Ecological observations on an East African bat community

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L'étude de la faune de chauves-souris du centre-sud du Kenya a été entreprise de mai 1973 à juillet 1974 : vingt-cinq espèces de chauves-souris appartenant à 7 familles ont été collectées; 24 d'entre elles étaient insectivores. Cette faune est pauvre quand on la compare aux régions néotropicales en raison de l'absence de non-insectivores. Le nombre d'espèces et de familles de chauves-souris insectivores, cependant, est presque identique à celui de Costa-Rica où un climat semblable est réparti de manière comparable.

La région subit une saison sèche prolongée de mai à la fin d'octobre, deux saisons des pluies en novembre et en mars-avril, et une saison sèche sourte et moins sévère de décembre à février. La moitié seulement des espèces ont été trouvées au cours de la longue saison sèche et beaucoup d'entre elles paraissent avoir de faibles densités. On pense que des migrations saisonnières vers des régions où il y a des pluies supplémentaires peuvent expliquer ces différences. Toutes les espèces sauf une se reproduisent avec les pluies les plus constantes de novembre, quelques-unes mettent bas au cours de la saison des pluies de mars-avril, mais aucune ne se reproduit pendant la longue saison sèche. La plupart des résidents annuels se reproduisent seulement en novembre et la plupart de ces espèces qui mettent bas en mars-avril sont probablement migratrices. Celles qu'on croit migratrices ont tendance à donner des portées plus petites.

INTRODUCTION

The structure and ecology of bat faunas is a subject of interest to mammalogists (Findley, 1976 ; Wilson, 1973). Syntopic African bat communities, however, have received little study in comparison with neotropical faunas (cf. Fleming *et al.*, 1972 ; LaVal and Fitch, 1977 ; McNab, 1971). Verschuren (1957) presented natural history information and species accounts for a localized central African bat fauna. Foraging related characteristics of a Rhodesian community have also been analyzed (Fenton, 1975 ; Fenton *et al.*, 1977), but not on a seasonal basis. Other reports on African bat faunas are restricted to regional summaries (cf. Koopman, 1975 or Rosevear, 1965) and do not consider ecological aspects of a single localized community. The purpose of our study was to follow species composition, reproduction, and foraging related characteristics of an East African bat fauna over a full annual cycle.

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METHODS AND MATERIALS

STUDY AREA

Collections and observations were made from late-May 1973 to late-July 1974 at Masalani (2°18'S and 38°7'E), 20.1 kilometers (km) northeast of Kibwezi, Machakos District, Kenya, elevation 704 meters (m). The Masalani site is occupied by Bushwhacker's Safari Camp, a small guest camp where we resided throughout the study. The surrounding vegetation is dense thornscrub with a few scattered patches of grassland. The bushland consists of thickets of shrubs, mainly *Combretum exalatum*, *Grewia villosa* and *Premna resinosa*, reaching heights of two to three m. Stands of *Commiphora* trees, mainly *C. africana* and *C. baluensis*, dominate the area and reach heights from three to six m above the shrub strata. Additional common trees and shrubs include *Acacia mellifera*, *A. senegal*, *A. tortillis*, *Adansonia digitata*, *Cassia abbreviata*, *Commiphora riparia*, *Terminalia prunoides*, *Barlaria taitensis*, *Boscia coriacea* and *Maerua kirkii*. The Athi River intersects the area and a very narrow strip of riparian vegetation here differs from the surrounding bushland. Trees reach heights of 15 m, and many are evergreen. Typical riverine trees include *Acacia elatior*, *Newtonia hildebrandti* and *Tamarindus indica*. During our study the entire area was wild and uninhabited, but since 1974 much of the bush has been cleared for subsistence farming.

The outstanding climatic feature of the area is seasonality of rainfall. Analysis of records collected at Masalani from 1969-1973 shows a cœfficient of variation of 150.3 percent in monthly rainfall ($\bar{x} = 39.4 \pm 59.2$ millimeters (mm)). Annual precipitation over this period averaged 473 mm, with 80.9 percent of the rain falling in two biannual peaks. A November-December rainy season accounted for 46.2 percent while March-April rains contributed 34.7 percent of the total. The November rains are also far more predictable in occurence than the April rains, as shown by long term records kept at DWA plantations, 14.3 km south of Masalani. These rains produced less than half of the average for this season ($\bar{x} = 308.6$ mm) in only five of the 54 years from 1919 to 1972 ; the April rains, in contrast, produced less than half of their mean ($\bar{x} = 209.5$ mm) in 14 of these years. The coefficient of variation in November-December rainfall at DWA is 45.1 percent, while in March-April this value rises to 61.1 percent. The two dry seasons between these biannual rainfall peaks also differ. Some rain occurs during the short dry season from late-December to March : the five year average for January at Masalani was 31.6 ± 18 mm ; February averaged 18.5 ± 18 mm. Rain is much rarer during the long dry season from May through October. The average total rainfall for May, June, July, August, and September at Masalani in 1969-1973 was 20.6 ± 5.9 mm, or 4.1 ± 6.1 mm per month.

This extreme seasonality of rainfall exerts dramatic effects on the flora and fauna. During rainy seasons productivity is at a peak, plant biomass is high, and insect abundance seems to be at its highest. The area is lush and green. In the short dry season some plants shed their leaves, but many retain foliage. A second flush of productivity and reproduction occurs during the March-April rains. Following this season, however, the landscape quickly becomes bleak, and with fex exceptions the vegetation becomes leafless.

METHODS

Harp traps (Tuttle, 1974) and mist nets were used to capture flying bats at night. We employed two traps for a total of 276 bat trap nights. Traps were set along walls, across trails, and occasionally over water or suspended beneath the *Commiphora* canopy. Nets were stretched across clearings, above the *Combretum* bush, or beneath the *Commiphora* canopy. These were usually tended until about 2200 hours (h) and then furled. Based on six m length nets, we used this method on 349 partial net-nights. From late January to early March 1974 we captured bats in nets across the Athi. A severe drought on the inland watershed reduced the flow of the river and made it possible to capture large numbers of molossids, bats which normally fly above the canopy, as they came to drink. At other times of the year the river was too wide to allow capture of molossids. Our data on this group of bats, therefore, are not comparable with data for other species taken in the bush throughout the year. We omit these when making comparisons within the fauna.

Captured bats were recorded by species, sex and age (juvenal or adult) ; weights and forearm lengths were taken when possible. Pregnancy was noted by palpation. Prominent teats indicative of lactation were also recorded. Litter size was determined by examining a small number of sacrificed females for embryos or uterine scars. Timing of parturition was estimated based on the presence of pregnant and lactating females or volant young. No attempts were made to collect large series of bats and the more common species were usually released. A total of 395 specimens was preserved, 225 as standard study skins, 123 in spirits, and 17 as skeletons. These are housed in the Northern Arizona University Vertebrate Museum. We identified bats in the field using Hayman and Hill (1971). Further confirmation or identification of specimens was made by staff of the Royal Ontario Museum, Toronto, Canada. For bats of the genus *Miniopterus* we follow a nomenclature proposed by R. L. Peterson (in prep.).

Data on wing morphologies were gathered on sacrificed or chloroform-anesthetized bats through wing tracings (Vaughan, 1959). Areas of tracings were determined with a compensating polar planimeter and aspect ratios were calculated as the ratio of wingspan squared to wing area. Ultrasonic frequency ranges were determined by releasing bats in an enclosed room and following them with a Holgate ultrasonic sensor. Some constant frequency (CF) emitting bats (see Simmons *et al.*, 1975) were hand-held during frequency determinations.

We measured the outside width across the last upper molars as an indicator of prey size selection and computed ratios of larger to smaller for each species pair. The measurement was taken to the nearest 0.1 mm on up to ten randomly selected skulls for each species, with nearly equal representaion of each sex when possible. If less than ten skulls were prepared we then measured all available skulls. Hutchinson (1959) and subsequent authors report that the ratio of larger to smaller « trophic structures » of coexisting species of closely related animals usually does not fall below 1.3. It is widely held that this ratio indicates coexistence due to food resource partitioning on the basis of prey size (but see Horn and May, 1977). We follow this reasoning in our study of horizontal gape ratios.

Foraging height data are based only on overall impressions of the more common species. We identified flying bats with the ultrasonic sensor or by watching them as they emerged, as they fed and were captured, or as they fed when released, until we could recognize them by stule of flight and silhouette. At the end of the study we compared our impressions of the heights at which the various species foraged and found good agreement in our range estimates. We used the midpoint of these estimates as the « typical » foraging height of each species and *a priori* assumed an arbitrary distance of at least 3 m between midpoints as indicating coexistence on the basis of vertical stratification. Our impressions are biased by time of the night, as most of our observations of feeding bats were made in early evening. They are also subject to criticism because of their subjectivity and lack of quantification ; we regret this but feel that they are still of value in the absence of more rigorously obtained information.

RESULTS AND DISCUSSION

Faunal composition and seasonal abundance

A total of 25 species representing seven families of bats was collected (Table 1). Vespertilionids dominated the fauna : ten species belonged to this group. Six of the remaining species were molossids and five were rhinolophids. Four families were represented by only one species each : Pteropodidae, Emballonuridae, Nycteridae and Megadermatidae.

This number of species is low compared to some Neotropical areas, which may possess up to 58 species in eight families (LaVal and Fitch, 1977). The lower species richness at the Kenya site is due primarily to a reduction in the number of trophic roles. Unlike Neotropical bat faunas, no carnivores, piscivores, sanguivores or nectarivores were found, and only one species was frugivorous. The Masalani fauna is remarkably similar to other tropical communities, however, in terms of numbers of species of insectivorous bats. Three sites in Costa Rica sampled similarly possessed 10 to 30 insect eaters in five to seven families (LaVal and Fitch, 1977). The one Costa Rican site with a rainfall pattern similar to that at Masalani held 22 species of insect feeders in six families (LaVal and Fitch, 1977), a species richness and familial diversity remarkably similar to the 24 species and six families of insectivorous bats comprising the Masalani fauna.

Strong seasonal differences in faunal composition were recorded (Table 1). This variation followed annual rainfall patterns. The highest number of species (25) was taken from November to May. Just ten species of insectivores and one frugivore were detected throughout the year, and it was our general impression that many of these species existed at lower densities during the long dry season (Table 1). An increase in the number of species occurred from November to May when fourteen additional species, all insectivores, were taken. Even disregarding opportunistically captured molossid bats, this represents a nearly two-fold increase in species richness from the long dry season to the November-May period : 18 non-molossid insectivorous species were detected during the latter period but only 10 from June-October.

The lower species richness and density during the long dry season is probably due to emigration. Such movements would allow bats to escape lengthy periods of food scarcity brought on by seasonal extremes of rainfall and community productivity. Other areas in Kenya show complementary rainfall patterns ; these could serve as sources of immigrants from November to May and as refugia in the long dry season. For example, at Masalani the five months from November to March receive 11 times more rainfall than the five months from May to September. Along the coast and in the highlands of western Kenya, however, the situation is nearly completely reversed. Here the five months from November to March receive two to seven times *less* precipitation than the five months from May to September (East African Meteorological Department, 1966). We suspect that through migration many species of bats follow these shifting geographic patterns of rainfall and subsequent community productivity during their annual cycles.

TABLE 1. — Composition, seasonal abundance and reproductive characteristics of the Masalani bat fauna. The number of females examined follows litter size in parentheses.

FAMILY AND SPECIES	NUMBER PRESERVED	SEASONAL PRESENCE	PARTURIENT SEASON	LITTER SIZE
Pteropodidae				
Epomophorus wahlbergi	19	Annual resident; low densities July to September	Nov. through April	1 (5)
Emballonuridae				
Taphozous mauritianus	10	Annual resident; low densities May to Oct.	Nov., March-April	1 (5)
Nycteridae				
Nycteris thebaica	23	Annual resident	November	1 (6)
Megadermatidae				
Cardioderma cor	9	Annual resident; low densities May to October	Nov., through March-April	1 (25)*
Rhinolophidae				
Rhinolophus landeri	7	October to March	November	1 (4)
R. hildebrandti	1	May	--	--
Hipposideros caffer	16	Annual resident	November	1 (1)
H. commersoni	6	Nov.-Dec.; Mar-Apr.	Mar-Apr.	1 (2)
Triaenops persicus	4	November-December	November	1 (4)
Vespertilionidae				
Myotis tricolor	1	November only	--	--
Nycticeius schlieffeni	17	Annual resident	November	2 (1); 3 (1)
Scotoecus hindei	31	Annual resident; low densities May-October	November	--
Pipistrellus nanus	41	Annual resident	November	2 (16)
Eptesicus somalicus	33	Annual resident	November	2 (15)
Scotophilus nigrita	19	Annual resident; low densities May to October	Nov., March-April	2 (1); 3 (1)
Miniopterus natalensis	28	Annual resident; low densities May to October	November	1 (1)
M. africanus	2	February only	--	--
M. fraterculus	8	November-April	November	1 (2)
M. schreibersi	1	January only	--	--
Molossidae				
Platymops setiger	10	--	Nov.-Dec.	1 (1)
Tadarida bemmelini	18	--	--	1 (1)
T. condylura	45	--	Nov., Mar-Apr.	1 (10)
T. bivittata	1	--	--	--
T. pumila	36	--	Nov., Mar-Apr.	1 (4)
T. aegyptiaca	9	--	--	1 (4)

* Based on captures of mother-young pairs (see Vaughan, 1976).

As a corollary to this probable migration, we noted buildups of subcutaneous fat in several of the suspected migratory species. These fat stores may provide energy for long distance movement. Among non-molossid bats large amounts of fat were found on individuals of four species either absent or noted in low numbers from May to October : *Hipposidderos commersoni, Miniopterus natalensis, Scotophilus nigrita* and *Scotoecus hindei*. Individuals of four species of molossids collected prior to the long dry season also possessed large reserves of subcutaneous fat (*Tadarida condylura*, *T. bemmelini*, *T. pumila* and *P. setiger*), indicating that some bats of this family probably also emigrate at the onset of this period.

REPRODUCTION

Parturition was strongly seasonal. Except for *H. commersoni*, every adult female of every species taken from late-October to December showed evidence of gestation or lactation. Some species also gave birth in March-April, but none bred during the May-October dry season. One species was polyestrous : volant young and gravid or nursing females of the frugivorous *Epomophorus wahlbergi* were continually evident from November to May. Eleven of the 14 non-molossid insectivorous species with data available (Table 1) were monestrous. Ten reproduced only in the November rains : seven of these were annual residents. Three of the remaining species, all four of which were probably migratory (Table 1), reproduced at both rainy seasons but not during the interim. *H. commersoni* gave birth in March-April but we did not detect parturition in this species in November.

The advantages of parturition in November are clear : females benefit from a predictably high productivity during late gestation and lactation, and the following months are relatively favorable to survival of young. The November rains contribute a greater proportion of the annual rainfall, are far more predictable, and are followed by five months in which some precipitation is received ; the April rains are more apt to fail and are followed by the five driest and least productive months of the year. Furthermore, those few species which do breed with the March-April rains all show evidence of emigration during the long dry season. Survival of young born in March-April may be enhanced by movements to more favorable areas. Non-migratory annual residents, in contrast, have such a lengthy and predictable dry season from May to October that the probability of survival of weaned young at these times is too low to warrant any attempts at reproduction.

Some patterns in litter size with respect to migration are also suggested by these data. Bats present only at rainy seasons and/or the short interval between tend to be monotoccus (four of four species with such data available). Most annual residents occuring at lower densities in the long dry season also have only one young per parturition (three of four species). Three of the six full resident species with available data, however, have two or three young per parturition. Perhaps longevity is enhanced by migration and these species find it more advantageous to funnel energy into stores for movements rather than into additional immediate offspring. Heavy fat deposits were observed, for example, in pregnant or recently lactated *H. commersoni*, a monotoccus species thought to migrate inland 250 km during rainy seasons (Vaughan, 1977). Among molossids, many species of which we suspected to be migratory, *Tadarida pumila* and *T. condylura* also had heavy fat deposits while in either gestation or lactation, but each had one young in two parturitions coinciding with the two rainy seasons.

FORAGING RELATED CHARACTERISTICS

Several studies have indirectly addressed the question of food resource partitioning in bat communities by examining differences in morphological and behavioral traits which logically seem to reflect underlying differences in food habits (see, for example, Fenton, 1975 ; Fenton *et al.*, 1977 ; Fleming *et al.*, 1972 ; Mc Nab, 1971 ; Tamsitt, 1967). We take that approach in this analysis. We consider sizes of bats, approximate foraging heights, wing morphologies, orientation pulses and unique pursuit strategies as indicators of food resource partitioning, although we also caution that a superior approach would involve determining the kinds of prey taken and their patterns of abundance and dispersion (cf. Anthony and Kunz, 1977 ; Black, 1974 ; Buchler, 1976 ; Bradbury and Vehrencamp, 1976).

Rare or unique species

Of 19 non-molossid bats four (*Rhinolophus hildebrandti*, *Myotis tricolor*, *Miniopterus africanus* and *M. schreibersi*) were captured only once or twice and were too rare for us to form conclusions on their roles in the bat community. These four species were detected from November to May and not during the long dry season (Table 1).

Among the remaining species, one was frugivorous (*E. wahlbergi*) and three possessed prey pursuit strategies unlike those of any of the other insectivorous species on the area. One (*Nycteris thebaica*) was primarily a foliage gleaner. Two species, *Cardioderma cor* and *H. commersoni*, hawked insects from perches ; details of their foraging strategies have been presented elsewhere (Vaughan, 1976, 1977). These two species did not forage in the same kinds of places or feed on the same kinds of prey. *H. commersoni* pursued large flying beetles from perches located in tall riverine trees at heights of 4 to 15 m. *C. cor* hawked terrestrial or low-flying prey from brushy perches at heights ranging from 0.3 to 3.5 m (Vaughan, 1976, 1977).

Wing morphology and foraging height

Wing morphology indicates style of flight, which in turn is adapted to characteristics of the habitat in which a bat forages. Masalani bats which hunt insects close to the ground where obstructions are prevalent require highly maneuverable flight. At the other extreme, species which fly above the canopy can sacrifice maneuverability in favor of speed, and thereby encompass a greater searching volume per unit time. Bats foraging at intermediate levels in woodland situations can be expected to show intermediate styles of flight. Two morphological indicators of style of flight are wing loading and aspect ratio. We investigate aspect ratio in our study but not wing loading because we also treat body size. Findley *et al.* (1972) have demonstrated a significant correlation between the latter two variables.

Aspect ratios (Table 2) show significant correlation with our qualitative estimates of foraging height midpoints ($r = 0.72$; $P < 0.01$, $t = 3.28$, 10 d.f.). This relationship is linear ($Y = 2.65 X - 11.94$) when molossids are omitted from the analysis. Molossid bats flew at heights too great to estimate accurately, but as a group had the highest aspect ratios (Table 2). If molossids were included the relationship would probably become exponential at an aspect ratio near 9.00 ; above the canopy no further obstructions are encountered and a variety of heights can be utilized equally effectively with the same wing form.

Species pair contrasts : size, height, and echolocation frequencies

Due to correlations of aspect ratio with foraging height and wing loading with size (Findley *et al.*, 1972), we have limited initial pair contrasts to foraging height and

TABLE 2. — Foraging-related characteristics of the Masalani bat fauna. Abbreviations for pursuit strategies are : A.I., aerial insectivore ; F., frugivore ; F.G., foliage gleaner ; H., hawker. Dashes indicate that no data are available. Sample sizes follow aspect ratios and gape distances in parentheses.

BAT SPECIES	PURSUIT STRATEGY	FORAGING HEIGHT MIDPOINT AND RANGE (M)	ASPECT RATIO	ULTRASONIC FREQUENCIES (kHz)	M^3-M^3 (mm)
Epomophorus wahlbergi	F	--	--		--
Taphozous mauritianus	AI	11.0 (7.0-15.0)	9.35 ± .34 (3)	50-30 (Fenton, 1975)	9.14 ± .14 (7)
Nycteris thebaica	FG	2.7 (.5-5.0)	5.61 ± .27 (11)	95-70 (Fenton, 1975)	6.81 ± .17 (10)
Cardioderma cor	H	1.7 (0-3.5)	5.66 ± .13 (9)	42; harmonics at 63	9.30 (1)
Rhinolophus landeri	AI	1.0 (0-2.0)	--	55 (hand-held; but see Novick, 1958)	6.60 ± .20 (3)
R. hildebrandti	--	--	5.33 (1)	--	--
Hipposideros caffer	AI	1.0 (0-2.0)	6.22 ± .40 (5)	155	6.10 ± .16 (10)
H. commersoni	H	8.5 (2.0-15.0)	6.54 ± .02 (2)	33; harmonics at 66 and 97 (hand-held)	11.05 ± .31 (4)
Triaenops persicus	--	--	--	83	6.4 ± .14 (2)
Myotis tricolor	--	--	--	--	7.6 (1)
Nycticeus schlieffeni	AI	5.0 (2.0-8.0)	6.45 (1)	70-30	5.95 ± .18 (10)
Scotoecus hindei	AI	6.0 (4.0-8.0)	6.71 ± .37 (4)	64-32	7.18 ± .30 (10)
Pipistrellus nanus	AI	3.6 (2.1-5.1)*	6.67 ± .09 (16)	115-65	4.71 ± .11 (10)
Eptesicus somalicus	AI	4.0 (2.0-6.0)	6.44 ± .25 (6)	70-35	5.05 ± .18 (10)
Scotophilus nigrita	AI	7.5 (3.0-12.0)	6.73 ± .35 (5)	72-34	9.22 ± .29 (10)
Miniopterus natalensis	AI	13.0 (6.0-20.0)	7.16 ± .23 (11)	85-45	6.10 ± .08 (10)
M. africanus	AI	--	--	--	6.65 ± .07 (2)
M. fraterculus	AI	7.0 (3.0-11.0)	7.71 ± .06 (2)	90-45	6.10 ± .13 (6)
M. schreibersi	AI	--	--	87-49 (Novick, 1958)	6.20 (1)
Platymnops setiger	AI	--	--	--	7.32 ± .18 (4)
Tadarida pumila	AI	--	8.90 ± .87 (5)	--	7.87 ± .16 (10)
T. aegyptiaca	AI	--	8.93 ± .36 (3)	--	8.62 ± .22 (7)
T. bemmelini	AI	--	8.81 ± .35 (3)	--	7.80 ± .14 (10)
T. bivittata	AI	--	--	--	9.05 (1)
T. condylura	AI	--	9.04 ± .36 (11)	--	9.25 ± .32 (10)

* Does not include extremes given by O'Shea (1977).

TABLE 3. — Horizontal gape ratios and distances between midpoints of foraging heights of the common non-molossid aerial insectivores. Distances between height midpoints (in m) occupy cells below the diagonal of the matrix.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) *T. mauritianus*	--	1.38	1.50	1.54	1.27	1.94	1.81	1.01	1.50	1.50
(2) *R. landeri*	10.0	--	1.08	1.11	1.09	1.40	1.31	1.40	1.08	1.08
(3) *H. caffer*	10.0	0	--	1.03	1.18	1.30	1.21	1.51	1.00	1.00
(4) *N. schlieffeni*	6.0	4.0	4.0	--	1.21	1.26	1.18	1.55	1.03	1.03
(5) *S. hindei*	5.0	5.0	5.0	1.0	--	1.52	1.42	1.28	1.18	1.18
(6) *P. nanus*	7.4	2.6	2.6	1.4	2.4	--	1.07	1.96	1.30	1.30
(7) *E. somalicus*	7.0	3.0	3.0	1.0	2.0	.4	--	1.83	1.21	1.21
(8) *S. nigrita*	3.5	6.5	6.5	2.5	3.5	3.9	3.5	--	1.51	1.51
(9) *M. natalensis*	2.0	12.0	12.0	8.0	9.0	9.4	9.0	5.5	--	1.00
(10) *M. fraterculus*	4.0	6.0	6.0	2.0	3.0	3.4	3.0	.5	6.0	--

size of gape. Eleven species of non-molossid aerial insectivores occured at Masalani that did not possess unique pursuit strategies and were not rare. We had information on both height and gape for ten of these (Table 2). When gape ratios rounded to 1.3 or greater we assumed coexistence at least partially on the basis of prey size (Hutchinson, 1959) ; if foraging height midpoint estimates were an arbitrary three m or more apart we assumed coexistence on the basis of vertical stratification. By these m criteria, 38 of the 45 possible species pair contrasts differ in at least one of these characters, 18 differ in both, and just seven fail to differ in either (Table 3).

Five of the seven pairs that overlap in both size and foraging height show little or no overlap when contrasted on the basis of echolocation frequencies. Two of these species produce CF orientation sounds *(Rhinolophus landeri* and *Hipposideros caffer)* but emit pulses at different, widely spaced frequencies (Table 2). Similar differences were noted among species which emit frequency modulated (FM) sounds. *Pipistrellus nanus* and *Eptesicus somalicus* show almost no overlap in range : *Eptesicus* sweeps from 70 to 30 kHz where as *Pipistrellus* sweeps from 115 to 65 kHz. *Miniopterus fraterculus* shows only partial overlap in frequency range with *Scotoecus hindei* and *Nycticeus schlieffeni* (Table 2), two species with which it otherwise shows both height and size overlap. Finally, *H. caffer* and *E. somalicus* emit sounds of different frequencies and of completely different design (CF vs. FM ; Table 2), design differences being related to divergent strategies of prey detection and tracking (Simmons *et al.*, 1975).

The ecological significance of gross differences in echolocation frequencies may be based on two frequency-related properties of sound. Objects of a size equal to the wavelength of the emitted sound will yield the strongest echoes, and bats producing pulses at higher frequencies should be more efficient at perceiving smaller particles (Novick, 1958). Secondly, atmospheric attenuation of ultra-sound is proportional to the square of the frequency (Griffin, 1971). At a given emitted intensity over a given distance echoes from higher frequency sounds will be less intense than those from lower frequency sounds. Sounds of lower intensity allow bats to forage closer to complex surfaces because they dampen the number and complexity of returning echoes (Novick, 1958). This relationship could be important, for example, in allowing the coexistence of *E. somalicus* and *P. nanus*. These two otherwise similar species differed in that *E. somalicus* (the lower frequency emitter) was consistently observed foraging in more open spaces whereas *P. nanus* was repeatedly seen feeding within one m or less of the surfaces of vegetation. It is probable that due to frequency design the latter species forages more efficiently on smaller insects taken closer to the vegetation.

In summary, most of the 45 bat species pair contrasts analyzed among aerial insectivores differ sufficiently in either gape ratio or foraging height to presume coexistence on these bases. Seven pairs do not, but five of these diverge widely in echolocation characteristics, suggesting food resource partitioning along lines reflected in contrasting perceptual abilities. Two species pairs, *N. schlieffeni* with *S. hindei* and *E. somalicus*, do not show these differences and perhaps partition resources along axes not reflected by this study.

Species pair contrasts : seasonal differences in gape overlap

Species pair contrasts based solely on gape ratios show noteworthy seasonal changes. There are 91 pair contrasts possible among the 14 species of non-molossid aerial insectivores detected from October to May. Fifty-three of these (58.2 percent) have rounded horizontal gape ratios less than 1.3 (Table 2). During the long dry season the number of possible contrasts falls to 28, but only 35.7 percent of these show ratios less than 1.3 ($P < 0.05$; $t = 2.104$, 117 df), indicating that at times of higher community productivity bats may be partitioning food resources on bases other than size alone. Anthony and Kunz (1977) have shown that as seasonal insect density increases the North American bat *Myotis lucifugus* becomes a more selective feeder. During the long dry season at Masalani bats may take prey more frequently on the basis of size. Hence a greater prevalence of overlapping gape ratios is not permissible among species coexisting at this time. During the wet seasons coexisting bat species may rely less on prey size partitioning but become more selective feeders and specialize on the basis of other prey characteristics. This would permit greater overlap in gape ratios of coexisting pairs. Greater insect abundance and a correspondingly finer selectivity on the part of the bats would allow for the higher species richness seen from November to May.

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SUMMARY

The bat fauna of a south-central Kenya study area was monitored from May 1973 to July 1974. Twenty-five species of bats in seven families were collected ; 24 of these were insectivorous. This fauna is depauperate compared to neotropical areas due to a lack of non-insectivorous feeders. The number of species and families of insect eating bats, however, is nearly identical to that found at a Costa Rican site with a similar climate sampled in a comparable manner (LaVal and Fitch, 1977).

The area had a pronounced dry season from May to late-October, two rainy seasons in November and March-April, and a short and less severe dry season from December through February. The maximum number of species was detected from November to May. Only about half of these species were found during the long dry season, and many of those present seemed to occur in lower densities. Seasonal migration to areas with complementary rainfall patterns is suggested to account for these differences. All but one species reproduced with the more predictable November rains, a few also gave birth in the March-April rainy season, but none bred in the long dry season. Most annual residents bred only in November and most of those species which gave birth in March-April were suspected to be migratory. Suspected migrants tended towards smaller litter sizes.

Several foraging-related characters were examined as indicators of food resource partitioning. Aspect ratio was significantly correlated with estimates of foraging height. It is suggested that most of the common non-molossid insectivorous bat species could coexist on the basis of differences in pursuit strategy, prey size, orientation pulses or feeding heights. A greater proportion of coexisting species overlap in size during the period from November-May than during the long dry season. This may indicate a greater degree of selective feeding when insect abundance is high, and greater partitioning on the basis of size when abundance is low.

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