus jamaicensis.*

During the March-May sampling, 27 percent of the *A. jamaicensis* adult females captured were nulliparous (Fig. 12,), and nearly all of these probably had been born in the first or second birth pulse of the previous year (8 to 12 months before). Through the next three bi-monthly periods the percentage of nulliparous females in the population steadily rose to 49 percent, as recruitment occurred from the off-spring of the year. Between November and the following March the proportion of nulliparous females declined, not from their having given birth, but presumably from higher mortality and/or dispersal rates than are found in older females.

GROUNDSTORY FRUGIVORE GUILD

Groundstory frugivores follow a reproductive pattern similar to canopy frugivores. There are two births per year per female, one in the dry-to-wet season transition and the other in mid-wet season (Fig. 14). Simultaneous pregnancy and lactation in March-May and recaptures of marked individuals indicate that females have a postpartum estrus. Females are reproductively inactive from mid-October through December.
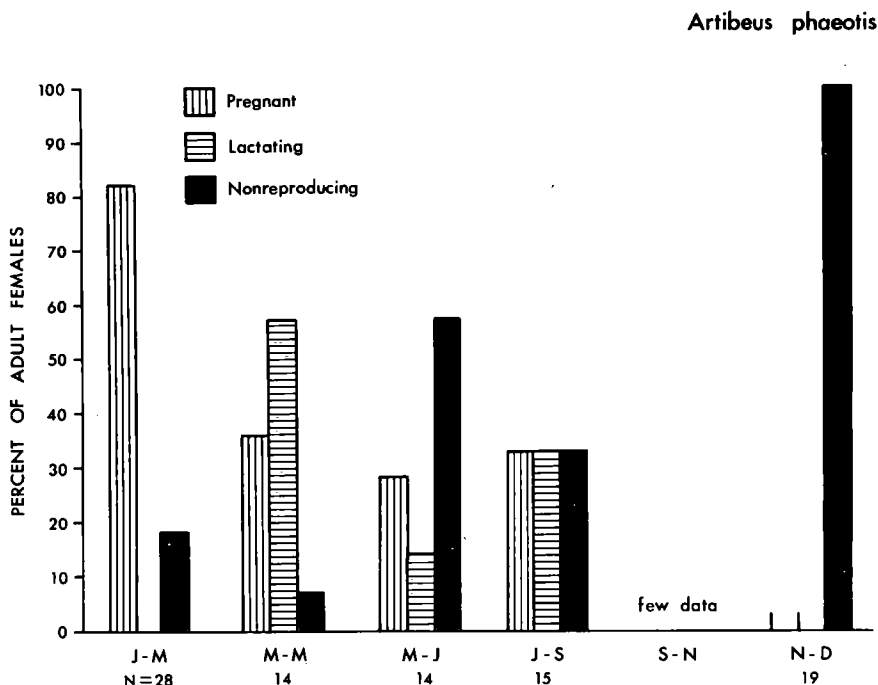

FIGURE 13.—Reproductive timing in female *Artibeus phaeotis*.

SCAVENGING FRUGIVORE GUILD

Though only two female *Centurio* were captured, one female pregnant in February and another lactating in November indicate that the wrinkle-faced bat is probably seasonally polyestrous like other fruit bats.

NECTAR-POLLEN-FRUIT-INSECT OMNIVORE GUILD

The only reproductive data available for this guild is for *Phyllostomus discolor,* which appears to follow the pattern of seasonal polyestry explained for frugivorous guilds (Table 17).

SANGUIVORE GUILD

Wimsatt and Trapido (1952) suggested that *Desmodus rotundus* females are seasonally polyestrous or polyestrous year round. Turner (1975) demonstrated that *D. rotundus* in cattle-raising areas of Dry Tropical Forest in Costa Rica are pregnant or lactating in all months of the year, but most pregnancies occur in the wet season. Although only six female vampires were captured in my study, the appearance of

TABLE. 17.—REPRODUCTIVE TIMING IN FEMALE BATS OF PANAMA.*

Bat species	Jan-Mar			Mar-May			May-Jul			Jul-Sep			Sep-Nov			Nov-Jan		
C. castenea	3	0	8	7	1	3	2	3	1	8	0	5	0	1	3	0	0	12
V. pusilla	2	1	0	5	7	2	3	1	2							3	0	2
C. trinitatum	2	0	0	0	0	1	1	0	1	0	1	0	1	2	0			
V. helleri	2	0	0	1	1	1	4	0	0	1	0	1	0	1	1	1	0	1
C. villosum	3	0	0	3	10	0							0	0	2	1	0	0
V. caraccioloi	2	0	0	1	1	1				0	2	2	0	0	1	0	0	4
C. senex	1	0	0													0	1	0
P. discolor	1	1	2	0	2	5	0	0	1	0	1	3	1	2	3	4	1	1
D. rotundus	0	1	1				1	0	0	2	0	0				0	0	1
M. megalotis	1	0	2	3	2	1							0	0	1			
M. brachyotis	1	0	0	1	1	1	1	0	1	0	0	1	0	1	1	1	0	2
M. crenulatum	1	0	4	5	0	0	0	3	1	0	1	4	0	0	1	0	0	2
M. hirsuta	0	0	1	0	0	1	0	0	1	0	0	1						
T. cirrhosus	4	0	4	0	0	1	0	1	0	0	0	1				1	0	0
T. sylvicola	1	1	0	1	0	0	2	0	0				0	0	2			
T. bidens	1	0	0															
P. hastatus				0	0	1	0	0	1									
C. maximiliani				1	1	0												
S. bilineata	1	0	1	2	0	0												
P. kappleri				0	0	1												
R. tumida				1	0	1												
M. nigricans	0	0	1	0	0	1												
P. suapurensis							0	1	0									
G. soricina																1	0	0

*Within each bimonthly period the numbers represent the number of pregnant, lactating, and nonreproductive females captured. Data for species in the accompanying figures are not duplicated here. Data are from this study and from bats captured in Panama by Fleming *et al.* 1972.

pregnant females in June, July, and August and a lactating female in January is consistent with either pattern.

GLEANING CARNIVORE GUILD

The fragmentary data available for this guild suggest a bimodal pattern of seasonal polyestry for the genera *Micronycteris, Trachops,* and *Tonatia.* The first birth pulse in these genera coincides with the beginning of the wet season (Table 17, Wilson 1979). A pregnant and lactating female *Tonatia sylvicola* captured in March provides the first evidence that this species has two litters per year and a postpartum estrus.

Mimon crenulatum has a monestrous reproductive cycle (Table 17). Pregnancy peaks in the dry-to-wet season transition with lactation peaking in the early wet season. *Mimon* are reproductively inactive from September through December.
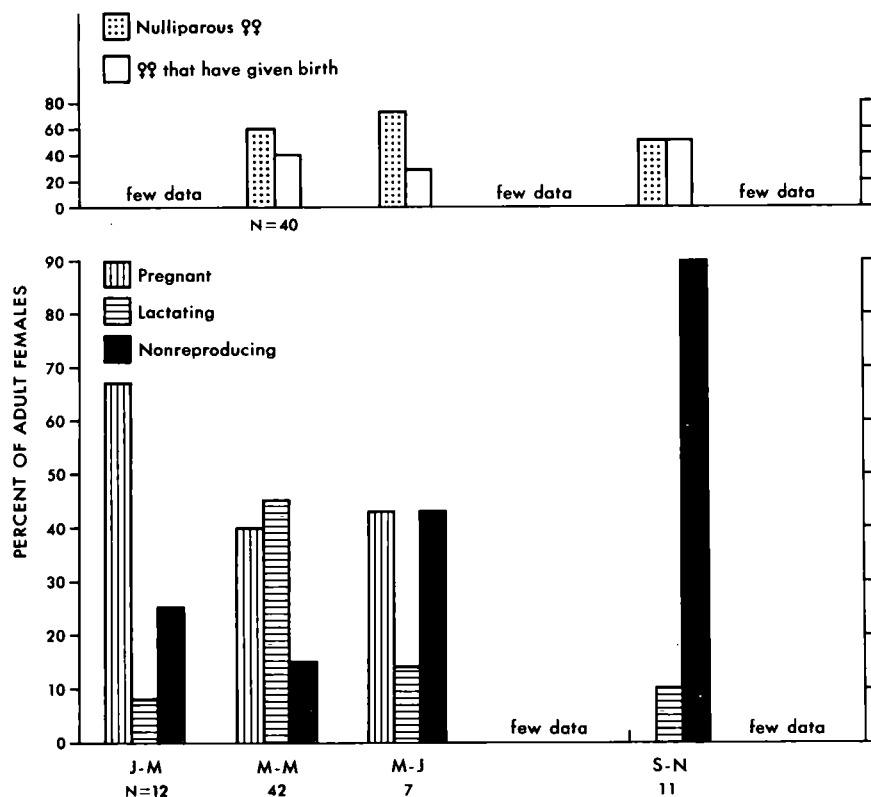

Carollia perspicillata

FIGURE 14.—Reproductive timing in female *Carollia perspicillata.*

SLOW-FLYING HAWKING INSECTIVORE GUILD

Female *Pteronotus parnellii* are monestrous (Fig. 15). Pregnancies occur from late December through mid-April. Lactation proceeds from mid-March through late October; however, most young bats are weaned by mid-July. The percentage of females sucking young in the May-July sampling indicates that at least 53 percent of the adult females succeed in raising young to the latter stages of nursing. This figure is actually larger, because some females already had weaned young by the end of this sampling period. Unfortunately juvenile *P. parnellii* were not distinguished from adults in the field.

During the March-May sampling 16% of the captured females were nulliparous adults, and these were probably all one-year-olds.
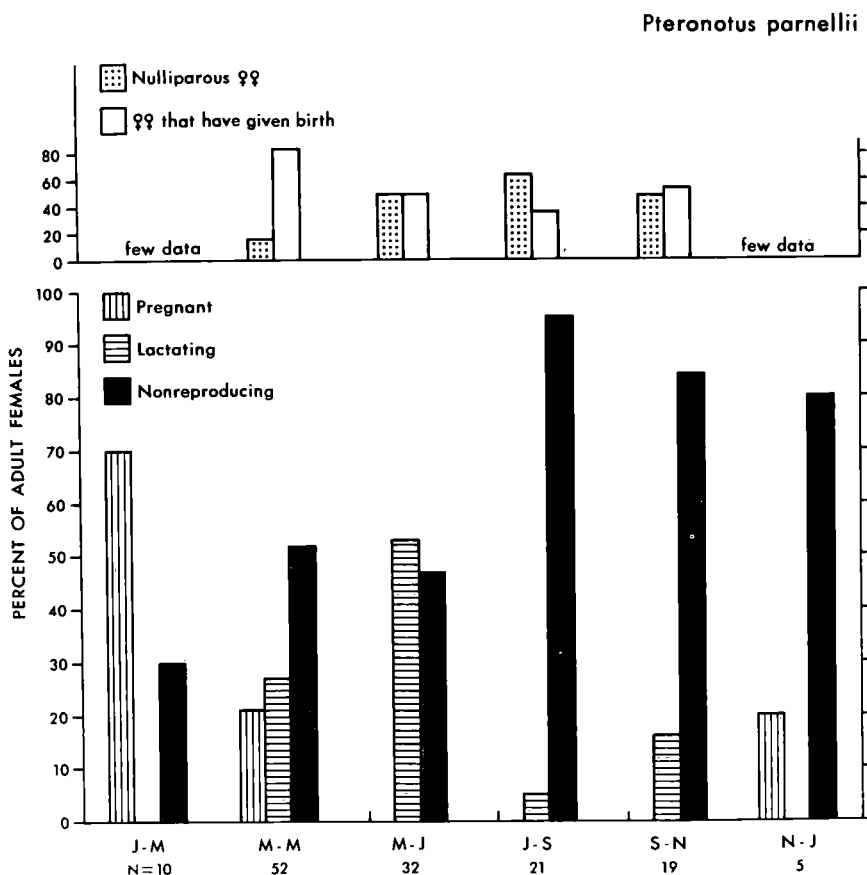

FIGURE 15.—Reproductive timing in female *Pteronotus parnellii*.

However, in the next sampling period 50% of the females captured were nulliparous, indicating that young of the year were entering the flying population (top graph in Fig. 15). In the July-September sample, 65% of the females were nulliparous. The proportion of nulliparous females then declined to 47% by the next sampling period. Associated with the fact that only 16% of the females were nulliparous in March, this pattern suggests a high mortality for females in the latter half of their first year. Such a pattern has been found in temperate *Myotis* (Humphrey and Cope 1976).

DISCUSSION

DIVERSITY AND PHENOLOGY

Maximal diversity in the bat community of BCI occurs from March through July (Bonaccorso and Humphrey, in prep.), the principal growing season. During this time rains are frequent yet light and many plants and insects, having passed through reproductive inactivity in the dry season, undergo rapid growth and reproduction. Deciduous trees produce new leaves, and mature fruits increase both in diversity and biomass. Most of the large orders of insects, including the Coleoptera, Lepidoptera, and Hymenoptera, explosively increase in numbers and biomass. In general most of the food resources eaten by bats, with the exception of nectar and pollen, are abundant during the March-July period, and many species of bats that move out of the forest habitat in the late wet season return by March.

Minimal diversity within the bat community occurs in the late wet season. Fruit is scarce both in kinds of mature fruits and biomass, and fruit bat species diversity is lowest during this period. The species diversity of insectivorous bats also reaches a minimum during the late wet season. Though the actual numbers and biomass of insects are slightly lower in the dry season, the availability of insects as food for bats is probably lowest in the late wet season, when frequent rains curtail insect and bat activity.

Communities formed by tropical bats are by far the most complex assemblages of sympatric mammalian species occurring anywhere in the world. Much simpler communities of bats are found in temperate latitudes. For example, Panama supports 104 known species of bats (Handley 1966), whereas similarly sized South Carolina contains only 14 species, and all of the United States and Canada contain only 39 species (Hall and Kelson 1959). Furthermore, 30 to 50 species of bats are commonly found coexisting within an area of a few square miles in Neotropical forests. Why are there so many more species of bats in tropical regions than are found in temperate regions of similar size?

What mechanisms permit so many similar species to occupy tropical forest communities?

Orians (1969) concluded that tropical forests support more bird species than temperate forests because of two attributes unique to the tropics. First, many kinds of food items that are ephemeral in temperate latitudes are available year-round in tropical latitudes (e.g. fruits and insects). Second, vegetation structure in tropical forests is much more heterogenous than in temperate forests, thus providing more microhabits for foraging specialization (e.g. more vertical layers, bromeliads and lianas).

The great variety of year-round food items and habitat heterogeneity explain to some degree the abundant numbers and kinds of bat species in the tropics. All Nearctic bats north of 32° N latitude are fully insectivorous. In Panama 42 species are probably fully insectivorous, but the other 63 species feed on fruit, pollen and nectar, fish, vertebrates, blood, or some combination of the above. At least 10 insectivore species in Panama feed to some extent by gleaning foliage, whereas only one bat species in South Carolina does so. A number of emballonurids appear to feed much of the time on aerial insects that are flying around foliage, flowers, or fruits. Several species feed chiefly on insects found over water or on its surface (Hooper and Brown 1968, Gardner 1977).

A third factor related to the high species diversity of the tropics is the great range in food particle sizes. Flowers, fruits, and insects available to bats all range widely in size. I earlier demonstrated that large canopy frugivores select fruits in proportion to their body size. It is worth considering whether such a mechanism is a common means of partitioning food resources both at intra- and interspecific levels of the bat community.

Hutchinson (1959), McNab (1971a and b), and May (1973) all theorized that similar species may avoid competition for food by differing in body weights by a factor of at least 1.3 (McNab and Hutchinson use the figure 2.0). Each species thus specializes in food particles proportional to its body weight, an easily measurable indicator of the linear dimensions of food handling apparatus such as tooth row, gape, tongue length, etc.

Food size plays an important role in the partitioning of food resources among similar species in many types of animals (e.g. Diamond 1973, Brown and Liberman 1973) and may be particularly important for fruit bats because of the behavior of carrying fruits in flight to feeding roosts. In accordance with Schoener's (1969) theory of optimal foraging, each bat should attempt to maximize the amount of food it harvests per unit of time and thus select the largest food par-

ticles it can efficiently find and handle. The weight that a bat can carry in flight without seriously impeding maneuverability probably sets the upper limit on food particle size for these animals. In fact, *A. jamaicensis* selects *F. insipida* fruits that are 1.7 times larger than the average weight of available fruits (Morrison 1978, this study). The largest figs are left because they are too heavy for effective flight.

The distribution of mean body weights for each bat species on BCI by guild is plotted in Figure 16. The species within the groundstory frugivore, canopy frugivore, and piscivore guilds increase in body weights by a geometric progression of 1.3 to 1.8, with one exception in the canopy frugivore guild. The relationship between body size and food size may also be important as a means of resource partitioning within other guilds: the two species of *Pteronotus* differ in mean weight by a factor of 1.4, the three species of *Mycronycteris* differ by a factor of 1.5, the males of the sexually dimorphic emballonurids differ by a factor of 1.2 to 1.5. Unfortunately adequate data on food particle selection exists only for the three largest canopy frugivores in this study and for the emballonurid insect-eaters studied by Bradbury and Vehrencamp (1976), all of which roughly select food particles in direct proportion to body weight. However, the circumstantial evidence of strictly adherable increments in body weight within a guild suggest that food particle size is an important mechanism of food partitioning and a selective factor controlling body size within the above mentioned guilds.

Foraging and Reproductive Strategies

Canopy Frugivores

Many fruits preferred by bats have attributes of color, odor, taste, etc. that reduce their availability to, or preference by, most other kinds of fruit-eating animals (Humphrey and Bonaccorso 1978). Hence, many of the competitive interactions any bat species encounters over fruit resources, either in ecological or recent evolutionary time, are with other species of bats of its own feeding guild or other individuals of its own species. However, competition between fruit bats and other frugivorous animals does occur. Morrison (1978) calculated that black howler monkeys (*Aloutata palliata*) and the Jamaican fruit bat (*Artibeus jamaicensis*) roughly consume 9% and 7% of the annual BCI fig crop respectively. The howlers prefer unripened figs (Hladik and Hladik 1969), while *Artibeus* and other bats will eat only mature fruits. Thus, howlers reduce the total fig crop that can become available to fruit bats. Fruits preferred by canopy frugivore bats seem to be unimportant food items for birds.
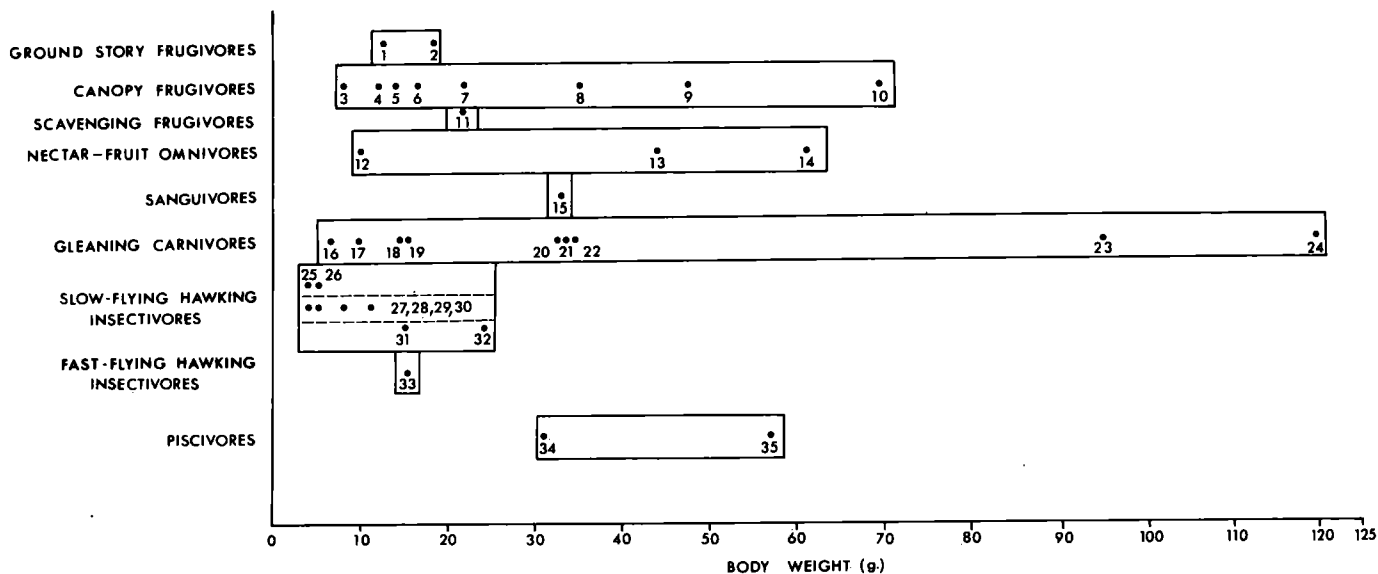
FIGURE 16.—Mean body weights of bat species by feeding guilds. (Dashed lines separate members of different families that belong to the same feeding guilds.) (1) *Carollia castanea*, (2) *C. perspicillata*, (3) *Vampyressa pusilla*, (4) *Chiroderma trinitatum*, (5) *Artibeus phaeotis*, (6) *Vampyrops helleri*, (7) *Chiroderma villosum*, (8) *Vampyrodes caraccioloi*, (9) *Artibeus jamaicensis*, (10) *A. lituratus*, (11) *Centurio senex*, (12) *Glossophaga soricina*, (13) *Phyllostomus discolor*, (14) *Phylloderma stenops*, (15) *Desmodus rotundus*, (16) *Micronycteris megalotis*, (17) *M. brachyotis*, (18) *Mimon crenulatum*, (19) *Micronycteris hirsuta*, (20) *Trachops cirrhosus*, (21) *Tonatia sylvicola*, (22) *T. bidens*, (23) *Phyllostomus hastatus*, (24) *Vampyrum spectrum*, (25) *Rhogeessa tumida*, (26) *Myotis nigricans*, (27) *Saccopteryx leptura*, (28) *Centronycteris maximiliani*, (29) *Saccopteryx bilineata*, (30) *Peroptery kappleri*, (31) *Pteronotus suapurensis*, (32) *P. parnellii*, (33) *Molossus molossus*, (34) *Noctilio labialis*, (35) *N. leporinus*.

Temporal partitioning of the access to a resource may arise when the resource is concentrated in a small space. Fruiting trees visited by canopy frugivores tend to be few or moderate in numbers of individuals, but very large per individual. Each individual tree produces thousands of fruits. Temporal differences in flight (and feeding) times between similar-sized species that feed in the same trees is a means to avoid behavioral interference between species when the food supply is abundant in amount but limited in spatial distribution.

The foraging strategies of fruit bats should optimize the intake of energy with respect to the density, abundance, spatial distribution, and particle sizes of available bat fruits. Moist forest sites throughout Central America usually contain 8 to 10 species of canopy frugivores (pers. obs.). Eight species of stenodermine bats form the canopy frugivore guild on BCI. These bats feed almost entirely on fruits growing in the forest canopy on trees, vines, and epiphytes. Individuals of most of these plants occur at very low densities and in patchy distributions within the forest. Most canopy trees producing bat fruits are large enough to feed hundreds of bats per night during their fruiting periods of about a week. Because a great range in size of preferred canopy fruits is available, it is possible for many bat species to specialize in taking food particles of different sizes. Seven species on BCI are fig specialists that partition figs primarily on the basis of size. The other species is a generalist with regard to the type of fruit in its diet.

The fig specialists appear to have large home ranges (about 3 km² for *A. jamaicensis*) compared to other bats of similar size, and travel through much of the home range in a night to obtain widely scattered food resources (Heithaus *et al.* 1974, Morrison 1978, Bonaccorso, unpubl. data). *Artibeus phaeotis*, the fruit generalist, appears to have a comparatively small home range for its size, probably because it feeds on more kinds of fruits and thus is more likely to encounter a suitable food resource in a smaller area than a specialist.

Frugivorous bats consume their own weight in fruit per night (Morrison 1978), because they appear to have low assimilation efficiencies and high metabolic rates (McNab 1969). Each bat must make about eight to a dozen visits to one or a few resource trees per night (Morrison 1978, in press). Each visit involves picking a single fruit and carrying it away to a feeding roost where the fruit is ingested. Once a tree with mature fruits is located an individual bat may return to it repeatedly for over a week, but some time and energy are spent scouting for trees that will be in fruit in future days (Morrison 1978).

For at least two weeks during the beginning of the dry season, when fruits are scarce and bat pollinated flowers are abundant, at least

three canopy frugivores switch partly to pollen and nectar diets. In drier forest habitats where suitable flowers are available over a longer dry season, stenodermine bats feed on nectar and pollen through much of the dry season (Heithaus *et al.* 1974).

Adult females of all species in this guild have two litters per year. Birth pulses are synchronized within populations and coincide with the two predictable seasonal peaks in fruit abundance. Late term pregnancy, lactation, and learning processes associated with foraging by young bats, the events of highest energetic cost in the life cycle of mammals (Miguela 1969; Studier et al. 1973), occur at times of food abundance.

GROUNDSTORY FRUGIVORES

Groundstory frugivores specialize in eating fruits that grow on shrubs, most of which are less than 3 m high. These bats also feed on some canopy fruits, and in the dry forest areas of Belize (Bonaccorso, unpubl. data) and Costa Rica (Heithaus *et al.* 1974) guild members also feed on nectar and pollen in the long dry season.

Two species in the subfamily Carollinae, *Carollia castanea* and *C. perspicillata,* form the groundstory frugivore guild on BCI. In closed canopy forest habitat throughout the Neotropical region, this guild contains fewer species than the canopy frugivore guild. In South America the other genus in the subfamily Carollinae, *Rhinophylla,* appears to fit the groundstory guild (Handley 1967). Some species of the genus *Sturnira* (Stenoderminae) also may belong in this guild.

Far fewer shrub species than tree species produce bat-dispersed fruits in tropical forests of Central America (12 versus 27 known species on BCI; also see Heithaus *et al.* 1974). Also, shrubs produce a much smaller range of fruit sizes than trees. On BCI shrub fruits preferred by bats range from about 0.2 to 2.0 g, a 10-fold range; whereas tree fruits range from about 2.0 to 30 g, a 15-fold range. Finally most shrub fruits are soft berries or catkins, but tree fruits additionally may be drupes, monkeypods, and other forms. Because of the greater variation in kinds, sizes, and shapes of canopy fruits there are many more ways to specialize on canopy fruits than on groundstory fruits, hence the larger numbers of species in the canopy frugivore guild.

Groundstory frugivores have small home ranges in comparison to large bats that specialize on canopy fruits. This probably occurs because shrub food species are abundant as individuals and more uniform in distribution than tree species. Groundstory frugivores usually must visit a large number of shrubs each night to find sufficient food. Each shrub has only a few small mature fruits available per

night (especially true of pipers) and a given shrub may be stripped of fruits by other bats before an individual visits it or between return trips from the feeding roost. When suitable canopy species are fruiting they are included in the diet. Fruits are picked from the resource plant and carried to feeding roosts for eating. Most fruits eaten by these bats are mature only from one to three consecutive months; thus groundstory frugivores must frequently change food species and search images. Some insects are eaten, but it is not clear whether these are taken with fruits or independently hunted.

The reproductive strategy of the groundstory frugivores on BCI is similar to that of canopy frugivores.

NECTAR-POLLEN-FRUIT-INSECT OMNIVORES

Moist and wet tropical forests have few large flowers suitable for bat pollination and feeding, and these are primarily available in the dry season (late December through March on BCI). Extreme nectar-pollen specialists among the Microchiroptera are common only in dry tropical forests and deserts (Humphrey and Bonaccorso 1978). Only species like *Phyllostomus discolor* and *Glossophaga soricina* that switch to other types of food in the wet season make prolonged use of dry season flowers in moist forest, though some frugivores occasionally visit flowers.

The mechanisms of resource partitioning among nectarivorous bats are poorly understood. My data and those of Heithaus *et al.* (1974) and Alvarez and Gonzales (1970) indicate almost complete overlap among bat species in the use of flowers. Flowers do have activity cycles with respect to nectar production, and it is suggested by Heithaus *et al.* that temporal differences in bat activity serve to partition nectar and pollen among bats. On BCI the foraging activity of *P. discolor* is compacted into the twilight and first hours of darkness, probably as a response to inter- and intraspecific competition over nectar. The first bats that arrive at a flower each night receive a maximal supply of nectar and successive visitors receive lesser amounts (Heithaus *et al.* 1974).

Both *Glossophaga* and *Phyllostomus* feed primarily on nectar and pollen as long as flowers are available. As the wet season begins, *Phyllostomus* switches to fruit and insects, and *Cecropia* fruits become particularly important. In the dry forests of Costa Rica where *Cecropia* is not a common tree, *Phyllostomus* disappears after the dry season flowering and does not reappear until the next flowering season (Heithaus *et al.* 1974). I expect that they migrate to and from habitats that have *Cecropia* fruits available in the wet season and large flowers in the dry season.

Glossophaga too switches to fruit in the wet season, and other authors have found it also eating insects then (Fleming *et al.* 1972; Howell and Burch 1974). *G. soricina* is a rare bat on BCI and becomes even more rare in the wet season, indicating that it may undergo seasonal habitat shifts.

The reproductive strategy of *P. discolor* appears to be similar to that of the frugivorous bats. Two birth pulses occur each year, the first of which is toward the end of the peak in flowering and at the beginning of the peak in fruiting. Females eat fruit and insects during both yearly periods of lactation. This diet may be richer in protein than a pollen and nectar diet.

GLEANING CARNIVORES

Nearly all gleaning carnivores depend on large insects as a primary food resource, though a wide range of vertebrates, invertebrates, and even fruits may supplement the diet. This large feeding guild has a more complex array of partitioning mechanisms than any other guild on BCI. Differences in body size, food types, foraging microhabitats, and possibly activity cycles operate to maintain the ecological distinctness among these species. Future investigators should consider potential competition between bats and other taxa that prey on large insects, such as nocturnal spiders, caprimulgid birds, and tree frogs.

Gleaning carnivores prey upon food items moderately large in relation to their own body weight just as fruit bats do. Also like fruit bats they carry prey items to feeding roosts whether the food be large insects (Wilson 1971b) or birds (Vehrencamp *et al.* 1977). Because of the high protein content of their diet these bats possibly eat a smaller weight of food in proportion to their body size and also fewer prey items per night than do frugivores. Thus, gleaning carnivores should spend less time and energy transporting food items between foraging sites and roost sites (and in total foraging time) than do frugivorous bats. Time budgets based on radiotracking by Vehrencamp *et al.* (1977) confirm this hypothesis in the case of *Vampyrum spectrum.* It would be interesting to compare guilds in more detail in terms of searching effort devoted to foraging.

Late in the wet season and in the dry season large insects are relatively scarce, and some gleaning species change foraging patterns. Several of the small- and medium-sized species become rare on the island late in the wet season, but return and eat mixed diets of fruit and insects through the dry season (Bonaccorso and Humphrey, in prep.). *Micronycteris megalotis* and *M. brachyotis* appear to use this strategy. *Tonatia sylvicola,* however, remains all year eating insects

and whipscorpions. Janzen (1973) and Janzen and Schoener (1969) reported that watersheds are dry season refugia for many insect groups in tropical forests. Perhaps some individuals or populations of gleaning carnivores move to riparian habitats off the island during lean times.

Micronycteris, Tonatia, and *Trachops* bear two litters per year. The first pregnancy of the year for these species occurs during relative food scarcity, but the birth pulse occurs as large insects are becoming abundant. The first lactation and the entire second reproductive cycle occur within months of food abundance.

The peak in pregnancy for *Mimon crenulatum,* a monestrous species, occurs about two months after those of the above gleaning carnivores. Thus both pregnancy and lactation occur within the year's peak of insect abundance. *Mimon* can time its reproductive activity in this manner because it does not squeeze two reproductive cycles within the months of large insect abundance as do the polyestrous species of the guild.

SLOW-FLYING HAWKING INSECTIVORES

Much less is understood about resource partitioning, foraging strategy, and reproductive strategy within this guild than in the guilds discussed above. It is possible that each family placed in this guild should constitute a distinct guild, but not enough is known to be certain. A common denominator among all these species is that they capture small aerial insects and eat them while flying. Some guild members have individual or group feeding territories. Territorial defense of foraging areas may serve as the primary means of decreasing intraspacific interference over food. Body size, microhabitat, and activity cycle differences are likely possibilities as primary mechanisms that reduce interspecific competition for food within the hawking insectivores.

Small insects are abundant all year long, although specific insects fluctuate in abundance (Smythe 1974). These bats do not undergo shifts in diet type as many other species are forced to do. Foraging activity occurs in bimodal periods on nocturnal or crepuscular regimes. Hundreds of very small food items must be eaten each night requiring very high capture and feeding rates (Gould 1955) compared to other bat guilds.

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