

*University of California, San Diego, Department of Biology,  
La Jolla, California*

## Lek Mating Behavior in the Hammer-headed Bat

By JACK W. BRADBURY

*With 13 figures*

*Received: November 29, 1976*

*Accepted: February 24, 1977*

### Abstract

Calling assemblies of *Hypsignathus monstrosus* were studied for 17 months in the field to determine if they were "leks" or mating arenas. Direct observations, netting of animals at the assembly sites, and radio-tracking of both ♂♂ and ♀♀ at the assembly sites, foraging grounds, and day roosts were all utilized to make this determination. Captive animals were maintained to establish growth rates. It is concluded that *Hypsignathus* exhibit lek behavior even by the most conservative definition and share many features with other avian and mammalian lek species.

### Introduction

The hammer-headed bat, *Hypsignathus monstrosus*, is the largest bat in continental Africa. It is a common species in the lowland rain forest of West and Central Africa, ranging as far east as Uganda. In addition to its large body size, the species is distinctive for showing the greatest degree of sexual dimorphism known in the Chiroptera. Adult ♂♂ are nearly twice the weight of adult ♀♀, sport a grotesquely swollen muzzle terminated with flaring lip flaps (see Fig. 1), and possess a greatly hypertrophied larynx that fills more than half of their body cavities. The smaller ♀♀ have a "fox-like" muzzle similar to other epomophorine bats and a larynx about  $\frac{1}{3}$  the size of that in an adult ♂. Numerous reports by field observers have noted the tendency for adult male *Hypsignathus* to aggregate at dusk in the same patches of forest where they "chorus" with loud monotonous honkings (ALLEN, LANG, and CHAPIN 1917; ROSEVEAR 1965; KINGDON 1974). The extreme sexual dimorphism, the modifications of the male larynx for repeated "display", and the aggregations of calling ♂♂ at fixed sites all suggested that this species exhibits lek mating behavior. This report summarizes the results of four field trips to the lowland forests of Gaboon to see if indeed, *Hypsignathus* does show lek behavior, and if it does, how it is similar to or differs from



Fig. 1: Adult male *Hypsignathus monstrosus*. A. (above) Lateral view of head. B. (below) Anterior view of mouth and nose. Photographs by A. R. DEVEZ, C.N.R.S. (France)

other lekking bird and mammal species. In a subsequent paper, field observations on the foraging energy budgets, and demographic profiles of the species will be presented along with comments on the forces leading to the evolution of leks in this species.

The use of the word "lek" has become quite indiscriminate in recent publications. Some authors have used it to describe any aggregation of territorial ♂♂ in which mating can occur (cf. WILSON 1975). I feel this broad definition of lek behavior leads to an indiscriminate lumping of quite different mating strategies. For example, the display territories of male sage grouse or hermit hummingbirds contain no resources required by ♀♀ except the ♂♂

themselves (WILEY 1973; SNOW 1968). If female choice occurs, it must be based on criteria other than enhanced access to some limited resource. In contrast, the territories of male Thompson's gazelles [cited by WILSON (1975) as "lek" species], do contain foraging sites which are usually used by ♀♀. Female choice in this context may involve quite different criteria than in the aggregations of male sage grouse. To distinguish between these systems, I favor a more restricted definition of lek involving the following criteria:

1. *An absence of male parental care.* ♂♂ make no contribution to the building of nests, incubating of eggs, defense or feeding of the progeny, or any other aspect of parental care.

2. *Existence of a mating arena.* Reproductive ♂♂ aggregate at a location fixed at least for one breeding period and establish display territories there. The area covered by any one male aggregation is significantly smaller than the normal home ranges of either ♂♂ or ♀♀ when not on the territories. All mating occurs at these aggregations.

3. *Male territories contain no resources.* Other than access to a ♂, a ♀ visiting an arena gains no enhanced access to any resource such as food, water, protection from predators, egg deposition or nesting sites, etc.

4. *♀♀ have an opportunity to select a ♂ for mating.* As opposed to some mating aggregations of male insects which mob any nearby ♀ (DOWNES 1969), ♀♀ approach ♂♂ on their display territories for mating. Thus the ♀ has some choice of a mate.

A primary goal of this paper is to show that the social system of *Hypsignathus monstrosus* meets all four of these criteria and hence is a "true" lek species.

In addition to the primary criteria used in distinguishing between leks and other mating systems, there are a number of "secondary" features which are common to many, though not all, of the species which do have true leks. These features are (BUECHNER and SCHLOETH 1965; HOGAN-WARBURG 1966; LILL 1974; VAN RHIJN 1973; SNOW 1968; SPIETH 1968; WILEY 1974):

1. Strong sexual dimorphism.
2. Sexual bimaturism with later-maturing ♂♂.
3. Traditional locations for arenas.
4. Extreme ritualization of male displays on the arena.
5. Highly skewed mating success among ♂♂ on any given arena.
6. The existence of a mating center: a region in the arena in which the more successful ♂♂ are aggregated.

Having shown that *Hypsignathus* does meet the primary criteria for lek behavior, a second aim of this paper will be to see to what degree these secondary features are also encountered in this species.

## Materials and Methods

### 1. Study Sites and Periods

This report is based upon four field trips to the lowland forests of Gaboon. Most work was carried out on the preserve of the Laboratoire de Primatologie et d'Ecologie Equatoriale, Makokou, Gaboon (latitude 0.4° N, longitude 13° E), a research station of the Centre National de la Recherche Scientifique (France). Additional data were collected north and south of the station along the Ivindo River and east and west along major roadways. Field trips were made in June—August, 1970, June—September, 1971, June—December, 1972, and May—September, 1974 for a total of 17 months field time.

## 2. Field Observations

Major singing aggregations of male *Hypsignathus* were located and roughly mapped in 1970. In 1971, trails were cut in the forest beneath three singing assemblies and marked at 10 m intervals. Censuses and spacings of singing ♂♂ were recorded by walking along these trails at night and noting the location of each ♂. Since the singing assemblies were typically linear in geometry, a single long trail was usually sufficient for this purpose.

Direct observations of calling animals required aerial platforms in the forest canopy. In several cases, these were constructed simply of wooden planks mounted in a canopy tree with a clear view of a calling ♂ 1 to 10 m away. Trees were climbed by nailing wooden steps to the tree boles, by direct ascent using a Tree Stand (Forestry Suppliers, Jackson, Mississippi), or by rigging trees with 1/2" Goldline for climbing with Jumar ascenders (DENISON et al. 1972). In 1974, we also used two light-weight metal frames, outfitted with plastic seats, and raised into the canopy to varying heights with blocks and tackles. The latter method was by far the best as the locations of observation platforms could be moved quickly to monitor different ♂♂, the height was variable and thus could be optimized as the ♂♂ moved around, and the seats were more comfortable for long hours of observation.

Male behaviour was monitored from canopy platforms with binoculars on moon-lit nights, with cameras and flash equipment, and with a starlight scope fitted with a 135 mm lens (Aspheronics, Leesburg, Virginia). A considerable amount of behavioral monitoring was also possible by simply listening to the sounds of ♂♂ from the ground, once canopy observations had provided the correct interpretations of different vocalizations.

## 3. Capture, Measurement, and Marking

Because roosting, feeding and nocturnal behaviors of this species are primarily restricted to the forest canopy, capture of sufficient individuals posed a considerable problem. An initial canopy net system at a singing assembly in 1970 showed that *Hypsignathus* of both sexes and of all volant ages were visiting the sites during the calling seasons. Accordingly, three 12 m net rigs were set up at 200 m intervals at the C.N.R.S. lek site. Because the bats tended to fly just over the canopy foliage and to follow natural "valleys" and flyways in the canopy, it was possible to select three sites in which bat traffic was relatively confined and frequent. In each site, all ground vegetation between two canopy trees 12 m apart was cleared and the two tree boles cleaned of epiphytes. Steel braided wires were strung parallel to each trunk as guides for the sliding net poles and fixed at the ground with a strong elastic band to maintain sufficient tension. Pulleys were mounted at heights of 20 to 25 m on the two trees and ropes were rigged so that the two poles could both be raised from a location near only one of the trees. This meant that one pulley rope passed between the two trees above the net. Capture rates were increased and injury rates decreased by shortening the shelf strings on the mist net to increase the pockets of the net. From 1971 through 1974, over 450 bats were netted at these three sites.

Because epomophorine bats seem particularly prone to net-induced wrist injuries, all nets were checked every 30 min and any captured bats were removed and placed in cloth bags. This frequency of checking nets eliminated all wrist injuries. Captured animals were examined and measured within 2 h of capture and then released. The following data were taken on all animals: weight, forearm length, length of nose (from anterior tip of eye to center of nostril), height of nose (from mouth to highest point of muzzle), size and location of testes in ♂♂, condition and evidence of prior use of teats in ♀♀, palpable pregnancies in ♀♀, and approximate age using tooth characteristics. These included the presence of milk teeth, the number of erupted cusps on premolars, and the degree of wear on molars. A total of 7 tooth categories coupled with weight and forearm data (calibrated using captive animals), permitted the assignment of all netted animals to one of four known age classes in 6 month intervals up to 2 years of age or to one of three relative age classes for bats older than 2 years. Most netted animals were also examined for expressible feces or seeds in the oral cavities.

Experiments with various forms of marking generated more failures than successes. Bands on the forearms, whether plastic spiral rings, metal wildlife rings, or soft Saflag (Safety Flag Co., Pawtucket, R.I.) loops all caused unacceptable irritation to wing membranes and forearm tissues. Because of the presence of inflatable pharyngeal pouches in ♂♂, collars of soft material were also not possible. Reflecting materials glued to the foreheads and backs of ♂♂ were quickly removed by the bats. Bleaching of numbers and designs into the dorsal fur with commercial hair lighteners and hydrogen peroxide did permit some short distance identifications, but only lasted a single season. In the end, permanent marking proved to be possible only by toe-clipping and ear notching. Recoveries of bats after 3 or 4 year periods showed that such marks were permanent and had no ill effects either on the health or expected numbers of recaptures of the bats. The most efficient short-term marking was achieved by gluing radio transmitters to the backs of selected animals (see below).

#### 4. Radio-Tracking

In 1970, several home-made radio transmitters following the design of COCHRAN (1967) were attached to adult *Hypsignathus* and the bats followed with a single Drake SPR-4 receiver with a Drake SC-2 converter. On subsequent trips, both homemade and commercial transmitters from AVM Co. were used for tracking these bats, and receivers from AVM were also used. All transmitters utilized a frequency of 148 MHz and were connected to mercury cells which would permit up to three months transmission life. Activated transmitters were dipped in paraffin for water proofing, potted in dental acrylic, and outfitted with 1/4 wavelength steel guitar strings for antennas. Attachment to the bats was accomplished by working Dow Corning Type RTV 732 silastic into the fur, applying the potted transmitter, and then working successive layers of fur and silastic over the transmitter. Radios were placed between the shoulder blades of the bats. Maximum package weights with the silastic averaged about 3–5 g, or less than 3% of the body weight of the smallest bats tracked. This method of attachment had the advantage that the bats were always able to scratch the radio transmitters off after several months with at most a loss of dorsal fur. Early removal of the transmitters was reduced by holding the bats for at least 1 h after placement of the transmitter, thereby permitting a firm setting of the silastic. Bats with transmitters were released by carrying them into a canopy tree and letting them leave from a branch at 20 to 25 m height when they wished. Tossing the bats into the air with the transmitters newly attached was attempted only twice and led to near tragedies when the exhausted and startled animals, not expecting the additional weight, fell into the nearby river.

Both types of transmitters emit pulses of radio energy at one to two times per s. Tracking was accomplished by outfitting two or sometimes three receiving stations at known locations up to 3 km apart. Aerial photos available through a local agency permitted accurate triangulations and locations of flight paths, roosts, and feeding sites of the bats. Yagi antennas (Cushcraft Co., Manchester, N. H.) were used for all receiving stations. One large 11-element Yagi was mounted on a rotatable shaft at the C.N.R.S. laboratory, and either 7-element or 4-element antennas were placed at various mobile sites. Walkie-talkies were used to coordinate data collection at the separate tracking stations. Food sites and day roosts were located by direct search in the forest on foot using a receiver and a 3-element Yagi antenna. Sometimes up to 2 km of forest travel were involved in locating a day roost. In all 77 radio transmitters were mounted and released from 1970 to 1974.

#### 5. Captive Animals

A total of 15 *Hypsignathus* of various ages was netted at the C.N.R.S. singing site and brought back to the research station and held in a large (20 × 3 × 4 m) flight cage. Each newly captured animal was force-fed bananas the first few nights in captivity and then allowed to feed itself from a mixture of peeled and unpeeled bananas placed in the cage. Access to a large pool of water was found to be essential since the bats typically drink water in flight. Whole milk powder was sprinkled over the peeled bananas to insure adequate protein and vitamins were also added at intervals. The bats thrived in captivity, even to the extent of setting up male singing posts, copulating, and raising many young on normal seasonal schedules. The captive bats permitted us to observe some of the calling behavior at close quarters and to obtain physical measurements as known aged animals matured. Bats captured in 1972 were subsequently brought to the Bronx Zoo (Bronx, New York), where they have continued to call and breed. A second group, brought back in 1974, are now split between the Bronx Zoo and the San Diego Wild Animal Park in Escondido, California.

#### 6. Vocalizations

Vocalizations were recorded in the field using a Nagra IV tape recorder at 15 i.p.s. and a Sennheiser directional microphone. Narrow and wide bandwidth sonagrams were made at original and reduced playback speeds with a Kay Sonagraph. Distances between a recorded animal and the microphone were always less than 20 m.

### Results

#### A. Location and Dispersion of male Calling Assemblies

Four calling sites were visited and mapped during calling seasons. Three were located along banks or islands of the Ivindo River, (the C.N.R.S. and

Bawaka sites south of Makokou, and the Mekob site north of Makokou), whereas a fourth was located on the Mté River north of the village of Edzua-meyen. Six other sites were identified through reports of local residents, but were visited out of the calling seasons. These sites were situated close to the villages of Ovan, Avil Nyabe, Tsetü, Eyameyong, at the confluence of the Mouianze and Ivindo Rivers, and several km south of the village of Yokob. Since the calling assemblies appear to be traditional, local villagers near true singing sites typically report that the sites were used as far back as the oldest inhabitants can remember. If placed on a map, these 10 locations around Makokou are spaced at from 5—18 km intervals; the average nearest neighbor distance between sites is 14 km.

All 10 of the calling sites are situated in riparian forest along streams or rivers. In some cases such as Mekob, Mté, and Avil Nyabe, the assembly areas are located along the mainland banks of the waterways; at C.N.R.S., Bawaka, and Ovan, the shorelines of river islands are used. The height and physiognomy of the forests used for singing sites appear to be quite variable. At Mekob, ♂♂ called in forest with a relatively closed canopy at heights of

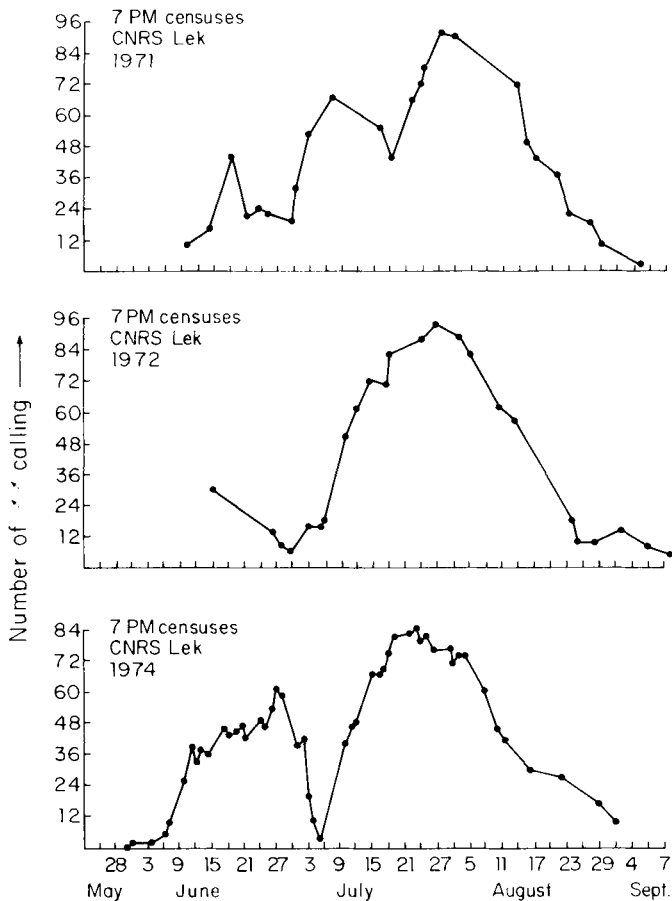


Fig. 2: Censuses of numbers of ♂♂ calling at C.N.R.S. assembly site at 19.00 h as a function of season in 1971, 1972, and 1974

25 m or more; at Bawaka, the forest consisted of many low trees and palms, and calling occurred at 10–15 m height.

### B. Shape and Size of Assemblies

The four calling assemblies mapped while  $\delta\delta$  were active all showed the same configuration. Even at peak levels,  $\delta\delta$  select calling perches which are at least 10 m apart. Since the riparian forest favored for calling is typically about 40 m thick, the width of the calling assembly rarely exceeded 4  $\delta\delta$  and was more frequently 2 to 3  $\delta\delta$ . The total numbers of  $\delta\delta$  calling during the peak periods ranged from 25–30 at Bawaka, 30–40 at Mté, 84–94 at C.N.R.S. and 130–132 at Mekob. Thus nearly all the assemblies consisted of linear arrays about 40 m in thickness and from 400 to 1600 m in length. The one exception to this geometry was the Bawaka site where the entire perimeter of a small (100 m by 170 m) island was occupied by calling  $\delta\delta$ , thereby producing a toroidal configuration.

### C. Seasonality in Calling Activity

All of the field trips reported in this paper occurred between May and December. This covers one of the annual dry seasons (June to early September) and one of the annual rainy seasons (September to December). On each trip, regular censuses of the numbers of calling  $\delta\delta$  at the C.N.R.S. site were made at 19.00 h. The results of these counts are summarized for 1971, 1972, and 1974 in Fig. 2. In each of these years, the numbers of calling  $\delta\delta$  have increased gradually from none in May to a peak in late July, and then have fallen rapidly during August to two or three in September. During September to December, a few  $\delta\delta$  may call for 5–10 min, but their behavior is erratic.

In 1971, coordinated censuses were attempted at the C.N.R.S., Mekob, and Bawaka calling sites. The results are shown in Fig. 3. All three sites show the gradual rise to a peak in late July and a more rapid decay to low levels during August. The C.N.R.S. and Mekob samples even share a common dip in the rising phase of the curves during mid-July. It thus appears that both for the same site in successive years and for different sites in the same year, there is a characteristic peaking of male calling activity in mid-dry season and a rapid fall-off thereafter.

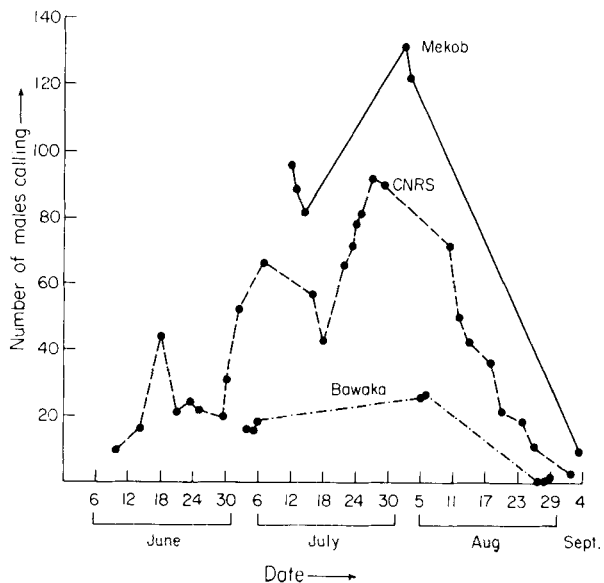


Fig. 3: Censuses of numbers of  $\delta\delta$  calling as a function of season in 1971 at three adjacent assembly sites. All censuses made at 19.00 h

All of the censuses graphed in Figs. 2 and 3 show conspicuous dips in the rising phases of the seasonal activity patterns. In 1971, several dips occurred in late June and mid-July, while in 1972 and 1974, a single large dip occurred in the last days of June or early July. The apparent synchrony in the dips in 1971 for the Mekob and C.N.R.S. sites suggested that some widespread environmental factor was modulating the numbers of calling ♂♂ at all locations. Comparisons of census data and graphs of moonlight intensity and moonrise, rainfall, humidity, and river levels suggested that none of these factors could account for the modulations in numbers of calling ♂♂. Contrasts between censuses and the graphs of minimum temperatures did suggest a relation. For example, in 1971, the three dips in numbers of ♂♂ at the C.N.R.S. site correlated within several days with decreases in the minimum temperature to values of 17°C or less. The large drop in ♂♂ in the 1972 census data in late June corresponded noticeably with a fall in temperature over a 5 day period to a low of 15°C on June 27. In 1974, minimum temperatures dropped below 17°C for 13 nights running in early July; this period corresponded to a nearly total abandonment of the C.N.R.S. singing site by calling ♂♂. One adult ♂ carrying a transmitter not only abandoned the singing site, but also moved its diurnal roost from a location within 1 km of the calling site to another 10 km away where it had been typically foraging before the cold period. When minimum temperatures again rose, the ♂ returned to the prior day roost, took up calling in its usual site, and reinstated its nightly commute to and from a feeding site 10 km away.

In order to see if any significant correlations existed between minimum temperatures and numbers of calling ♂♂, multiple regressions were run with numbers of ♂♂ calling and temperatures on the night censused as the dependent and one of the independent variables respectively. To control for the seasonal rise and fall in ♂♂ already noted, a second independent variable based on a seasonal model was added. The model was developed by approximating the rising and falling phases of all censuses at the C.N.R.S. site with straight lines as follows:

$$\begin{array}{ll} \text{Number of } \text{♂♂} = 1.28 \times \text{Day} - 9.82 & \text{if Day was between 9 and 68} \\ \text{Number of } \text{♂♂} = 78 & \text{if Day} = 69 \\ \text{Number of } \text{♂♂} = -2.35 \times \text{Day} + 239 & \text{if Day was between 70 and 101} \end{array}$$

Here Day was the number of days which had passed between May 21 and the census date in question. The seasonal model accounted for 81%, 74%, and 70% of the variance in the numbers of ♂♂ calling for years 1971, 1972, and 1974 respectively (all regressions with  $p < .0001$ ). Temperature, entered as the minimum temperature on the night the census was performed, explained a significant 7% and 15% additional variance for the years 1972 and 1974 ( $p < .01$  or smaller). When entered in this manner, temperature did not explain a significant amount of variance for 1971. This latter failure is not disturbing to the basic thesis since the entering of minimum temperatures on the night of censusing, while the simplest, is probably not the most realistic relation between calling ♂-numbers and ambient temperatures. More realistic models would incorporate time lags (e.g., entering the temperatures 1, 2 or 3 days prior to the censusing), cumulative effects (e.g., only entering periods when temperatures dropped below a given level for a given number of nights), and non-linearities in the physiological responses of the bats to lowered temperatures. Rather than experiment with all these possibilities, direct physiological measurements on captive *Hypsignathus* are currently being attempted by Dr. Roger CARPENTER (San Diego State University). These should provide insights into the actual relation between low temperatures and the energy budgets of calling ♂♂.

Reports by local residents and colleagues at the C.N.R.S. laboratory in Gaboon made it obvious that the *Hypsignathus* calling behavior was biannual with a second calling season in December to February. Recently, Dr. Louise EMMONS was able to census the C.N.R.S. site monthly from November, 1975 through March, 1976 and has kindly provided the data summarized in Fig. 4. Because the data were collected monthly, the exact peak cannot be ascertained, but it is apparent that maximal levels were reached in January. The duration (about 3 months) and size (max. of 112 ♂♂) of the assembly are quite similar



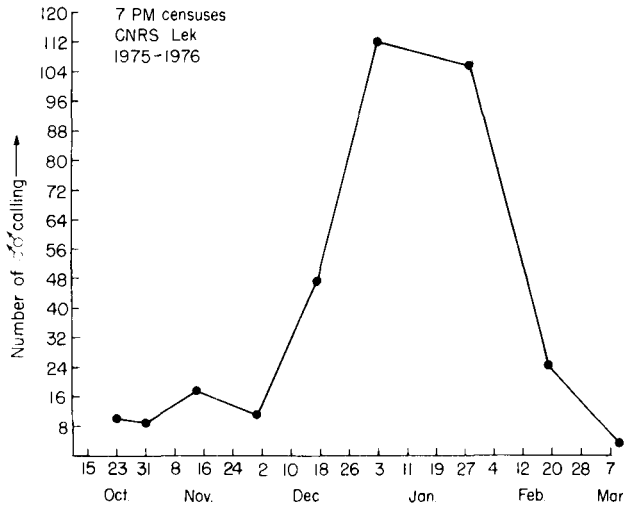


Fig. 4: Numbers of  $\sigma\sigma$  calling at C.N.R.S. assembly site during December to February calling period. Censuses taken at 19.00 h. Data supplied by Dr. L. EMMONS

to values recorded at the same site during the June to August seasons of 1971—1974. If the peak levels were to occur at the end of January, the interval between the peaks of the two calling seasons would be exactly 6 months.

#### D. Male Behavior at the Calling Sites

The behavior of calling  $\sigma\sigma$  has proved to be fairly simple and predictable. Just at dusk (18.30 h), adult male *Hypsignathus* can be seen flying at canopy level en route to the calling sites. At the C.N.R.S. location, most calling  $\sigma\sigma$  apparently roost on the mainland during the day and cross the river to the island calling area at dusk. Fig. 5 illustrates the dispersion of calling  $\sigma\sigma$  at this site and the major routes of approach to the island.

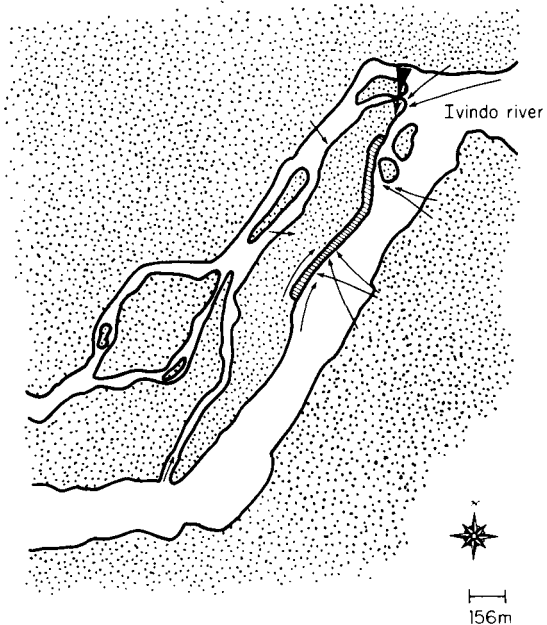


Fig. 5: Topographical configuration of C.N.R.S. calling assembly. Calling assembly is shaded while forested areas are stippled. Arrows indicate major routes followed by adult  $\sigma\sigma$  to the assembly site at dusk. Dark arrow indicates most heavily used access route

Once arriving at the calling area, ♂♂ may swoop low over the river and drink while in flight. They then land in the canopy of the forest bordering the river. The typical roost consists of several horizontal branches beneath a dense umbrella of foliage. In many cases, the side facing the river is more open and the bats are easily visible from the water. ♂♂ approaching their calling branch often make 5—10 passes before landing. Some land for a few s and then leave to land again. Bats appear to use exactly the same spot on a branch night after night and the repeated approaches may reflect the difficulty that so large a bat encounters in achieving purchase at just the right spot. Once there, the ♂♂ usually groom themselves for 2—3 min and then begin to call.

The first calls are always raspy and harsh but within 4—5 renditions take on the clear metallic note so characteristic of this species. A pharyngeal pouch over each shoulder appears to become inflated during these first few calls and subsequently expands and contracts with the emission of each normal note.

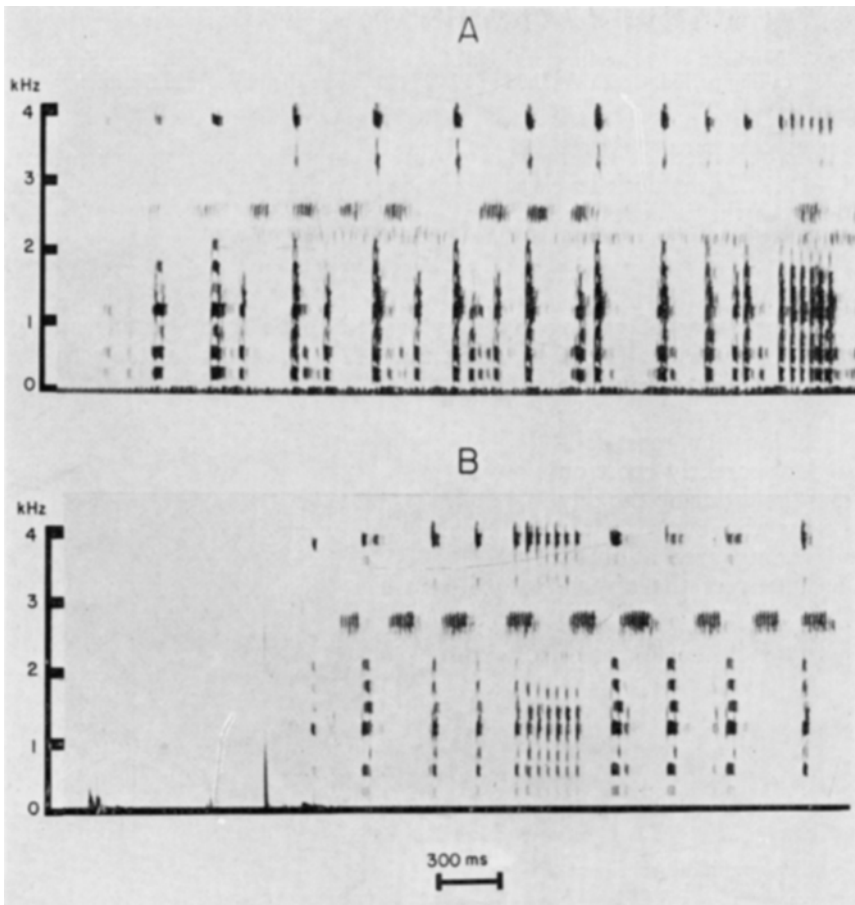


Fig. 6: Sonograms of display calls of male *Hypsignathus* recorded in the field. In both sonograms, the columns of harmonics are the bat calls; the pulsed sounds at 2.2 and 2.6 kHz are insects. In A, several ♂♂' calls are evident, and one performs a staccato-buzz at the end of the record. In B, a single ♂ is present and a staccato-buzz occurs at the mid-point of the record

The call itself is simple with no modulations of frequency. On an oscilloscope, it can be seen to have a periodic or pulsatile waveform with a repetition rate of about 290 pulses/s. These are presumably glottal pulses as in most mammalian sounds. On a sonagram, the periodic structure of the call appears as a harmonic series with a fundamental of 290 Hz (Fig. 6). Energy is not equally distributed among the harmonics but occurs in three bands. The first consists of harmonics 1—7 and covers frequencies from 290 Hz to 2 kHz; the peak value occurs at harmonic 4 (1150 Hz) or 5 (1450 Hz). A second band of energy is composed of harmonics 11—15 with a peak at 4 kHz. These two bands have similar energy levels at their peak frequencies. The third band occurs around harmonics 26—28 (7500—8000 Hz) and is typically several db lower in amplitude than the lower two bands. The selective accentuation of certain harmonic bands could be due to any or all of the large boxy larynx, the pharyngeal pouches, or the enlarged nasal cavities. The resulting call is very loud and resembles the sound of a glass being rapped hard on a porcelain sink.

While the  $\delta\delta$  are calling, they typically extend their half-opened wings and beat them at about twice the rate of call emission. The latter varies from about 50 calls/min to about 120 calls/min. A calling  $\delta$  approached by another in flight accelerates his calling and wing flapping and turns his head and body towards the other animal.  $\delta\delta$  appear to see well and can follow the movements of a flying conspecific quite accurately even under low light levels. Auditory cues may contribute to this following behavior, but since flying bats often glide rather silently and the ambient sound levels are so intense due to the calling of  $\delta\delta$ , these are probably of less value than vision.

During the first 30 min after arriving at the calling areas, agonistic behavior between adult  $\delta\delta$  is pronounced. Typically, a calling  $\delta$  is approached by another flying  $\delta$ . The former breaks off the normal calling and emits a series of harsh gasps and honks. He may also lash out at the flying animal with his wings. Usually the volant bat veers aside and avoids the roosting individual. A more contested location may be the scene for alternate attacks and supplants at the perch by several  $\delta\delta$ . Often the perching animal will flee as the intruding bat approaches and then the latter will in turn abandon the roost as the first bat returns. Several times we have observed overt attacks in which the  $\delta\delta$  will grapple, bite, and slap at each other in flight. Physical attacks are much rarer than passes and supplantings without contact. By about 19.00 h agonistic behavior becomes sporadic and  $\delta\delta$  spend most of their time calling.

Normal calling is interrupted at intervals for two reasons. The most common interruption is due to a shift of calling position by the  $\delta$ . Each  $\delta$  appears to have 2—3 preferred calling positions within several m of each other. At intervals of about 17 min (mean of 47 multiple h samples at 25 locations throughout the calling season), a  $\delta$  will terminate one calling bout, fly out silently in a wide arc, and return to begin calling at an adjacent branch. Bout length is highly variable, often reaching 65% variation for a given  $\delta$  on a single night.

The second perturbation of normal calling is caused by visiting  $\text{♀♀}$ . Direct visual observation of  $\text{♀♀}$  (some carrying newborn young in flight), indirect monitoring with radio transmitters, and netting of  $\text{♀♀}$  at the C.N.R.S. site have all provided evidence that  $\text{♀♀}$  visit the male assembly sites in considerable numbers.  $\text{♀♀}$  typically fly along the axis of the calling assembly and make short hovering inspections of particular  $\delta\delta$ . Whenever a  $\text{♀}$  hovers near



Fig. 7: Displaying male *Hypsignathus* at the C.N.R.S. assembly site with partly opened wings and inflated pharyngeal pouches emitting normal call

a calling ♂, the latter accelerates its calling rate and performs a “staccato buzz” display. This consists of an increase in call emission up to a rate of 2–3/s. As the ♀ flies to within a m of the ♂, the latter pulls its wings tightly against its body and emits several long buzz notes. As seen in Fig. 6B, these are spectrographically identical to normal call notes but are twice as long in duration (90–100 ms for buzz notes vs. 45–50 ms for normal call notes). As the ♀ turns and leaves, the ♂ extends his wings and returns to normal calling and wing-flapping. An example of a typical calling ♂ is shown in Fig. 7.

The number of staccato buzzes performed by a given ♂ on a particular evening, and thus the number of female visits, varies with the calling location of the ♂, the season, and the identity of the ♂. Here rates were measured by counting the number of staccato buzzes performed by a ♂ during a 30 to 210 min sampling period in the calling session just after dusk. Rates were computed as number of staccato buzzes (SB) per min of sampling. The range in this rate was 0 to 1.10 SB/min and the average of 274 samples at the C.N.R.S. and Bawaka sites was 0.143 SB/min. If calling locations sampled in the same year are treated as belonging to the same ♂ but when sampled in different years as belonging to different ♂♂, these 274 samples from all four years (1970–1974) represent about 136 different ♂♂. Location effects are summarized in Table 1. Here the C.N.R.S. site has been divided into approximately 200 m segments with the north end containing the trail marker 0 and the south end the marker 1000 m. It is clear that as one passes from 0 m to the assembly center at about 500 m, staccato buzz rates steadily increase. From 600 to 800 m the rates drop again, and then rise in the south end of the site to a second smaller peak about 900 m. The differences between adjacent segments are all significant except for the first two (t Test, 2-tailed,

Table 1: Effect of male location on staccato-buzz rates for the C.N.R.S. site. All years pooled

Male Calling Location	Average Display Rate (SB / min)	Number of Samples
0 - 200 m	.100 ± .088	58
210 - 400 m	.116 ± .070	26
410 - 600 m	.280 ± .289	45
610 - 800 m	.110 ± .087	78
810 - 1000 m	.170 ± .171	48

$p < .05$  or smaller). This locational variation in staccato buzz rates exactly matches the distribution in copulations to be discussed below.

The seasonal effects are most easily seen by comparing the frequency distributions of different staccato buzz rates for June, July and August samples (Table 2). In all months, a significant fraction of the  $\delta\delta$  sampled had staccato buzz rates below the overall average of .143 SB/min. During June, as the singing assembly is rising to its peak and prior to the first copulations (first week in July), most  $\delta\delta$  have low rates and none exceeds 0.400 SB/min. With the onset of copulations in July, staccato buzz rates for some  $\delta\delta$  rise dramatically and during this month, 9% of the samples give rates between 0.400 and 1.100 SB/min. In August, the extremely high rates disappear again, but the rest of the distribution remains statistically indistinguishable from that for July. If rate categories are lumped to eliminate zero cells, the distribution for June is significantly different from that for July and August pooled (G Test,  $G = 14.4$ ,  $df = 2$ ,  $p < .01$ ).

In addition to seasonal and regional variations in staccato buzz rates, there was pronounced heterogeneity among neighboring  $\delta\delta$  in the numbers of female visits even on the same nights. Initial sampling of pairs of  $\delta\delta$  showed that staccato buzz rates on the same evening might differ by factors of 10 to 20 times. To quantify this variation further, simultaneous samples on triplets of adjacent  $\delta\delta$  were taken at various points in the C.N.R.S. assembly at different times during the season. If  $\text{♀♀}$  visited  $\delta\delta$  within any such triplet at random, we would expect each  $\delta$  to perform about 33% of the total staccato buzzes recorded from the triplet in a given sample. In fact, analysis of 41 such triplets, pooled over all locations within the assembly and over all times during the calling season, shows significant heterogeneity in the distributions of staccato buzzes. For the average trio of  $\delta\delta$ , one  $\delta$  typically obtained 57% ± 16% of the group's total staccato buzzes, a second performed 29% ± 11% of the total, and the third was responsible for only 15% ± 9% of the total. Taking as the expected values  $1/3$  of the total staccato buzzes

Table 2: Seasonal changes in frequency distributions of staccato buzz rates. C.N.R.S. and Bawaka sites pooled, and all years pooled

Staccato Buzz Rates	June		July		August		Total	
	Number	%	Number	%	Number	%	Number	%
0 to .100	37	74	83	48	28	54	148	54
.101 to .200	10	20	40	23	14	27	64	23
.201 to .300	2	4	25	15	7	13	34	12
.301 to .400	1	2	9	5	2	4	12	4
.401 to .500	0	0	3	2	1	2	4	1
.501 to 1.100	0	0	12	7	0	0	12	6
Total Samples	50	100	172	100	52	100	274	100
Presumed No. of $\sigma\sigma$	30	-	73	-	34	-	137	-

by a trio in a given sample, the 41 trios examined gave a total chi-square of 680. This is highly significant (for  $df = 82$ ,  $p < .0001$ ). When examined individually, 25 of the 41 triplets (61%) differed significantly from equitable partitionings of the total staccato buzzes in the sample (chi-square = 5.99 or greater,  $df = 2$ ,  $p < .05$ ).

There are not enough data to identify the factors which generate the local heterogeneities in female visits and thus staccato buzz rates. In some cases, return visits by the same ♀ were observed, and this would tend to accentuate the effects of any female preferences. Hints of other factors were noted. In several cases, staccato buzz rates for the same ♂ in each of his adjacent calling branches were recorded separately. In one particular example, samplings on two successive nights each involving 4–5 branch changes suggested that calling from one branch consistently led to more female visits than did calling from the adjacent branch. Unfortunately, the samples are too small for statistical testing of this impression.

### E. Patterns of Territorial Settlement

Early in the June to August calling period, only a few ♂♂ visit the site and defend calling territories. Some can be seen to fly in to calling positions but simply land on the branch without calling for 30–40 min and then leave. The distributions of calling ♂♂ in the early and late parts of the calling season are interesting. Instead of settling at a few concentrated loci and spreading out to the maximum assembly area, initial settlement is widely scattered along the whole length of the eventual assembly and subsequent territories appear between those of established ♂♂. This process is summarized in Table 3 in which the length of the assembly and the average nearest neighbor distances between established ♂♂ are given for the C.N.R.S. site in 1974. Assembly length is measured as the linear distance between the two most terminal ♂♂. As early as June 6 when only 4 ♂♂ were present at the site, the assembly length was already 80% of its eventual maximum length. During the ensuing rise to peak densities in late July, nearest neighbor distances dropped to 6% of their June 6 levels. During the decline in numbers of ♂♂ in August, territorial abandonment was dispersed relatively evenly throughout the whole assembly area and thus the same effects were found in this period as well.

Table 3: Settlement patterns of the C.N.R.S. site in June to August, 1974

Date	No. of ♂♂	Assembly Length	Average Nearest Neighbor Distances
		(m)	(m)
June 6	4	835	230 ± 335
June 7	10	830	99 ± 88
June 10	25	795	47 ± 82
June 11	39	930	25 ± 29
June 20	47	905	22 ± 24
June 26	54	960	18 ± 17
July 15	66	915	15 ± 15
July 23	84	1040	13 ± 14
August 5	60	1000	18 ± 20
August 13	30	905	35 ± 49
August 26	17	890	60 ± 57

By radio-tracking 9 adult ♂♂ in 1974 which eventually sang at the C.N.R.S. assembly site, it was possible to identify the basic steps in territorial settlement. Several case histories are illuminating. ♂ 1 was captured June 10. From June 11 to June 14, it sang regularly in the early evening at trail marker 190 m. In the early morning of June 15, ♂ 1 appeared and took up a singing post at 490 m (a location within 30 m of what became later the major site of copulations). On subsequent evenings, this animal flew directly to the 490 location at dusk and called there regularly. Early in the evening of June 28, ♂ 1 and another ♂ had a loud and conspicuous fight at the 490 location which was terminated when ♂ 1 flew to its former 190 m site. From this date until July 23 when the radio came off the bat (a total of 43 days of tracking), ♂ 1 called regularly and only at the 190 m site. Not only was this the only site used by ♂ 1 after its initial displacement, but on occasions when it was not present, no other bats used the same calling territory. Two other ♂♂ had similar histories. One initially took a singing territory within 100 m of the major mating center, but in July moved (or was forced to move) to a new singing site 235 m from the major mating center and 100 m from the secondary mating center. (See below for locations of these centers.) Another began with a singing territory in early June near the northern end of the assembly, but had moved by June 17 to a site within 30 m of the major mating center. Both of these bats returned to the new singing sites night after night for as long as their radios remained attached and functioning (50 and 60 days respectively). A fourth ♂ sang nightly for several weeks in June at a site near the northern end of the assembly. On June 24, he suddenly failed to appear in the evening and his position was filled by another unmarked ♂. Two tracked ♂♂ established singing territories in June, but alternated with unmarked bats in their use of the sites. In one case, alternation occurred on successive nights, while in the other, supplants occurred several times nightly. Both of these ♂♂ disappeared from the C.N.R.S. assembly after several weeks. Three other ♂♂ called at the C.N.R.S. site for a few nights only and then disappeared. Each attempted to establish a territory intermediate between those of two already established ♂♂ and apparently failed to do so. One called for two successive nights in late June, one for a single night at peak levels in July, and a third for a single night on August 14.

The radio-tracking data from 1974, along with scattered observations on ♂♂ marked with bleached fur or conspicuous scars and wounds, all suggest that after the initial settlement period in June, most ♂♂ tend to occupy the same calling site for the rest of the calling season. Long hours of direct observation of individual calling locations certainly yield the impression that the same individual bats are being observed on consecutive nights. In each of these cases, marked quirks of behavior such as short calling bouts, preferred perching positions, or unusual grooming behavior are seen in the bat occupying the same position night after night. Unfortunately, none of these quirks nor the marking methods used allow one to assess whether the same ♂♂ return to the same singing sites in *successive years*: bleaching is detectable only for the period between molts and clipped toes are impossible to see when the bats are calling in the forest canopy. Of 108 male bats marked at the C.N.R.S. site in 1971 and 1972, only 5 were recaptured at the same location in 1974. 3 of these were adults when first captured in 1972, one was a subadult at that time, and the fifth was a juvenile when first netted (see below for aging methods). While 3 of these bats (two trapped originally as adults and one as a

juvenile), were radio-tracked and shown to establish singing territories in 1974, I have no data on their prior status in 1972.

During the decline in ♂-numbers in August, several peculiar patterns were noted. Usually about mid-August, ♂♂ with a much more raspy and rough call (called "honkers"), begin to appear at various points in the assembly. Sonagrams of these calls show a similar harmonic structure to that of normal calls but with the presence of more energy at higher harmonics around 4 kHz. It was first supposed that honkers were juvenile or subadult ♂♂ which were attempting to take up calling positions in the assembly as the more established ♂♂ abandoned their territories. However, the facts that the fundamental frequency of honker calls is identical to that of normal ♂♂, and that 12 honkers collected at several assembly sites in August and September all had normal adult laryngeal dimensions suggest that this is not the case. Collected honkers were also indistinguishable from adults in all other morphological attributes including the presence of active sperm in the epididymides. It now seems most likely that honkers are normal adult ♂♂ which, perhaps because of submaximal inflation of pharyngeal pouches, are simply not producing the normal metallic call. Careful monitoring of specific sites suggests that most ♂♂ phase out the calling season with the following sequence: a) a reduction in the duration of calling in a given night, b) a reduction in the rate of call emission while at the assembly (from normal rates of 60—120/min down to 30—40/min), c) a change in the energy distribution of the call to produce "honkers", d) the cessation of any calling while visiting the calling territory, e) the cessation of any visiting to the assembly. The intermediate stage of roosting for 30—60 min in the calling territory without calling or wing-flapping is common to both the onset and decline of the calling season.

#### F. Nocturnal Activity Patterns of Calling ♂♂

♂♂ do not call all night. Activity is bimodal with peaks in the numbers of calling ♂♂ at 1900 and 0400 h. Fig. 8 summarizes a series of all-night hourly censuses at the C.N.R.S. site throughout the June to August season. With the exception of the mid-June sample, the evening calling sessions are always attended by 2—10 times as many ♂♂ as attend the subsequent morning sessions. There is some evidence that evening and morning calling sessions have different "functions" and that shifts in relative size of morning and evening peaks reflect seasonal changes in the importance of each function. In particular, agonistic encounters between ♂♂ during the evening sessions are primarily limited to the first 30 min after arrival at the assembly sites. By 19.00 h, most ♂♂ have settled any new territorial disputes and devote nearly all of their attention to calling and staccato buzzes. In contrast, morning sessions are characterized by repeated and noisy agonistic interactions between adjacent ♂♂. While ♀♀ visit ♂♂ during both sessions, staccato buzz rates during morning sessions are usually lower than those during evening sessions. More strikingly, copulations have been recorded exclusively during evening sessions (see below). Analysis of the all-night census data shows that an average of only 26% ± 14% of the singing territories occupied during the evening calling sessions were again occupied in the subsequent morning sessions. The highest values of joint evening and morning usage occurred on June 14 and June 21 when 53% and 31% respectively of the occupied evening territories were also filled the next morning. By the same analysis, an average of 44% ± 30% of the singing sites occupied in the morning sessions were



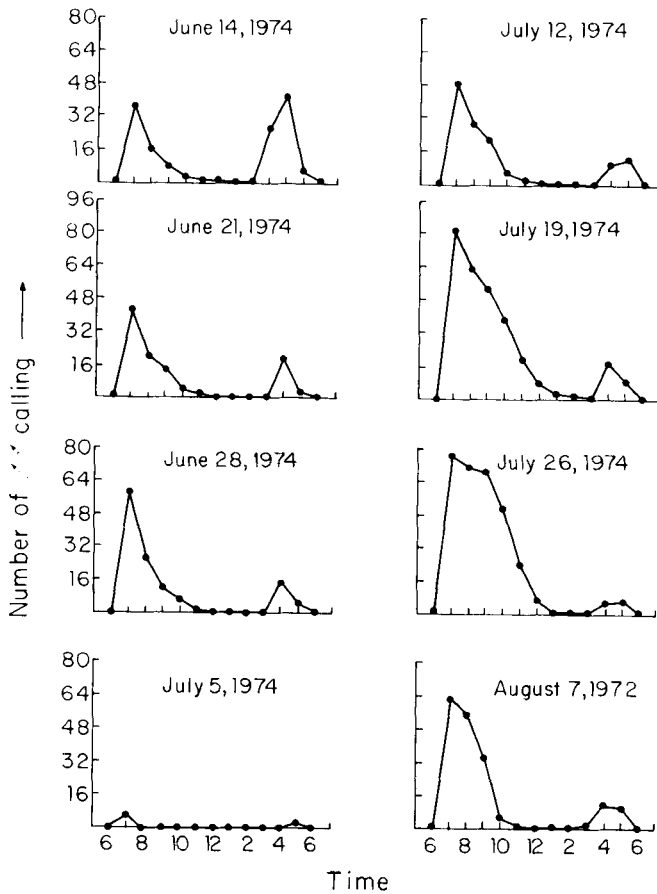


Fig. 8: All night hourly censuses of the numbers of  $\delta\delta$  calling at the C.N.R.S. assembly site. All data taken in 1974 except for the last sample which was taken in 1972. The lower axis indicates time with the left-hand "6" corresponding to 18.00 h and the right-hand "6" to 06.00 h

vacant the previous evening session. Thus about half of the sites occupied in either session are not utilized in the preceding or successive sessions.

The differences in agonistic and sexual behaviors, the fairly disjunct occupancy of territories, and the seasonal shifts in the relative sizes of the morning and evening sessions can all be understood best by referring to the radio-tracking data on calling  $\delta\delta$ . All first attempts to settle a new singing territory by radio-tracked  $\delta\delta$  occurred during a morning session. This was even true of the established  $\delta\delta$  which attempted to relocate during the season in a new territory. Radio-tracking also showed that the hours when  $\delta\delta$  were not calling at the assembly were occupied by foraging at distances of up to 10 km from the calling assembly.  $\delta\delta$  which called in the evening session often spent the whole remainder of the night foraging in these distant locations. Since evening sessions were the only periods likely to lead to copulations, calling during this period is presumably more critical for established  $\delta\delta$  than would be the morning sessions. If foraging times prohibit visits at both sessions on occasion, it is apparently the morning session which is missed.

The absence of more established  $\delta\delta$  during the morning session may be one reason why initial settlement of new territories is attempted at this time. The fact that up to 50% of the established  $\delta\delta$  returned to their sites in the morning sessions in June suggests that, at least early in the season, control of a territory in the morning sessions in some way enhances the probabilities of holding that territory during the evening sessions. Once territory settlement has stabilized for most  $\delta\delta$ , return visits in morning sessions do not seem to be as frequent. In short, morning sessions seem most concerned with territorial establishment and  $\delta-\delta$  interactions; evening sessions do include agonistic behaviors, but display and mating are the major activities during this period. Morning sessions are largest early in the season when territorial settlement, and thus male interactions, are maximal.

Evening sessions not only involve greater numbers of  $\delta\delta$ , they also tend to be longer in duration. This is mostly due to more prolonged occupation of territories in evening sessions at the peak of the season. Whereas only 34%  $\pm$  3% of the calling territories occupied at 19.00 h during the June 14 to July 12 period were still occupied at 20.00 h, an average of 72%  $\pm$  6% were continuously occupied at both times for samples in the July 19 to August 7 period. This is a significant difference (t-Test, 2 tailed,  $t = 10.2$ ,  $df = 2$ ,  $p < .05$ ). At the peak season in late July, some  $\delta\delta$  were observed to call continuously except for minor perch relocations for up to 6½ h.

### G. Copulation Behavior at Calling Assemblies

Copulations have been observed with either moonlight or the starlight scope. A  $\delta$  selected by a  $\text{♀}$  for copulation is usually visited several times within a short period before she lands on the branch next to him. During each approach, the  $\delta$  performs one or more staccato buzz displays. On several occasions, it has been possible to watch the same  $\text{♀}$  hover to each of 4–6 neighboring  $\delta\delta$ . It is interesting that in these cases, the  $\text{♀}$  appears to visit each  $\delta$  at least once, then returns to two or three for repeated and alternating visits over a 3–5 min period, and finally concentrates on repeated hovering before a single  $\delta$ . An observer certainly gains an impression of direct comparisons of  $\delta\delta$  by the  $\text{♀}$  until she has chosen one for mating. Once a  $\text{♀}$  has landed, copulation is rapid. The  $\delta$  ceases all calling abruptly, mounts the  $\text{♀}$  from behind and the two animals remain in contact for only 30–60 s. Copulation is always terminated by several loud whinings by the  $\text{♀}$  before she flies off.  $\delta\delta$  typically resume calling within a min after the termination of copulation.

The characteristic sequence of repeated staccato buzzes, abrupt arrests in the calling of one  $\delta$ , and the  $\text{♀}$  whining after 30–60 s of local silence permitted the acoustical tabulation of copulations at different seasons and at different locations within an assembly. Table 4 summarizes the seasonal distribution of the 58 copulations recorded during four June to August watches at the C.N.R.S. site. Copulations have also been noted at the Bawaka and Mekob sites and fit the same patterns shown in Table 4. No copulations are recorded at any sites before July 1 or after August 18. At the C.N.R.S. location, the number of copulations rises rapidly during July to a peak in the third week, and then declines to only a few by mid-August. Comparisons of Table 4 and Fig. 2 will show that copulation rates roughly follow the numbers of calling  $\delta\delta$ , but peak about one week earlier. Table 4 also gives the numbers of  $\text{♀♀}$  netted on the C.N.R.S. site per h of netting. If we assume that the numbers of  $\text{♀♀}$  netted reflect the numbers visiting the site for copulation,

Table 4: Seasonal distributions of copulations and numbers of ♀♀ netted at C.N.R.S. site. All years are pooled for copulation data, but netting data are given for 1974 only

Sample Period	Copulations	% of Total Copulations	♀♀ netted / h netting
All of June	0	0	.379
July 1 - July 7	2	3	.229
July 8 - July 14	6	10	.480
July 15 - July 21	25	43	1.000
July 22 - July 28	16	28	1.381
July 29 - August 4	4	7	1.100
August 5 - August 11	4	7	.444
August 12 - August 18	1	2	.100
August 19 - August 31	0	0	.229

we get a not surprising correlation between the numbers of copulations for each period and the numbers of ♀♀ visiting the site ( $r = .72$ ,  $r^2 = 52\%$ ,  $df = 7$ ,  $p < .05$ ).

As with staccato buzz rates, copulations are not evenly distributed over the whole calling assembly. Fig. 9 plots the distribution of the 50 copulations recorded at the C.N.R.S. site in 1974 according to the location at which acoustic monitoring of activity was undertaken. Because sampling was not equal at all points, values are given as the number of copulations per h of sampling at a given location. It is clear that copulation rates are quite unevenly distributed and that there are two regions of max. mating activity. The first and major peak is located at approximately 520 m along the assembly trail, or roughly near the center of gravity of the assembly. The second and minor peak occurs near the south end of the assembly. This distribution matches closely the distributions in average staccato buzz rates presented in Table 1. A more precise comparison was achieved by computing the average staccato buzz rates in 1974 for all ♂♂ within 20 m to either side of the copulation sampling points:

- .058 ± .023 SB/min (N = 21 samples) for ♂♂ in the 150—190 m interval
- .109 ± .035 SB/min (N = 4 samples) for ♂♂ in the 230—270 m interval
- .152 ± .140 SB/min (N = 7 samples) for ♂♂ in the 450—490 m interval
- .370 ± .318 SB/min (N = 29 samples) for ♂♂ in the 500—540 m interval
- .137 ± .103 SB/min (N = 13 samples) for ♂♂ in the 620—660 m interval
- .086 ± .084 SB/min (N = 21 samples) for ♂♂ in the 730—780 m interval
- .180 ± .186 SB/min (N = 33 samples) for ♂♂ in the 870—910 m interval

A linear regression of the copulation rates in Fig. 9 against the staccato buzz rates above gives a highly significant result (Copulations/h = 3.53 SB/h — .22,  $r = .94$ ,  $df = 5$ ,  $p < .01$ ). Thus the assembly regions most frequently

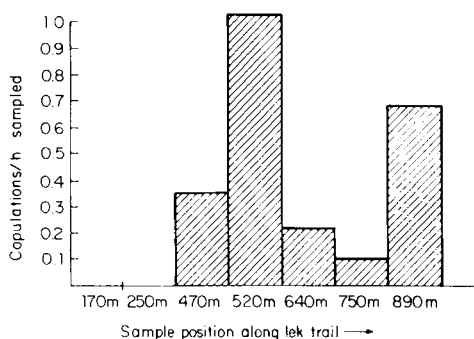


Fig. 9: Copulation rates as monitored acoustically at 7 locations along the C.N.R.S. assembly site in 1974. The data represent a total of 50 recorded copulation sequences

visited by ♀♀ (including repeat visits), are also those in which the greatest numbers of copulations are occurring.

In addition to seasonal and regional effects, there were marked differences among adjacent ♂♂ in the same sampling period as to the numbers of copulations achieved. For example, of the 9 ♂♂ easily sampled from the 520 m observation site, one obtained 17 copulations, one 13, two received one each, and 5 obtained no copulations at all. Assuming that all 9 ♂♂ were equally likely to receive copulations if these were distributed at random, this distribution is a significant deviation from the random case (chi-square = 97,  $p < .005$ ).

The summed effects of seasonal variations in female visits, regional differences in female visitation rates within the aggregation, and local differences between adjacent ♂♂ yield a pronounced skew in mating success among ♂♂ at any given aggregation. In Fig. 10, the copulation rates per h of sampling for the C.N.R.S. site in 1974 are plotted for individual calling positions. As noted earlier, little relocation by ♂♂ occurred after the onset of copulations and hence all copulations at a given calling site are probably attributable to a single ♂. If we assume that these rates reflect the seasonal totals in mating success for each ♂, Fig. 10 indicates that 2 of the 85 ♂♂ in the aggregation (or 2%) accounted for 40% of the season's copulations; the 5 top ♂♂ (6%) accounted for 79% of the copulations. To test for randomness in this distribution, we would need to have sampled for equal times at all calling sites. However, if we presume that the measured rates are representative, we can compute a "standardized" distribution of the observed 50 copulations among the 85 ♂♂ in 1974. This can then be tested against a Poisson expectation. When this is done, the distribution is highly non-random (chi-square = 43.2,  $df = 3$ ,  $p < .005$ ). If we make a similar calculation but only for the top 12 ♂♂ which were observed to copulate in 1974, the distribution is still highly non-random with several ♂♂ getting more and many getting less than their share by chance (chi-square = 7.11,  $df = 1$ ,  $p < .01$ ).

Whether looking at the whole assembly or only the successful ♂♂, copulations are distributed in a highly skewed fashion.

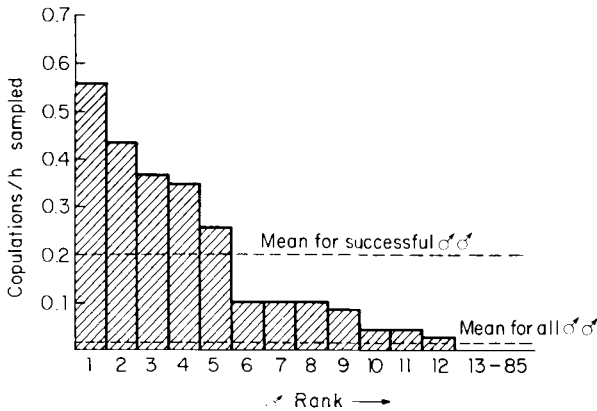


Fig. 10: Copulation rates of calling territories ranked according to copulation rate. It is presumed that each value represents the success of a single ♂. Dotted lines denote the average copulation rates of all ♂♂ monitored and of all ♂♂ which obtained any copulations respectively

### H. Day Roosts

Bats netted at the C.N.R.S. assembly site were subsequently radio-tracked to their day roosts. In some cases, it was possible to follow individual animals through a succession of day roosts over periods of several months. Between

1970 and 1974, 35 different day roost locations were mapped and 24 of these were actually visited and monitored for extended periods. In 1974, the nearest neighbor distances between *known* roosts of *Hypsignathus* ranged between 0.4 and 6 km. As will be shown below, the cryptic nature of the day roosts and their sparse distribution over kilometers of uniform habitat make it virtually impossible to locate them by any means other than radio-tracking.

All day roosts show a similar configuration. The bats typically roost high in the forest canopy at heights of from 20 to 30 m. Roosts are always exposed branches beneath a dense umbrella of vegetation. Usually access to the roosting branch is guaranteed by apparent selection for sites with few nearby lianas and epiphytes and several m gap between roost and understory. No preference for particular species of roost trees was noted.

Of the 24 roosts which were visited regularly, 18 contained only a single bat (9 ♂♂ and 9 ♀♀). In the other 6 roosts, more than one bat was present, at least for part of the time the roost was censused. Roosting groups can contain both sexes and apparently all age classes. However, adult ♂♂ seem to be present with a lower frequency than adult ♀♀. For example, 2 of the 6 groups noted above only contained ♀♀ and young and the average for all 6 groups was only 26 % adult ♂♂. When several bats are present in a roost, the individuals maintain a strict 10–15 cm spacing except for mothers with nursing young. There seems to be a tendency for adult ♂♂ to roost more at the periphery of groups than we would expect by chance, but our samples are small. The largest group examined in the study reached a peak size of 17 bats consisting of at most 6 adult ♂♂. Mean group size, averaged both over many censuses for any one site and over the 6 monitored groups, was  $4.4 \pm 2.0$  bats/group.

Behavior at the day roosts is minimal. During most of the day, the bats cover their noses with their wings and appear to be asleep. They are extremely wary, however, and the slightest noise will open all eyes immediately. Further disturbance causes the bats to lower their heads, survey the immediate vicinity as they rotate around their feet, and perhaps to fly off even in daytime to a new roost. Early in the day, individuals may clamber up on the branch, and hanging by the wing claws, defecate. Some grooming may occur during the day, but it is most likely just before dusk. Except for mothers and nursing young, allogrooming has never been observed. Just at sunset, all bats groom and eventually each leaves either for foraging or to visit the calling assembly. There is no coordination in the departures of members of a roosting group, and no vocalizations are emitted as bats leave. Adult ♂♂ tend to leave roost groups before other group members. In general, there appear to be no detectable interactions between roosting group members except use of a common site. ♂♂ have never been seen to approach ♀♀ at such a roost, and as noted, if anything tend to roost at the periphery of the group.

Group size at day roosts is extremely labile. Three groups monitored in 1974 for several months showed coefficients of variation in group size of 42 %, 44 % and 53 % per census. Each site was censused every 2–3 days. Because usually only one member of each group carried a radio or some other mark, estimates of compositional stability are difficult to make. In two groups which periodically contained adult ♂♂, the coefficients of variation in numbers of ♂♂ were 50 % and 100 % per census. A third group consisted only of adult ♀♀ and juveniles and was censused 20 times over a 38-day period. During this censusing, group size ranged from 0 to 7. Using the number of

juveniles in the group as an index of compositional stability, on 65 % of the censuses, at least one juvenile was present, while on 15 % of the censuses two juveniles were present. Attendance rates for any one individual juvenile must thus be 65 % or less; since several juveniles were visiting the site, the average value is clearly lower than 65 %. In short, both group sizes and presumed compositions of day roost groups show considerable temporal variation.

Much of this variation in roost group size is related to the tendency of bats to shift day roosts at short intervals. A solitary ♀ followed in 1972 utilized one day roost for 8 days after capture and then moved to a new day roost 3.5 km away. She resided daily in this new site (again solitarily), for another 8 days and then moved to a third site 1 km from the second. Still roosting by herself, the bat used the third roost for 10 days and then moved out of radio contact. A similar history was obtained with a second ♀ in 1974 which moved every 5 to 6 days to a new roost 50–60 m from the prior one. One subadult ♂ used a given roost for 5 days after capture, moved out of radio contact for 3 days, and then returned to the original site for 8 days. The shortest continuous use of a given day roost observed was one day and the longest was 10 days. The latter may be an underestimate since in several cases a marked animal dropped the radio but could have continued to be a resident in a given day roost group. Based on animals which retained the radios through at least one roost move, the typical time in one spot appears to be 5 to 9 days. The distance moved between day roosts appears to have a distinctly bimodal distribution. On the one hand, some bats may remain within a local area for an extended period, but move 50–100 m to a new tree every 5 to 9 days. Others, such as the first ♀ mentioned above, move longer distances between day roosts and use only a single tree while within a given area. If we divide all the recorded moves between day roosts into those occurring over distances of 100 m or less and those occurring over distances greater than 100 m, we find an average local shift in day roosts of  $54 \pm 20$  m (10 moves by 8 bats) and an average long distance shift of  $5 \pm 5$  km (8 moves by 7 bats). A few bats showed both patterns during the periods they were being tracked.

The locations of the calling assemblies seem to modulate the positioning of male day roosts in a manner different from that for female roosts. In Table 5, the distances between the C.N.R.S. assembly site and all known female and male roosts are summarized. Two totals are given for ♂♂: that for all ♂♂ regardless of mating status, and that for ♂♂ known to be holding territories on the C.N.R.S. assembly site. The distributions of male day roosts relative to the C.N.R.S. site for territorial versus all ♂♂ are not significantly different. However, both differ significantly from that for ♀♀ (♀♀ vs. all ♂♂,  $G = 9.82$ ,  $df = 2$ ,  $p < .01$ ; ♀♀ vs. territorial '♂♂',  $G = 10.32$ ,  $df = 2$ ,  $p < .01$ ). While ♀♀ appear to be most frequent at inter-

Table 5: Distances between day roosts and the C.N.R.S. assembly site for all bats known to be carrying working transmitters and for all bats roosting in group roosts

Distance	# of ♀♀	# of ♂♂	# of Assembly ♂♂
0 - 1 km	5	9	7
2 - 8 km	16	3	1
8 + km	11	12	5
Totals:	32	24	13

mediate distances from the calling site (2—8 km), both all ♂♂ and territorial ♂♂ are roosting either very close to the assembly (1 km or less) or very far from the assembly (more than 8 km). This is a curious finding since the territorial ♂♂ with more distant roosts must commute each night over 8 km to get to their singing territories.

### I. Foraging and Resource Distributions

Radio-tracking data have now been obtained on 27 foraging *Hypsignathus monstrosus*. 8 of these animals were adult ♂♂ currently holding display territories and 19 were either ♀♀, subadult ♂♂, or adult ♂♂ not currently holding display territories. Foraging schedules of tracked bats fell into two categories as a function of whether the tracked animal was or was not a displaying ♂. All displaying ♂♂ tracked once copulations had begun left the day roost immediately at dusk and flew directly to their display territories. They remained displaying at these territories until 22.00—23.00 h, and then flew nearly bee-line paths to foraging sites. The average distance between foraging sites and the assembly site was 6.7 km (N = 8). One ♂ with a day roost close to the assembly site commuted nightly over 10 km each way to its foraging sites. Many of the ♂♂ foraged until dawn and then flew directly to their day roosts. A few, as noted above, returned to the assembly site to call between 03.00 and 05.00 h. In contrast to this pattern, all non-displaying bats flew directly from day roosts to foraging grounds at dusk. Some ♀♀ were observed to make detours to pass over the assembly sites en route to foraging locations. A few ♀♀ flew to these sites after foraging. Many of the non-displaying bats were observed to make long non-foraging flights (no repeated passes to fruit trees noted) between the hours of 22.00 and 03.00 h. A few appeared to spend these hours roosting and fed a second time before dusk. The average distances flown between day roosts and foraging sites for non-displaying bats were under 5 km for all sex and age classes. Displaying ♂♂ thus differed from non-displaying bats both in the scheduling of nocturnal activities and in the average distances flown to feed. (A more detailed analysis of the differences in foraging between different age and sex classes will be published elsewhere.)

A total of 133 oral swab and feces samples was taken from animals netted at the C.N.R.S. site between 1970 and 1974. All samples were taken in May to October; thus statements as to dietary preferences apply only to this period. Of the 133 samples, 88 % contained seeds of only two genera of plants: *Ficus* and *Anthocleista*. The remaining 12 % of the samples contained seeds of *Musanga cecropioides* and *Solanum spp.*, both of which are common in secondary growth areas and in old plantations. *Anthocleista* occurs in certain river border sites and is also very common in secondary growth areas. The *Ficus* species obtained in the seed samples were mostly epiphytic forms of mature forest, although a few were free-standing figs of secondary growth.

To determine whether any of these food plants occurred within the calling territories of ♂♂, 19 ha of island forest including 90 % of the C.N.R.S. calling assembly were rigorously censused for possible food trees. *Anthocleista* was only identified as the other major food component late in the study, and searches for it were less intense. However to date, no *Anthocleista* have been located within or adjacent to the calling assembly. *Solanum* and *Musanga* are also absent from the site. On the other hand, a total of 68 *Ficus* was

located in the 19 ha, of which 35 were located within the calling assembly. It is obvious that the distribution of *Ficus* is higher within the calling area than outside it: 51 % of the *Ficus* plants located were found in the assembly area which accounts for only 18 % of the area sampled (assuming a roughly uniform distribution, the probability of finding this degree of bias is  $p < .001$ ). A 24 month survey of these *Ficus* in collaboration with M. Georges MICHALOUD showed that very few of them fruit during the calling seasons. In July, 1974, only two of the 35 *Ficus* on the assembly site fruited and in August, 1974, only one did so. In June of 1974, and in June—August of 1975, no *Ficus* fruited on the assembly sites. The max. fraction of *Ficus* fruiting anywhere within the 19 ha study area during one month in the calling seasons of 1974 and 1975 was 7 % in July, 1974. On the three occasions in 1974 and on one in 1972 when *Ficus* did fruit within the assembly, canopy platforms were used to monitor feeding activity. In all four cases, both adult male and smaller (female and young male) *Hypsignathus* were observed to feed on the fruit. In spite of the proximity of feeding sites, no established  $\delta\delta$  were observed to defend the fruit trees or to alter their nightly calling behavior in any way. The large *Ficus* which fruited in 1972 clearly attracted a large number of bats, and staccato buzz rates for nearby  $\delta\delta$  did increase (though not statistically), during this period.

The low frequency of fruiting of *Ficus* in the assembly area, the absence of other known food sources in this habitat, and the lack of altered behavior when *Ficus* fruit on the assembly all argue that  $\delta\delta$  are not adopting a strategy of defending a food resource which  $\text{♀♀}$  require and that  $\text{♀♀}$  visit the assembly for some purpose other than to feed. These conclusions are totally consistent with the radio-tracking data, all of which implicated feeding sites other than the assembly areas. In fact, given the evidence, it is likely that the higher density of *Ficus* noted in the assembly area is the *result* of frequent defecations by calling  $\delta\delta$  and visiting  $\text{♀♀}$  and not the *cause* of such aggregations.

### J. Sexual Dimorphism and Bimaturism

The sexual differences in anatomical features of this species have been adequately noted by prior authors (ALLEN, LANG, and CHAPIN 1917; ROSEVEAR 1965; KINGDON 1974). To these, it may be instructive to add the weights and linear measures of 91 adult  $\delta\delta$  and 83 adult but non-pregnant  $\text{♀♀}$  netted at the C.N.R.S. site from 1970 to 1974. These measures are summarized in Table 6.

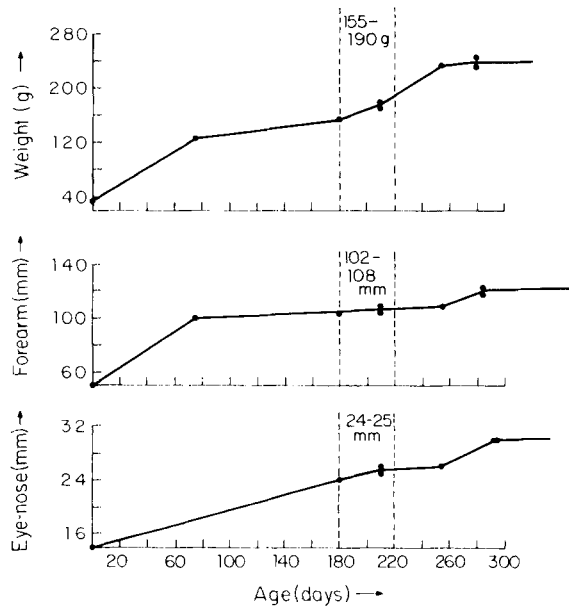
Rates of maturation of the two sexes have been monitored by maintaining animals in captivity both in Gaboon and in the New York Zoological

Table 6: Weights and linear dimensions for adult male and adult but non-pregnant female *Hypsignathus monstrosus*. Nose height was measured from the upper lip to the max. height of the nose; nose length was measured from the anterior tip of the eye to the center of the nostril. Variations are standard deviations

Measure	$\delta\delta$		$\text{♀♀}$		$\delta / \text{♀}$ Ratio
	Sample Size	Value	Sample Size	Value	
Weight (g)	91	420 $\pm$ 1	74	234 $\pm$ 19	1.79
Forearm (mm)	87	134 $\pm$ 3	83	120 $\pm$ 3	1.12
Nose Height (mm)	65	34 $\pm$ 2	77	16 $\pm$ 1	2.13
Nose Length (mm)	71	42 $\pm$ 1	77	30 $\pm$ 1	1.40



Fig. 11: Growth curves for female *Hypsignathus* with respect to weight, forearm length, and nose length. Dotted lines demarcate the values of each parameter for the "small size" class of ♀♀ netted at the C.N.R.S. site in June—August. "Large" ♀♀ have size ranges given in Table 6. Parameter values for newborn ♀♀ are the averages of 17 measured babies. The other points reflect measurements on four bats of known age



Society's Bronx Zoo. Several young born in captivity have now matured to full sexual activity and complete records on these animals are plotted in Figs. 11 and 12. In Fig. 11, weight, forearm and nose length are plotted as functions of age for ♀♀. ♀♀ are netted on the C.N.R.S. site in the June—August display period in two distinct size classes. It is clear from Fig. 11 that the smaller ♀♀ netted (155—190 g, 102—108 mm forearms, and 24—25 mm nose lengths) are 6 months of age. These are thus the young born the previous December—February. All other ♀♀ are full sized and fall within the values given in Table 6. 6 month old ♀♀ taken visiting the assembly areas in August have been found to be pregnant. Thus sexual maturity for ♀♀ is achieved at about 6—7 months when the animals have not yet even reached full size.

Equivalent data are given for ♂♂ in Fig. 12. As for ♀♀, the measured growth curves for weight, forearm length, nose length and nose height in captive animals are superimposed upon observed categories of ♂♂ netted at the C.N.R.S. site in the June—August calling period. The first category corresponds to very small ♂♂ with weights of 210—240 g, forearms of 115—120 mm, nose lengths of 29—31 mm, and nose heights of 17—19 mm. These are clearly the 6 month old ♂♂ born the previous December—February. A second class of ♂♂ (weights 310—340 g, forearms of 127 to 128 mm, nose lengths of 34—36 mm, and nose heights of 21—22 mm) are yearlings born the previous July—August. The third class of ♂♂ represents 18 month old or older ♂♂ with weights and dimensions as noted in Table 6. While weight, forearm length, and nose length appear to grow almost linearly with age for ♂♂ between 2 and 18 months of age, testis size and nose height both show a dramatic increase in mean values in the period between 12 and 18 months of age. Epididymal biopsies indicate that 12 month old ♂♂ do not have viable sperm while 18 month old ♂♂ do. Sexual maturity for male *Hypsignathus*, evidenced both by testis activity and achievement of the enlarged muzzle of the adult, clearly occurs between 12 and 18 months of age. Fig. 13 shows that up until this sudden change, subadult ♂♂ are very difficult to differentiate from adult ♀♀ in external configuration.

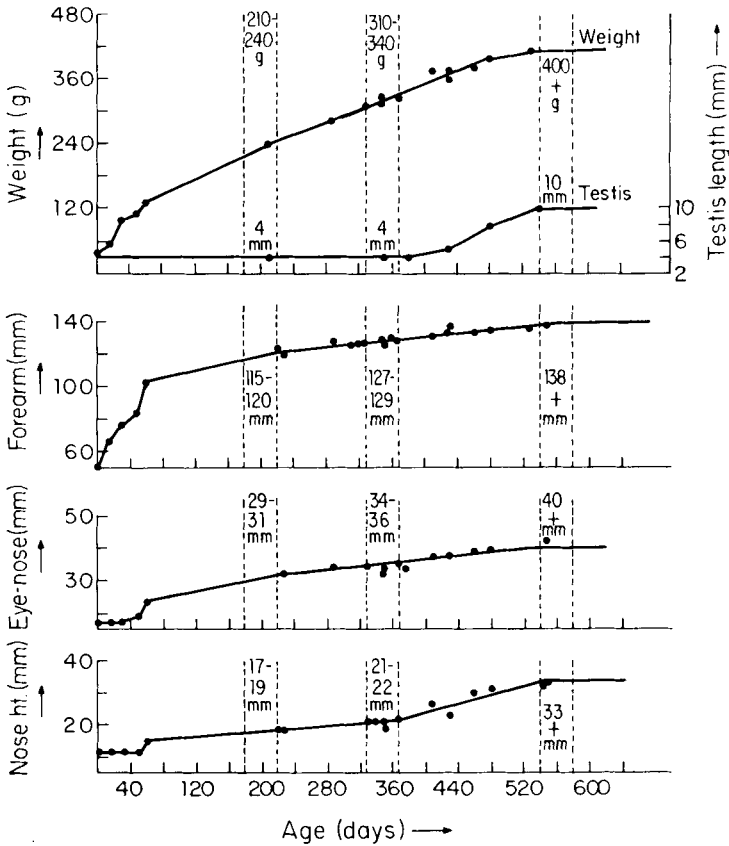


Fig. 12: Growth curves for male *Hypsignathus* with respect to weight, forearm length, nose length, nose height and testis length. Bats netted at the C.N.R.S. site during June—August fall into three discrete categories (excluding newborn ♂♂). Dotted lines indicate the presumed ages as indicated by the growth curves and the values of each parameter for each size class. Data of newborn ♂♂ are the averages of 20 examples. Other points represent measurements on 7 ♂♂ of known ages

## Discussion

It is clear from the data presented here that even by a conservative definition, the calling assemblies of *Hypsignathus monstrosus* are true leks. There is no male parental care, and in fact, many of the bats roost solitarily in the daytime. The assembly sites have all the characteristics of a classical lek "arena" and the display territories of ♂♂ are only tiny fractions of their own as well as female home ranges. Mating appears to occur exclusively on these display territories. ♀♀ are not coerced into male territories, but appear to visit them selectively and select one ♂ for mating. Male display territories do not contain resources utilized by ♀♀ in any significant quantities. Thus, at least by the definition given at the beginning of this report, the mating system of this bat is a true lek.

In addition to meeting the definition of a lek, *Hypsignathus* shows nearly all of the secondary features which have been reported for other lek

species. It is extremely sexually dimorphic and  $\delta\delta$  mature a full 12 months later than  $\text{♀♀}$ . The assembly areas are traditional, at least over periods of up to 60 years, and seem to occur in quite specific types of habitats. Male display repertoires are tiresomely simple and ritualized, and the basic displays are repeated without variation for many h at a time. Mating within any assembly is highly skewed with the top 6% of the  $\delta\delta$  achieving 79% of the total matings. Successful  $\delta\delta$  appear to be aggregated in mating centers as in other species. However, as might have been predicted given the linear geometry of *Hypsignathus* leks, several such mating centers may occur in a given assembly.

Contrasts in the calling behaviors and emitted sounds of *Hypsignathus* and *Epomophorus wahlbergi* have been recently summarized by WICKLER and SEIBT (1976). It now seems clear that nocturnal calling behavior is typical of  $\delta\delta$  of most if not all of the larger epomophorine bats: *Hypsignathus*, *Epomops*, *Micropteropus*, and the 8 species of *Epomophorus* (ALLEN, LANG, and CHAPIN 1917; EISENTRAUT 1945; BOOTH 1960; ROSEVEAR 1965; BROSSET 1966; KINGDON 1974; WICKLER and SEIBT 1976). Nocturnal behavior in the smaller epomophorines such as *Scotonycteris* or *Nanonycteris* is as yet poorly known (BROSSET 1966; ROSEVEAR 1965). From the available data, it appears that while  $\delta\delta$  call in most of these species, *Hypsignathus* is the only one with a true lek. In all of the others for which reports are available,  $\delta\delta$  are much more widely spaced, although they may be roughly clustered within a given area. Behavior of *Epomops franqueti* in Gaboon is probably typical of these more spaced species (BROSSET 1966; BRADBURY, unpubl. obs.). In this bat, in-

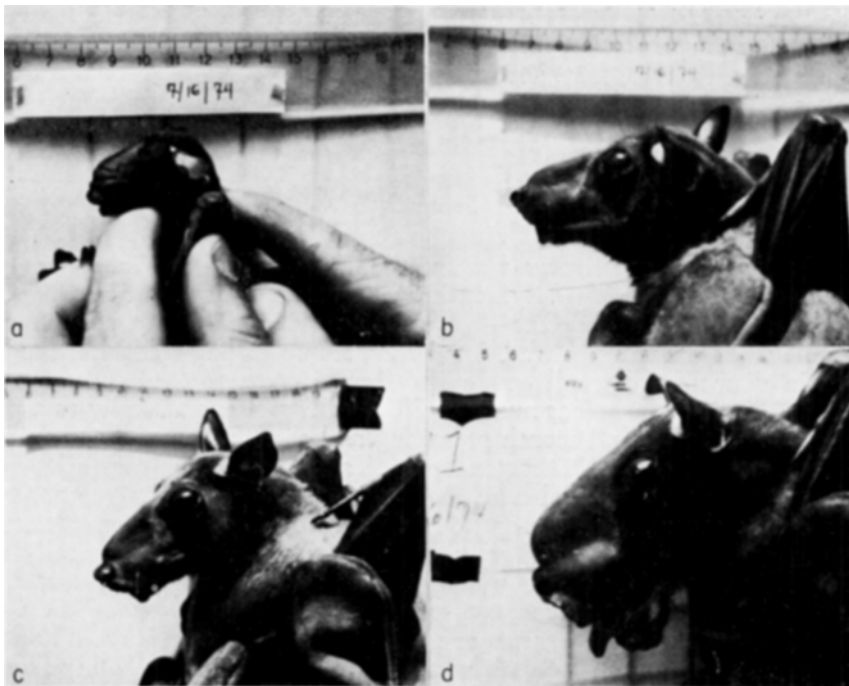


Fig. 13: Head configuration for different age and sex classes of *Hypsignathus*. a. Day-old  $\delta$ . b. Fully adult  $\delta$ . c. Yearling  $\delta$ . d. Adult  $\delta$ . Changes in head shape between c. and d. occur over a 6-month period between 12 and 18 months of age

dividual ♂♂ have their own calling territories which are usually 100—200 m in diameter. They call within these territories from any of four to five different perches spaced at intervals of 20—50 m apart. As with *Hypsignathus*, male *Epomops* call in bouts of 20—30 min and then shift calling perches. ♀♀ visit these calling ♂♂ and hover in front of them while the ♂ performs a modified version of the regular call. Female *Epomops* are more vocal than their *Hypsignathus* counterparts, and approach to a calling ♂ may involve a vocal exchange between the two animals. Copulations have not yet been observed in these bats. On several occasions, I have observed female or juvenile *Epomops* feeding on resources near the territory of a calling ♂. Without quantitative information on the frequency of this latter finding, it is difficult to decide whether the loose aggregations of calling male *Epomops* are to be considered leks or not. In behavior and configuration, they seem analogous to the “exploded leks” of bellbirds (SNOW 1970). However, as noted in the introduction to this paper, it is critical to know whether the ♂♂ are visited by ♀♀ primarily for mating, or whether instead the ♂♂ are defending territories around crucial resources needed by ♀♀. I suspect that subsequent work on other epomophorines will reveal a gradient of strategies ranging from complete resource defense (like some antelopes) to true leks as in *Hypsignathus*. Field studies of mating territories and resource distributions in the intermediate species, such as *Epomops* and *Epomophorus*, will be extremely interesting.

The finding in this study that mating and parturition in *Hypsignathus* are semiannual is consistent with recent reports by OKIA (1974 a, b) that both *Epomops franqueti* and *Epomophorus anurus* breed twice a year at intervals of 6 months. In all three species, parturition and copulation appear to be synchronized with the dry seasons or the end of the dry seasons. The finding that *Hypsignathus* follows a similar pattern of breeding provides a major exception to OKIA's (1974 a) contention that smaller African fruit bats tend to breed twice a year while larger ones might be expected to breed only once annually.

### Summary

*Hypsignathus monstrosus* were studied in the field in Gaboon over a four year period. A total of 17 months was spent in the study, most of which were concurrent with the June—August calling periods. ♂♂ were found to assemble twice annually at traditional sites, set up calling territories roughly 10 m in diameter, and call each night from 18.30 h to 23.00 h and again from 03.00 h to 05.00 h. The number of ♂♂ calling rises erratically to a peak at the end of the second month of calling and then falls rapidly to zero in the third month. While ♂♂ may shift positions and contest territories early in the season, few territorial relocations seem to occur after copulations begin midway through the season. ♂♂ display by hanging from a branch, flapping the partially opened wings, and emitting a loud harmonically rich call at rates of roughly once a second. ♀♀ visit the assembly sites, hover before ♂♂ while the latter perform a stereotyped syncopation of the usual call, and eventually settle next to one ♂ for mating. Mating is rapid and the ♂ resumes calling immediately afterwards. Mating success was highly skewed in the major assembly studied with 6 % of the ♂♂ accounting for 79 % of the 50 copulations recorded in 1974. Successful ♂♂ were aggregated into “mating centers” as has been reported for other lek species. Given the pe-

culiar linear geometry of these leks, several mating centers may occur within any one site.

Most day roosts located contained only solitary animals. Groups of bats do occur and can contain adult ♀♀, recent juveniles, newborn young and even adult ♂♂. All day roosts are located in the foliage of the forest canopy and all behavior at the roosts is extremely cryptic and subdued. No interactions between ♂♂ and young have ever been noted at the day roosts.

Both sexes fly several km to feed, and ♂♂ currently displaying at assembly areas may fly as far as 10 km between the assembly sites and foraging grounds. Several tropical fruit trees dominate the diets and sample distributions both on and off the assembly areas were surveyed. It is concluded that there are few if any food resources within the assembly areas during the period of calling and mating.

Captive animals indicated that ♀♀ can become sexually active at 6 months of age while ♂♂ are neither sexually potent nor fully developed until 18 months of age. The matching of several discrete size classes of ♀♀ and ♂♂ netted at the assembly sites in June—August with growth curves indicates that both ♂♂ and ♀♀ born the previous mating season 6 months earlier and all older age classes visit the assembly areas.

Since *Hypsignathus a*) show no male parental care, b) display and mate at arenas, c) have no significant resources within male display territories which ♀♀ need, and d) exhibit female choice of mates, it is concluded that this species has a lek mating system in the classical sense. In addition, the species shows many other features commonly associated with leks: strong sexual dimorphism, sexual bimaturism, traditional arena locations, highly ritualized male displays, extreme skew in mating success among ♂♂, and the existence of mating centers on the lek sites.

### Zusammenfassung

Hammerkopf-Flughunde, *Hypsignathus monstrosus*, wurden insgesamt 17 Monate lang in 4 Jahren (meist in den Monaten Juni—August) im Freien in Gabun beobachtet. Die ♂♂ sammeln sich zweimal im Jahr an traditionellen Plätzen, besetzen Ruf-Reviere von etwa 10 m  $\phi$  und rufen von 18.30 bis 23.00 und von 3.00 bis 5.00 h. Die Zahl der Rufer nimmt bis zum Ende des zweiten Monats unregelmäßig zu und fällt dann schnell auf Null. Zu Beginn der Saison gibt es noch Revierstreitigkeiten zwischen den ♂♂, später — wenn etwa in Saisonmitte die Paarungen beginnen — kaum noch. Die ♂♂ hängen beim Rufen am Zweig, schlagen mit den halboffenen Flügeln und stoßen laute, an harmonischen Obertönen reiche Rufe aus, etwa einen je s. ♀♀ kommen zu diesen Rufplätzen, rütteln im Flug vor den ♂♂, die dann ihren Ruf modifizieren, und hängen sich schließlich neben ein ♂ zur Paarung. Die Kopula ist kurz; unmittelbar danach ruft das ♂ weiter. 6% der ♂♂ tätigten 79% der beobachteten Paarungen. Diese erfolgreichen ♂♂ waren in Paarungs-Zentren beisammen, wie es auch für andere arena-balzende Arten bekannt ist.

Tagsüber ruhen die Tiere im Blätterdach und halten sich dort sehr ruhig. Sie ruhen meist einzeln; wenn sich Gruppen bilden, dann gibt es darin keine sozialen Interaktionen mit den ♂♂.

Ihre Nahrung suchen die Tiere mehrere km im Umkreis und bis zu 10 km von den Rufplätzen entfernt. Zur Rufzeit gibt es an den Rufplätzen wenig Freßbäume.

In Gefangenschaft wurden ♀♀ mit 6 Monaten, ♂♂ nicht vor 18 Monaten nach der Geburt geschlechtsreif.

Die Art zeigt ein klassisches Arena-Balzverhalten, denn: 1. die ♂♂ beteiligten sich nicht an der Brutpflege; 2. sie balzen und paaren sich an Arena-Plätzen; 3. in der Nähe der Balzplätze gibt es keine für die ♀♀ wichtigen Ressourcen; 4. die ♀♀ suchen sich das ♂ aus. Ferner reifen die Geschlechter in verschiedenem Alter, die Tiere sind stark sexualdimorph, die ♂♂ haben eine hochritualisierte Balz und extreme individuelle Unterschiede im Paarungserfolg.

### Acknowledgments

I am grateful to M. A. BROSSET, Director of the Laboratoire de Primatologie et d'Ecologie Equatoriale, for his unstinting generosity and encouragement in this study. To my many other colleagues at the Museum National d'Histoire Naturelle, Brunoy, France, and at the C.N.R.S., I am also deeply thankful for field assistance, suggestions, criticisms of field design, and general intellectual stimulation. My colleagues and former students first at Cornell University and then at Rockefeller University played major roles in designing and analyzing these studies, and I wish to acknowledge their many contributions. Drs. L. EMMONS, S. VEHRENCAMP, I. LIEBERBURG, and D. MORRISON and Mr. A. MILLER all worked with me in the field on this study between 1970 and 1974. This work was supported in part by a grant from the Bache Fund of the National Academy of Sciences, by research funds of the Centre National de la Recherche Scientifique (France), and by NSF Grant GB-30478 to the author.

### Literature cited

- ALLEN, J. A., H. LANG, and J. P. CHAPIN (1917): The American Museum Congo Expedition collection of bats. *Bull. Amer. Mus. Nat. Hist.* 37, 405—563.
- BOOTH, A. H. (1960): Small mammals of West Africa. Longmans, Green and Co., London • BROSSET, A. (1966): Les chiroptères du Haut-Ivindo (Gabon). *Biol. Gabon.* 2, 47—86 • BUECHNER, H. K., and R. SCHLOETH (1965): Ceremonial mating behavior in Uganda Kob (*Adenota kob thomasi*). *Z. Tierpsychol.* 22, 209—225.
- COCHRAN, W. W. (1967): 145—160 MH7 beacon (tag) transmitter for small animals. AIBS-BIAC Information Module M-15. AIBS-BioInstrumentation Advisory Council, Washington, D.C., 12 pp.
- DENISON, W. C., D. M. TRACY, F. M. RHOADES, and M. SHERWOOD (1972): Direct, nondestructive measurement of biomass and structure in living, old-growth Douglas fir. *Proceedings — Research on Coniferous Forest Ecosystems — A Symposium.* Bellingham, Washington, U.S. Government Printing Office, 147—158 • DOWNES, J. A. (1969): The swarming and mating flight of Diptera. *Ann. Rev. Entomol.* 14, 271—298.
- EISENTRAUT, M. (1945): Biologie der Flederhunde (Megachiroptera). *Biol. Generalis* 18, 327—435.
- HOGAN-WARBURG, A. J. (1966): Social behavior of the ruff, *Philomachus pugnax*. *Ardea* 54, 1—45.
- KINGDON, J. (1974): East African Mammals. Vol. II, Pt. A.: Insectivores and Bats. Academic Press, New York.
- LILL, A. (1974): Social organization and space utilization in the lek-forming white-bearded manakin, *M. manacus trinitatis*. *Z. Tierpsychol.* 36, 513—530.
- OKIA, N. O. (1974a): The breeding pattern of the eastern epauletted bat, *Epomophorus anurus* in Uganda. *J. Reprod. Fert.* 37, 27—31 • OKIA, N. O. (1974b): Breeding in Franquet's bat, *Epomops franqueti*, in Uganda. *J. Mammal.* 55, 462—465.
- VAN RHIJN, J. G. (1973): Behavioral dimorphism in male ruffs, *Philomachus pugnax*. *Behaviour* 47, 153—229 • ROSEVEAR, D. D. (1965): The Bats of West Africa. The Trustees of the British Museum (Natural History), London.
- SNOW, B. K. (1970): A field study of the bearded bellbird in Trinidad. *Ibis* 112, 229—239 • SNOW, D. (1968): The singing assemblies of little hermits. *The Living Bird*, 7th Annual, 47—55 • SPIETH, H. T. (1968): Evolutionary implications of sexual behavior in *Drosophila*. *Evol. Biol.* 2, 157—193.
- WICKLER, W., and U. SEIBT (1976): Field studies of the African fruit bat, *Epomophorus wahlbergi*, with special reference to male calling. *Z. Tierpsychol.* 40, 345—376 • WILEY, R. H. (1973): Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*.

Anim. Behav. Monographs 6, 85—169 • WILEY, R. H. (1974): Evolution of social organization and life history patterns among grouse (Aves, Tetraonidae). *Quart. Rev. Biol.* 49, 201—227 • WILSON, E. O. (1975): *Sociobiology: the new synthesis*. Harvard/Belknap Press, Cambridge, Mass.

Author's address: Jack W. BRADBURY, Department of Biology, C-016, University of California at San Diego, La Jolla, California, 92093.