Ecological observations on an 
East African bat community

by Thomas J. O'SHEA and Terry A. VAUGHAN

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011. 
(Present address of O'Shea : U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, 
Laurel, Maryland 20724)

L'étude de la faune de chauve-souris du centre-ouest du Kenya a été entreprise de mai 1973 
à juillet 1974 : vingt-cinq espèces de chauve-souris appartenant à 7 familles ont été collectées, 
34 d'entre elles étaient insectivores. Cette faune est pauvre quand on la compare aux régions 
neotropicales en raison de l'absence de non-insectivores. Le nombre d'espèces et de familles de 
chauve-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 courte et modérée de décembre à février. La 
mortalité élevée 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 pourraient expliquer ces différences. Toutes les 
espèces sont une s'adaptent avec les pluies les plus constantes de novembre, quelques-unes 
mortent 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 reproduit 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 de petites portées.

INTRODUCTION

The structure and ecology of bat faunas is a subject of interest to mammalogists 
(Pindley, 1970 ; 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.

Mammalia, 1. 14, n° 1, 1980.
MAMMALS

METHODS AND MATERIALS

STUDY AREA

Collections and observations were made from late-May 1973 to late-July 1974 at Masafile (19°18′ and 36°7′E; 20.1 kilometers [km] northeast of Eldoret, Nakuru District, Kenya, elevation 704 meters [m]). The Masafile site is occupied by Bish- 
whacker'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 caudatum,

Grevia nitens and Premna reichenii, reaching heights of two to three m. Stands of

Combretum trees, mainly G. africana and C. balsamum, dominate the area and reach

heights from three to six m above the shrub strata. Additional common trees and

shrubs include Acacia mellowii, A. senegal, A. tortilis, Adansonia digitata, Canis

africana, Combretum riparium, Terminalia peregrina, Baronia taliensis, Sclerocarya

birrea and Marua kriri. 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 riparian trees include

Acacia elata, Neobalanus kilembendi and Tamarindus indica. During our study the entire

area was wild and unembellished, 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 Masafile from 1968-1979 shows a coefficient of variation of

105.3 percent in monthly rainfall (\(E = 30.4 \pm 52.2\) millimeters [mm]). Annual precip-

itation over this period averaged 473 mm, with 80.9 percent of the rain falling in two

bimodal peaks. A November-December rainy season accounted for 42.2 percent

while March-April rains contributed 32.7 percent of the total. The November rains

are also far more predictable in occurrence than the April rains, as shown by long term

records kept at DWA plantations, 14.3 km south of Masafile. These rains produced

less than half of the average for this season (\(E = 305.6\) mm) in only five of the 54

years from 1919 to 1972; the April rains, in contrast, produced less than half of their

means (\(E = 200.0\) mm) in 14 of these years. The coefficient of variation in November-

December rainfall at DWA is 48.1 percent, while in March-April this value rises to

51.1 percent. The two dry seasons between these bimodal rainfall peaks also differ.

Some rains occur during the short dry season from late-December to March; the five

year average for January at Masafile was 31.6 \(\pm 18\) mm; February averaged 18.5

\(\pm 18\) mm. Rain is much scarcer during the long dry season from May through October.

The average total rainfall for May, June, July, August, and September at Masafile

1969-1973 was 20.6 \(\pm 9.8\) mm, or 4.1 \(\pm 6.1\) 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 peak of pro-

ductivity and reproduction occurs during the March-April rains. Following this season,

however, the landscape quickly becomes bleak, and with exceptions the vegetation

becomes leafless.

METHODOLOGY

Harpy traps (Tottle, 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 lines

across trails, and occasionally over water or suspended beneath the Combretum canopy. Nets were stretched across clearings, above the Combretum bush, or beneath the Combretum canopy. These were usually tended until about 2200 hours (h) and

then furled. Based on six long net sets, we used this method on 249 partial net-nights.

From late January to early March 1974 we captured bats in nets across the Athi.

A severe drought on the hinterland 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 com-

parable 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, age and sex (Juvenile or adult); weights and

forearm lengths were taken when possible. Pregnancy was noted by palpation.

Prominent tests 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,

255 as standard study skins, 123 in spirits, and 17 as skretons. These are housed in

the Northern Arizona University Vertebrate Museum. We identified bats in the field

using Heyman 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 K. 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

pygmy size selection and compared 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 representation 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 "crown length" of

coveting species of closely related animals usually does not fall below 1.3. It is widely

held that this ratio indicates coexistance due to food resource partitioning on the basis of

pygmy size (but see Horn and May, 1977). We follow this reasoning in our study of

horizontal gap 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 flew and were captured, or as they fed when released, until we

could recognize them by state 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 an 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
RESULTS AND DISCUSSION

FAUNAL COMPOSITION AND SEASONAL ABUNDANCE

A total of 25 species representing seven families of bats was collected (Table 1). Vespertilionoids dominated the fauna: ten species belonged to this group. Five of the remaining species were molossoids and five were pteropalephiles. Four families were represented by only one species each: Pteropodidae, Emballonuridae, Myotidae and Megadermatidae.

This number of species is low compared to some Neotropical areas, which may possess up to 56 species in eight families (LaVal and Fitch, 1977). The lower species richness at the Kinyinya site is due primarily to a reduction in the number of trophic roles. Unlike Neotropical bat faunas, no carnivores, phyllostomids, sanguivores or nectarivores were found, and only one species was frugivorous. The Massai Mara fauna is remarkably similar to other tropical communities, however, in terms of numbers of species of insectivorous bats. These three sites in Costa Rica sampled similarly possessed 10 to 30 insectivores in five to seven families (LaVal and Fitch, 1977). The one Costa Rican site with a rainfall pattern similar to that at Massai Mara held 22 species of insect feeders in six families (LaVal and Fitch, 1977), a species richness and family diversity remarkably similar to the 24 species and six families of insectivorous bats comprising the Massai Mara 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 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 molossoids bats, this represents a nearly two-fold increase in species richness from the dry 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 Massai Mara 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, 1968). We suspect that through migration many species of bats follow these shifting geographic patterns of rainfall and subsequent community productivity during their annual cycles.

As a corollary to this probable migration, we noted buildups of subadults 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: Roussettus aegyptiacus, Miniopterus schreibersi, Stenodorus nigripes and Stenomys hirtus. Individuals of four species of molossids collected prior to the long
dry season also presented large reserves of subcutaneous fat (Tadrida condylura, T. murina, T. pumila and T. zeyheri), 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. One species also gave birth in March-April, but none born during the May-October dry season. One species was polyovular; ventral young and gravid or nursing females of the frugivorous Eupom pictus calabarensis were continually evident from November to May. Eleven of the 14 non-mammalian insectivorous species with data available (Table 1) were monomorphic. 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 interrain. 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 migration 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 unpredictable dry season from May to October that the probability of survival of weaned young at this time 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 the short interval between tend to be monomorphic (four of four species with such data available). Most annual residents occurring at lower densities in the long dry season also have one or 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 those species find it more advantageous to forest 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 monomorphic species thought to migrate inland 250 km during rainy seasons (Vaughan, 1977). Among mammals, many species of which we suspected to be migratory, Tadrida condylura and T. murina 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, Fonton, 1975; Fonton et al., 1977; Fleming et al., 1972; Me Noh, 1971; Tamsitt, 1977). We take this 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. Anseller and Koes, 1971; Blak, 1974; Buckler, 1978; Bradbury and Hvelechenk, 1976).

**Rare or unique species**

Of 19 non-mammalian bats four (Echinosia bimaculata, Myops trinotus, Miniopea africana and M. schreiberi) were captured only once or twice and were too rare for us to form conclusions on their role 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. callithrix) and three possessed prey pursuit strategies unlike those of any of the other insectivorous species in the area. One (Nigerian thelecan) was primarily a foliage gleaner. Two species, Cardiodromus arc and H. commersoni, hunted insects from perchs: 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 butterflies from perchs located in tall riverine trees at heights of 4 to 15 m. C. arc hunted terrestrial or low-flying prey from broken perchs at heights ranging from 0.3 to 5.5 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. Maximal bat which hunt insects close to the ground are likely to experience high maneuverability 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, r = 0.38, p < 0.05). This relationship is linear (Y = 2.94 X - 11.84) when moths are omitted from the analysis. Mothless fly at heights too great to estimate accurately, but as a group had the highest aspect ratios (Table 2). If moths were included the relationship would probably become exponential at an aspect ratio near 8.00; 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 exploitation 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 Mammals bat forms. Abbreviations for prey size categories are: A.L., aerial insects; P., frugivores; P.S., Palaeotricha sp. *H. sabasi*, *H*. longicalcar. Dashes indicate that no data are available. Sample sizes follow aspect ratios and gape sizes in parentheses.

<table>
<thead>
<tr>
<th>BAT SPECIES</th>
<th>FORAGING</th>
<th>PERCENTAGE</th>
<th>PERCENTAGE</th>
<th>PERCENTAGE</th>
<th>PERCENTAGE</th>
<th>ASPECT RATIO (N=10)</th>
<th>GAPE SIZE (N=10)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. longicalcar</em></td>
<td>A.L.</td>
<td>11.5</td>
<td>11.5</td>
<td>11.5</td>
<td>11.5</td>
<td>11.5</td>
<td>11.5</td>
</tr>
<tr>
<td><em>H. sabasi</em></td>
<td>A.L.</td>
<td>3.7</td>
<td>3.7</td>
<td>3.7</td>
<td>3.7</td>
<td>3.7</td>
<td>3.7</td>
</tr>
<tr>
<td><em>H. longicalcar</em></td>
<td>P. sp.</td>
<td>5.7</td>
<td>5.7</td>
<td>5.7</td>
<td>5.7</td>
<td>5.7</td>
<td>5.7</td>
</tr>
<tr>
<td><em>H. sabasi</em></td>
<td>P. sp.</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td><em>H. longicalcar</em></td>
<td>P.S.</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td><em>H. sabasi</em></td>
<td>P.S.</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
<td>0.5</td>
</tr>
</tbody>
</table>

**TABLE 3.** Foraging height midpoints and distances between midpoints of foraging heights of the common non-muscular aerial insectivores. Distances between height midpoints in m m/s below the diagonal of the matrix.

<table>
<thead>
<tr>
<th>BAT SPECIES</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. longicalcar</em></td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
</tr>
<tr>
<td><em>H. sabasi</em></td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
</tr>
<tr>
<td><em>H. longicalcar</em></td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
</tr>
<tr>
<td><em>H. sabasi</em></td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
</tr>
<tr>
<td><em>H. longicalcar</em></td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
</tr>
<tr>
<td><em>H. sabasi</em></td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
<td>1.8</td>
</tr>
</tbody>
</table>

* See note 1 for data sources given by *Perez* (1979).
complex surfaces because they dampen the number and complexity of returning echoes (Norwick, 1966). This relationship could be important, for example, in allowing the coexistence of E. amandus and P. annuus. These two otherwise similar species differed in that E. amandus (the lower frequency emitter) was consistently observed foraging in more open spaces whereas P. annuus was repeatedly seen foraging within one or in less of the enclosures of vegetation. It is probable that due to frequency design the latter species forages more efficiently on smaller insects taken close to the vegetation.

In summary, most of the 45 bat species pair contrasts analyzed among equidistantly spaced foraging heights were consistent with the perception of the echolocating bats. These contrasts are consistent with the echolocation characteristics observed at the species level.

Species pair contrasts: seasonal differences in gape overlap

Species pair contrasts based solely on gape ratios show noteworthy seasonal changes. There are 14 pair contrasts possible among the 12 species of non-seed eating bats foraging on insects detected from October to May. Fifty-five of these (48.2 percent) have rounded horizontal gape ratios less than 1.3 (Table 2). Among the long dry season the number of possible contrasts falls to 28, but only 32.7 percent of these show ratios less than 1.3 (P = 0.05; 1 = 2.106, 114 df), indicating that at times of low community productivity bats may be partitioning foraging resources on bases other than size alone. Anthony and Kuss (1977) have shown that as seasonal insect density increases the North American bat Myotis fusipes becomes a more selective feeder. During the long dry season at Mbasani bats may take prey more frequently on the basis of size. Hence a greater variation of overlapping gape ratios is not permissible among species coexisting at this time. During the wet season 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 species. Greater insect abundance and a corresponding lower selectivity on the part of the bats would allow for the higher species richness seen from November to May.

Acknowledgements

R. L. Peterson and staff at the Royal Ontario Museum kindly identified specimens. For assistance with field work thank M. H. and B. F. Fowler, T. M. Hirst, S. A. O’hen, D. B. Patten, and the T. A. Vanfossen family. Mr. and Mrs. Harriet Sturton generously allowed us to use the facilities of the Newfoundland Museum. The U.S. National Museum of Natural History Assoclates with the National Museum of Kenya thanks Lenker, P. W., for help in field and laboratory studies. Permission to do research was granted by the government of the Republic of Kenya. Field studies were partially supported by grants from the National Geographic Society and the Loyala Foundation.

SUMMARY

The bat fauna of a south-central Kenya study area was monitored from May 1975 to July 1976. Twenty-five species of bats in seven families were recorded. Of these there were two species, E. amandus and P. annuus, that were significantly different in their foraging patterns. The two species exhibit significant differences in the amount of energy they require to forage on different insects. The differences in foraging patterns are caused by differences in the physical environment and the size of the insects they catch.

BIBLIOGRAPHY


Humphreys, G. W., 1950. - Vespids in the genus Vespa are they more or less aggressive than other kinds of animals? Am. Nat., 84: 141-150.

